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Cover image:
Transverse section of *Caninophyllum tomiense* (Tolmatchev, 1931) from Tournaisian (Carboniferous) strata of Dolomite Quarry near Dokuchaevsk town, Ukraine. From Ohar (this volume, p. 212).

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PALEO-ARCHIVES OF CNIDARIA AND PORIFERA IN SPACE AND TIME

GUEST EDITORS:
FRANCESCA R. BOSELLINI, CESARE A. PAPAZZONI & ALESSANDRO VESCOGNI

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Paleo-archives of Cnidaria and Porifera in space and time

Proceedings of the 13th International Symposium on Fossil Cnidaria and Porifera

Francesca R. Bosellini, Cesare Andrea Papazzoni & Alessandro Vescogni

F.R. Bosellini, Dipartimento di Scienze Chimiche e Geologiche, Università degli Studi di Modena e Reggio Emilia, Via Campi 103, I-41125 Modena, Italy; francesca.bosellini@unimore.it

C.A. Papazzoni, Dipartimento di Scienze Chimiche e Geologiche, Università degli Studi di Modena e Reggio Emilia, Via Campi 103, I-41125 Modena, Italy; papazzoni@unimore.it

A. Vescogni, Dipartimento di Scienze Chimiche e Geologiche, Università degli Studi di Modena e Reggio Emilia, Via Campi 103, I-41125 Modena, Italy; alessandro.vescogni@unimore.it

This Thematic Issue hosts the Proceedings of the 13th International Symposium on Fossil Cnidaria and Porifera, held at the Università degli Studi di Modena e Reggio Emilia (Italy) on September 3-6, 2019. It was the congress of the International Association for the Study of Fossil Cnidaria and Porifera, organized every four years since the first edition in Novosibirsk (Russia) in 1971, and then hosted by many different countries all over the world (France, Poland, USA, Australia, Germany, Spain, Japan, Austria, Russia again, Belgium, Oman). In Modena, the general Assembly changed the name and statute of the association, now named International Fossil Coral and Reef Society (IFCRS: https://www.cnidaria.nat.uni-erlangen.de/IFCRS/).

For the first time organized in Italy, the Symposium aimed to bring together participants from all over the world to discuss and share the most recent advances of studies on fossil corals and sponges, coral reefs and associated biota. The congress theme "Looking back to see ahead" was chosen to highlight the importance of the fossil archives to understand the response of the biosphere to long-term environmental perturbations and to promote interdisciplinary approaches from a body of interested palaeontologists, biologists but also specialists in other disciplines.

There is a striking evidence that coral reef systems are currently navigating a world of warming temperatures, rising sea levels, and changes in oceanographic conditions and water quality. This combination of direct and indirect anthropogenic stressors is severely threatening coral reefs causing their decline worldwide (Pandolfi et al., 2003; De'ath et al., 2009; Harborne et al., 2017), and predicting their future development is thus a priority challenge (Pandolfi et al., 2011).

Coral reefs, and in general reef environments, have experienced a variety of climate boundary conditions during the recent and the geological past, and investigating their evolution in the fossil record is crucial to place the observed changes in modern reefs into a long-term context. Reefs, reef organisms and reef attributes of the past are precious archives for tracing the impact of transient, oscillatory and abrupt changes of environmental factors over large-time and spatial-scales, from yearly to millennial, and from individual reefs to entire oceans (Kiessling, 2005, 2009; Pandolfi & Kiessling, 2014; Renema et al., 2016).

Contributions to this Thematic Issue are organized by stratigraphic order and provide a multi-scale overview of Cnidaria, Porifera, reef organisms and reef environments across the Phanerozoic by a broad spectrum of approaches (systematic palaeontology, palaeoecology, palaeobiogeography, taphonomy, facies analysis, etc.)

The Issue starts from the deep time, with a thorough overview of the long fossil record (from the Cambrian to the Eocene) of cnidarian medusae (jellyfish)-bearing deposits and analysis of the palaeoenvironmental conditions and factors that progressively led to the restriction of their preservational potential through the Phanerozoic (Young & Hagadorn, 2020).

The Palaeozoic record is represented in this Issue by the Carboniferous-Permian time window. Lower Carboniferous solitary rugose corals from Ukraine (Ohar, 2020) and tabulate and rugose corals from the Moscow Basin (Russia) (Somerville et al., 2020) are described and framed into the palaeogeographic context of the period, providing new data about possible connections between the Eastern European basin, Palaeotethys and North America. Still from the Carboniferous (Upper Mississippian), but from South China, is reported and interpreted the endosymbiotic relation between solitary rugose corals and large soft-bodied worm-like organisms, as evidence of the importance of the symbiotic interactions between organisms to better understand exploitation of ecospace and the formation of specific niches within the ecosystem (Lin & Herbig, 2020). Contributions related to the Carboniferous period end with the Pennsylvanian of the Cantabrian Mountains (northern Spain), where a combined palaeontological-sedimentological study reveals the presence of remarkable algonspongia-chaetetid mounds (Rodríguez-Castro et al., 2020). A detailed systematic description of lower Permian solitary rugose corals from Slovenia underlines a gregarious mode of growth for these corals (Kossovaya et al., 2020); whereas a rarely preserved case of intraspecific competition in rugose corals is explored from Permian (Guadalupian) reef blocks of Oman (Weidlich, 2020).

From the Palaeozoic, this Issue moves forward in time until the Cenozoic, with contributions spanning from the

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lower Eocene to the Miocene, and from Mediterranean to Caribbean and western Atlantic regions. The discovery of the new aphroid scleractinian coral genus *Nancygyra* in the lower Eocene (upper Ypresian) reef limestones of Monte Postale (northern Italy) highlights the diversification of scleractinians during a time represented by a marked decline of coral reefs (Bosellini et al., 2020a). The Eocene deposits of northern Italy are also well known for the occurrence of siliceous sponges and are herein investigated from the Lutetian of the Chiampo area in order to provide a first interpretation of their taphonomic history and depositional environment (Frisone et al., 2020). A peculiar coral-larger foraminifera association is documented from the upper Eocene of Jamaica, with the first record of a solitary discoid coral settled on a *Lepidocyclina* test (Stemann & Robinson, 2020). The Oligocene, well known as the apex of Cenozoic coral reef growth, is documented in this Issue by the description of reef corals from Austria that represent the northernmost fauna reported to date for Rupelian time (Baron-Szabo & Sanders, 2020), and by the study of the coeval reef coral assemblages and facies of the Lessini Shelf as a base to review and assess the alternative reef depositional models proposed for this area (Bosellini et al., 2020b). The reconstruction of the Oligo-Miocene diversification patterns of the staghorn coral *Acropora* in the western Atlantic is the subject of the last paper of this Issue, testifying the role of the fossil record for better understanding the present-day success of the most diverse living genus of reef-building corals (Wallace et al., 2020).

Finally, we would like to underline once again the importance of this international effort in providing precious contributions to the knowledge of the reef systems of the past as the basis for modelling the future of our richest marine biological systems. Looking back to see ahead!

REFERENCES

Baron-Szabo R.C. & Sanders D. (2020). Scleractinian corals (Anthozoa) from the lower Oligocene (Rupelian) of the Eastern Alps, Austria. *Bollettino della Società Paleontologica Italiana*, 59: 319-336.

Bosellini F.R., Stolarski J., Papazzoni C.A. & Vescogni A. (2020a). Exceptional development of dissepimental coenosteum in the new Eocene scleractinian coral genus *Nancygyra* (Ypresian, Monte Postale, NE Italy). *Bollettino della Società Paleontologica Italiana*, 59: 291-298.

Bosellini F.R., Vescogni A., Kiessling W., Zoboli A., Di Giuseppe D. & Papazzoni C.A. (2020b). Revisiting reef models in the Oligocene of northern Italy (Venetian Southern Alps). *Bollettino della Società Paleontologica Italiana*, 59: 337-348.

De'ath G., Lough J.M. & Fabricius K.E. (2009). Declining coral calcification on the Great Barrier Reef. *Science*, 323:116-119.

Frisone V., Preto N., Pisera A., Agnini C., Giusberti L., Papazzoni C.A., De Angeli A., Beschin C., Mietto P., Quaggiotto E., Monaco P., Dominici S., Kiessling W., Luciani V., Roux M. & Bosellini F.R. (2020). A first glimpse on the taphonomy and sedimentary environment of the Eocene siliceous sponges from Chiampo, Lessini Mts, NE Italy. *Bollettino della Società Paleontologica Italiana*, 59: 299-313.

Harborne A.R., Rogers A., Bozec Y.M., Mumby P.J. & Annual R. (2017). Multiple stressors and the functioning of coral reefs. *Annual Review of Marine Science*, 9: 445-446.

Kiessling W. (2005). Long-term relationships between ecological stability and biodiversity in Phanerozoic reefs. *Nature*, 433: 410-413.

Kiessling W. (2009). Geologic and biologic controls on the evolution of reefs. *Annual Review of Ecology, Evolution, and Systematics*, 40: 173-192.

Kossovaya O., Novak M. & Weyer D. (2020). New data on lower Permian rugose corals from the Southern Karavanke Mountains (Slovenia). *Bollettino della Società Paleontologica Italiana*, 59: 261-280.

Lin W. & Herbig H.-G. (2020). A soft-bodied endosymbiont in Serpukhovian (late Mississippian, Carboniferous) rugose corals from South China. *Bollettino della Società Paleontologica Italiana*, 59: 235-245.

Ohar V. (2020). Tournaisian (Carboniferous) rugose corals of the Donets Basin, Ukraine. *Bollettino della Società Paleontologica Italiana*, 59: 205-224.

Pandolfi J.M., Bradbury R.H., Sala E., Hughes T.P., Bjorndal K.A., Cooke R.G., McArdle D., McClenachan L., Newman M.J.H., Paredes G., Warner R.R. & Jackson J.B.C. (2003). Global trajectories of the long-term decline of coral reef ecosystems. *Science*, 301: 955-958.

Pandolfi J.M., Connolly S.R., Marshall D.J. & Cohen A.L. (2011). Projecting coral reef futures under global warming and ocean acidification. *Science*, 333: 418-422.

Pandolfi J.M. & Kiessling W. (2014). Gaining insights from past reefs to inform understanding of coral reef response to global climate change. *Current Opinion in Environmental Sustainability*, 7: 52-58.

Renema W., Pandolfi J.M., Kiessling W., Bosellini F.R., Klaus J. S., Korpanty C., Rosen B.R., Santodomingo N., Wallace C.C., Webster J.M. & Johnson K. G. (2016). Are coral reefs victims of their own past success? *Science Advances*, 2: e1500850.

Rodríguez-Castro I., Rodríguez S. & Fregenal-Martínez M. (2020). *Donezella*-chaetetids mounds in the Valdeteja Formation (Bashkirian, Pennsylvanian) at Truébano, Cantabrian Mountains, northern Spain. *Bollettino della Società Paleontologica Italiana*, 59: 247-259.

Somerville I.D., Kossovaya O.L., Rodríguez S. & Cózar P. (2020). New data on the Serpukhovian (carboniferous) coral assemblages from the northwestern part of the Moscow Basin (Russia). *Bollettino della Società Paleontologica Italiana*, 59: 225-233.

Stemann T.A. & Robinson N. (2020). A solitary coral-larger benthic foraminifera association from the late Eocene of Jamaica. *Bollettino della Società Paleontologica Italiana*, 59: ……

Wallace C.C., Portell R.W. & Muir P.R. (2020). Lineages of *Acropora* (staghorn) corals in the Oligocene to Miocene of Florida and SW Georgia (USA). *Bollettino della Società Paleontologica Italiana*, 59: ……

Weidlich O. (2020). Intraspecific competition in Guadalupian fasciculate rugose coral clusters (Hawasina Nappes, Oman Mountains). *Bollettino della Società Paleontologica Italiana*, 59: 315-317.

Young G.A. & Hagadorn J.W. (2020). Evolving preservation and facies distribution of fossil jellyfish: a slowly closing taphonomic window. *Bollettino della Società Paleontologica Italiana*, 59: 185-203.

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Evolving preservation and facies distribution of fossil jellyfish: a slowly closing taphonomic window

Graham A. Young* & James W. Hagadorn

G.A. Young, Manitoba Museum, 190 Rupert Avenue, Winnipeg, Manitoba, Canada; gyoung@manitobamuseum.ca **corresponding author*
J.W. Hagadorn, Department of Earth Sciences, Denver Museum of Nature & Science, Denver, CO 80205, USA; jwhagadorn@dmns.org

KEY WORDS - Cnidaria, medusae, jellyfish blooms, taphonomy, fossilisation, Konservat-Lagerstätten.

ABSTRACT - Although medusoids (medusa-like fossils, putative medusae) are widely reported in the literature, there are only thirteen confirmed medusa-bearing deposits. These have a predictable and evolving distribution through time and across facies - including in coarse clastic sand flats where mouldic preservation predominates, restricted lagoonal facies where anoxia and hypersalinity fostered preservation, and offshore settings where rapid burial and early diagenetic mineralisation catalysed preservation. The medusan preservational window became progressively more restricted through the Phanerozoic. Preservation in sandy beach and sandflat facies is only known from the Cambrian, there are no open shelf medusa-bearing deposits after the Carboniferous, and the latest known lagoonal fossil medusae are from the lower Cenozoic. This restriction in occurrence through time is associated with changes in bioturbation, evolution of scavengers, occurrence of microbial mats, and possibly evolution of microbial communities. There is evidence of jellyfish blooms in five of the thirteen deposits, and medusan fossilisation may have been associated with anoxia caused by the partial decomposition of large masses of dead medusae.

INTRODUCTION

Jellyfish (cnidarian medusae) occur in immense numbers in modern oceans, with some taxa having nearly global occurrence (Jarms & Morandini, 2019). Due to their remarkable reproductive capacity, medusan populations can quickly "bloom" to phenomenal numbers when conditions are favourable, to the extent that jellyfish blooms have become a significant issue for people and economies in some regions (Lynam et al., 2005; Purcell, 2005; Condon et al., 2012; Schnedler-Meyer et al., 2018). In spite of their abundance in modern marine settings, and inferred abundance in ancient oceans, medusae have a very poor fossil record because they possess almost no mineralised hard parts and quickly decay or are scavenged after death. Medusae have existed since at least the early Cambrian, yet even in the hundreds of known Konservat-Lagerstätten, non-mineralising Cnidaria are among the rarest major metazoan groups.

Although there have been some new discoveries of fossil medusae in recent years (e.g., Han et al., 2016; Fu et al., 2019), they are still only known from 13 distinct fossil deposits (or groups of genetically related deposits), where their presence is an indicator of exceptional preservational conditions (Pl. 1). The fossilisation of medusae is not only rare, but in some ways it may be distinct from the preservation of other soft-bodied organisms. By examining specimens from all bona fide medusan-bearing deposits, we have often observed that fossil jellyfish are different from other fossils in colour and texture, even within a single horizon in a Konservat-Lagerstätte. The composition and form of the medusan body may have been different enough from those of other animals that it induced unique variations on the fossilisation processes. For example, within many Konservat-Lagerstätten, medusae are not as frequently preserved as cuticular organisms such as arthropods, but they are frequently better preserved than the other entirely soft creatures.

Given these considerations, we hypothesise that a major factor in this differential preservation is the presence of mesoglea, an elastic, fibre-bearing proteinaceous tissue present in Cnidaria and Ctenophora (see also mesohyl in Porifera; Brusca & Brusca, 2003, p. 183). To test this hypothesis, one needs a synoptic temporal, palaeobiologic, and environmental framework for assessing preservational patterns in the medusan fossil record and distinguishing these from evolutionary or other causative/mitigating factors. With this in mind, here we present a detailed assessment of the jellyfish fossil record, aimed at helping our community better understand the environmental conditions, ocean chemistry, and evolution of groups of organisms that had an impact on the preservation or non-preservation of medusae, including scavengers, decomposers, burrowers, and microbial communities (sensu Fernandez-Lopez, 2013). This assessment may also provide useful criteria for searching for additional deposits that contain medusae.

Young & Hagadorn (2010) reviewed the fossil record of medusae, established criteria for recognition of fossil jellyfish (vs. "medusoids" or "possible jellyfish"), and interpreted the systematic affinities of confirmed fossil medusae. This contribution is a companion piece, examining the facies distribution of medusa-bearing deposits, and discussing possible reasons for their distinctive pattern of occurrence, including evolutionary, environmental, taphonomic, and/or biological influences. This work only covers macroscopic medusan cnidarians lacking hard parts, and thus excludes porpitid (chondrophorine) hydromedusae, hydroid colonies, conulariids, and olivooids and other microscopic medusoids (see e.g., Fryer & Stanley, 2004; Van Iten et al., 2006; Muscente et al., 2016; and Wang et al., 2017 for coverage of those groups).

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The fossil jellyfish literature is marred by a very high "noise to signal ratio" because most of the structures that have been interpreted as medusae represent other phenomena, such as trace fossils, non-medusan body fossils, or equivocal forms (e.g., Young & Hagadorn, 2010). To develop an improved understanding of the actual medusan fossil record, we have been working over the past decade to review all reported occurrences. Our database currently includes over 120 reports, of which we recognise about 20 taxa, occurring in 13 deposits or deposit groups. In each case we have applied recognition criteria that include morphology of the medusoid structure, co-associations, and evidence that the palaeoenvironment and taphonomy are consistent with interpretation as a preserved medusan. These criteria include: 1) evidence of original morphology consistent with medusae; 2) evidence of preburial transport, deformation, tearing, and/or desiccation; 3) evidence of appropriate palaeoenvironment (based on lithology, biota, sedimentary structures); 4) multiple individuals and horizons; and 5) evidence that the medusoid(s) can't be readily ascribed to other phenomena (for details, see Young & Hagadorn, 2010).

From this curated record we assessed facies occurrences through time, to better understand the factors that permitted or prohibited preservation of these unusual fossils. All known fossil medusae occur within a somewhat limited suite of palaeoenvironmental settings: shallow to emergent sandy coasts, muddy lagoons or estuaries, and deeper mud-dominated subtidal environments. They are not known from other settings, most notably normal marine open shelves, but also rocky shores, reefs, and the deep sea. Each occurrence of fossil medusae exhibits unique palaeoenvironmental conditions and a distinct taphonomic signature. The purpose of this contribution is to review the depositional and preservational conditions of medusan occurrences, thus revealing potential trends in preservation through geological time.

FOSSILISATION OF MEDUSAE

In general terms, soft tissue preservation can occur in several ways: as organic residues (modified original material), through early diagenetic mineralisation by minerals such as pyrite and phosphate, and as sediment impressions or casts (see syntheses in Briggs, 2003; Briggs & McMahon, 2016; Parry et al., 2018; MacGabhann et al., 2019). Fossil medusae can be preserved through all of these pathways, and in many instances a single fossil can exhibit two or more preservational modes. Mineralisation conditions for medusan soft tissue preservation are often unique.

Fossil medusae always show evidence of decay, and it is clear that each fossil reflects a dead, partly-decomposed jellyfish, not a freshly-killed one. This situation mirrors that of fossil anemones (Alpert, 1973; Pemberton et al., 2011; Plotnick et al., 2017), which are generally buried when dead; in deeper settings, living anemones and jellies that encounter burial events (hyperpycnal flows, turbidity currents, etc.) may leave behind trace fossils of their escape, or if escape is unsuccessful, they decay after burial but before they are completely cast. Even in shallower, intermittently exposed settings, jellyfish that are stranded alive tend to have time to decompose at least partially before or after burial - but prior to fossilisation.

EXPLANATION OF PLATE 1

Examples of fossil medusae (color online).

Fig. 1 - Undescribed scyphozoan from a Cambrian arenite of the Potsdam Group, Carrières Ducharme, Québec, Canada; Pointe-du-Buisson/Musée Québéquois d'archéologie, Québec, Canada, JF-67ME.

Fig. 2 - Upper Carboniferous (Moscovian) chirodropid cubozoan *Anthracomedusa turnbulli* from the Mazon Creek Lagerstätte (Francis Creek Shale Member, Carbondale Formation), Illinois, USA, showing abundant tentacles; Field Museum of Natural History, Chicago, USA, FMNH 38977.

Fig. 3 - Upper Jurassic (Tithonian) rhizostome scyphozoan *Rhizostomites admirandus* from the Solnhofen Formation, Franconian Alb, Bavaria, Germany, showing muscles, possible gonads, and conjoined mouth-cross near the axis; Bayerische Staatssammlung für Paläontologie und Geologie (BSPG), Munich, Germany, Nr. 1885.

Fig. 4 - Undescribed upper Carboniferous (Moscovian) chirodropid cubozoan from the Mecca Quarry Shale, Indiana, USA, with bell filled with quartz sand and tentacles preserved as mineralized and carbonaceous films; FMNH PE 23963.

Fig. 5 - Cluster of small upper Carboniferous (Moscovian) *Octomedusa pieckorum* from the Mazon Creek Lagerstätte (Francis Creek Shale Member, Carbondale Formation), Illinois, USA, with distinct bell margins and tentacles; Royal Ontario Museum (ROM), Toronto, Canada, ROMIP65605.

Figs 6-8 - Upper Jurassic (Tithonian) probable semaeostome *Myogramma speciosum* from the Solnhofen Formation, Franconian Alb, Bavaria, Germany;

6-7 - images of specimen BSPG 1959 I 365 with 6 being a detail showing small fish skeleton inside the specimen, and 7 illustrating "feathered" muscle pattern at top of slab;

8 - specimen BSPG 1909 I 21 showing muscles and discrete axis.

Figs 9-10 - Eocene (upper Ypresian) medusae from the Calcari Nummulitici formation of the Bolca Lagerstätten, Bolca, near Verona, Italy;

9 - unnamed probable semaeostome scyphozoan with gonads and ring muscles, Museo Civico di Storia Naturale di Verona (MCSNV), Italy, m.B.3;

10 - rhizostome *Simplicibrachia bolcensis* with bell and oral arms, Museo dei Fossili di Bolca, Verona, Italy, I.G.132586.

Each scale bar represents 20 mm.


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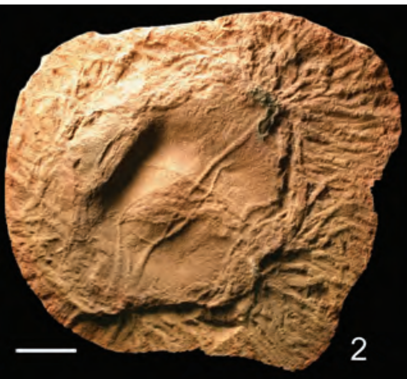
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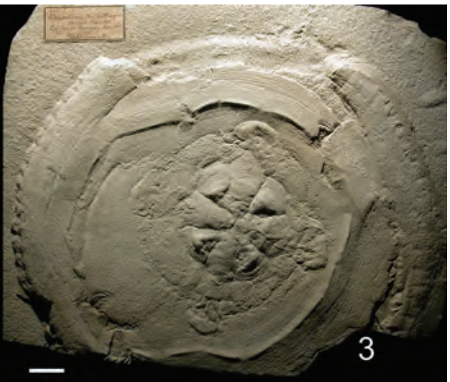
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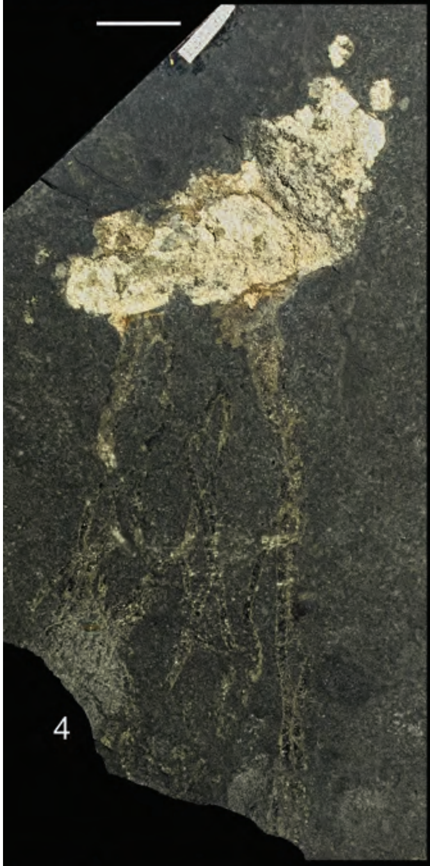
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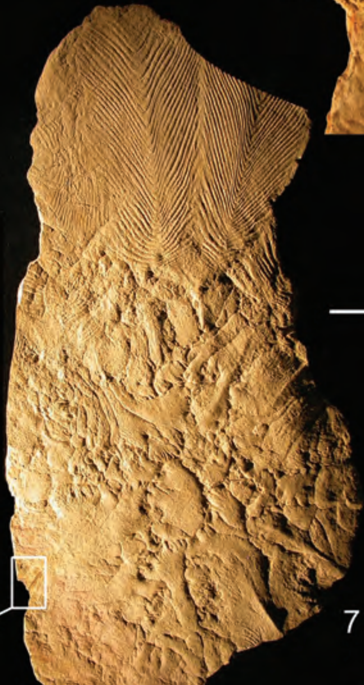
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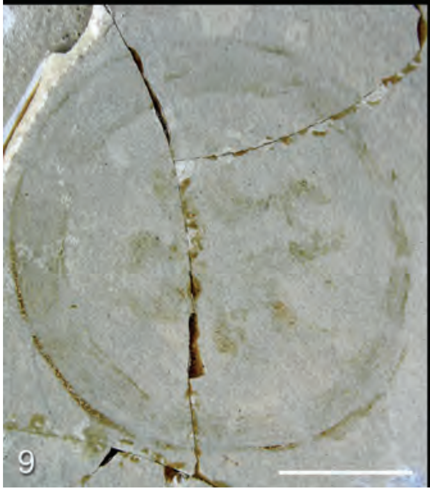
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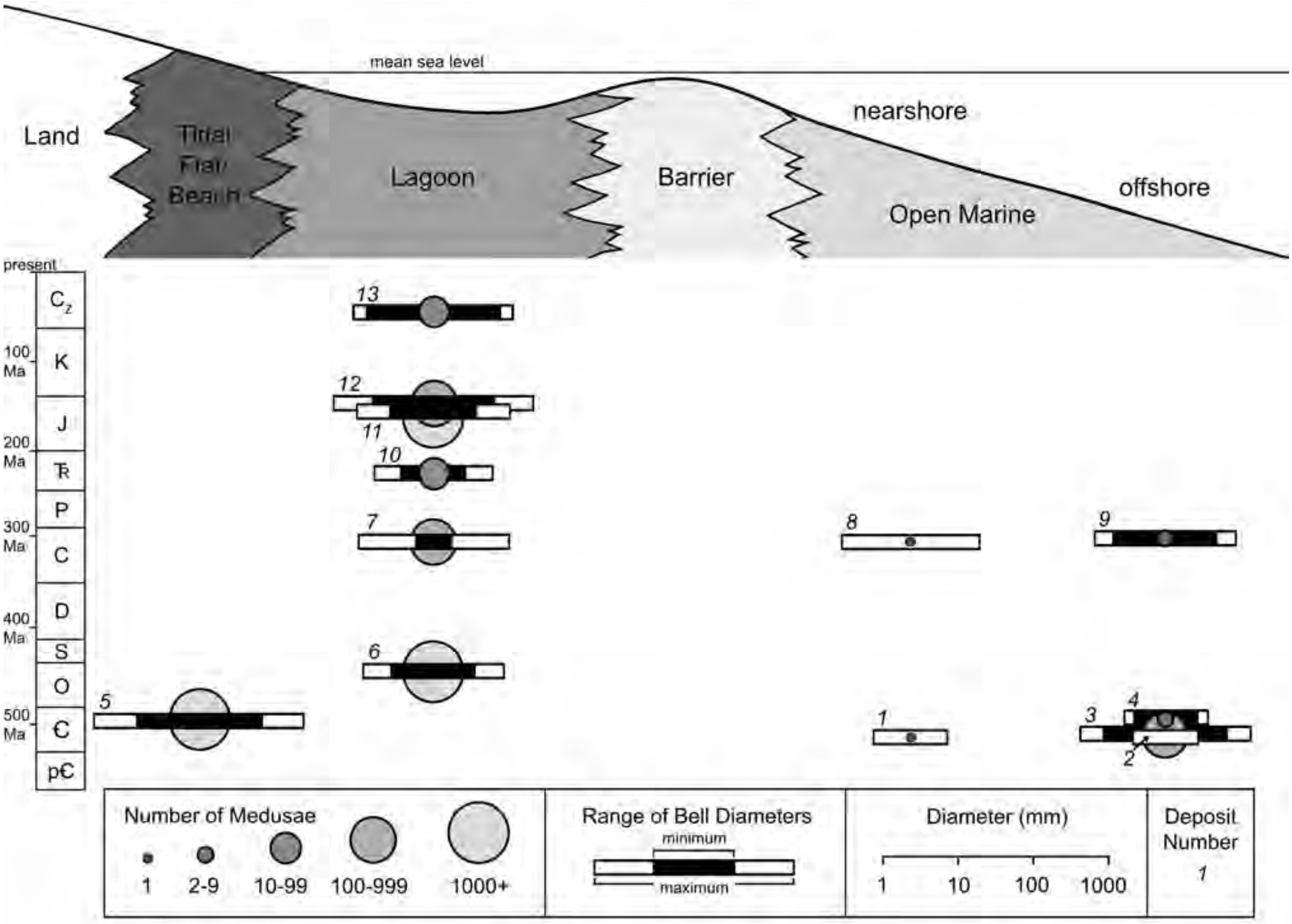

Fig. 1 - Synoptic temporal, facies, and size distribution of verified occurrences of fossil medusae. Deposits are plotted against both geological time and generalised facies. Minimum and maximum bell diameter in each deposit are represented by solid and open bars, and abundances are represented by circles (note logarithmic scales); missing circle in locality 2 indicates that the number of specimens is currently unknown. Deposits include: 1, Chengjiang Lagerstätte, Yunnan Province, China; 2, Qingjiang Lagerstätte, Hubei Province, South China; 3, Burgess Shale Lagerstätte, British Columbia, Canada; 4. Marjum Formation, House Range, Utah, USA; 5, Cambrian arenites, Elk Mound Group, Wisconsin, USA, Keeseville Formation, Potsdam Group, New York, USA and Cairnside Formation, Potsdam Group, Québec, Canada; 6, Williams Member, Stony Mountain Formation, Manitoba, Canada; 7, Mazon Creek Lagerstätte, Illinois, USA; 8, Mecca Quarry Shale Member, Linton Formation, Carbondale Group, Indiana, USA; 9, Stark Shale Member, Dennis Formation, Iowa and Nebraska, USA; 10, Grès à Voltzia Formation, Vosges Septentrionales, France; 11, Cerin Formation, Jura Mountains, France; 12, Solnhofen Formation, Bavaria, Germany; 13, Bolca Lagerstätten, near Verona, Italy.

Which features may be lost through decay, and what remains of the jellyfish, are critical to interpretation of a fossil. Evidence from the sedimentary record indicates that tentacles, manubria, and oral arms are likely to be lost through transport and/or decay (Adler, 2013). Muscles, mesenteries, gonads, and canals can be rather robust and thus may be preserved in detail depending on the taxon and mode of transportation, as may the oral arms of rhizostomes and rhizostome-like forms. Sediment casts of internal structure, along with mesoglea, may survive after everything else has gone (see Adler, 2013).

Studies of modern medusae pertinent to fossilisation processes fall broadly into two categories: observations of dead or moribund medusae in marine environments, and laboratory experiments and observation of premortem behaviour or postmortem deposition. Key studies of medusan burial, decay, and cast formation on shorelines include Nathorst (1881), Schäfer (1941, 1972), Kornicker & Conover (1960), Thiel (1971), Hamada (1977), and Müller (1984, 1985). These works provide useful observations on what parts of a jellyfish tend to survive the longest, on orientation of medusae, and on collapse and potential cast formation. Unfortunately, they provide few insights into the form and preservation of actual fossil medusae. In recent years, observation of dying medusae in deep water has added considerably to our understanding of jellyfish deposition in such environments (e.g., Billett et al., 2006; Titelman et al., 2006).

The deposition and potential fossilisation of medusae have been the subject of experimental studies over many years, going back to pioneering work by Nathorst (1881) and Walcott (1898), and subsequent studies by Kornicker & Conover (1960), Schäfer (1972), Norris (1989), Bruton (1991), Rozhnov (1998), and Adler (2013). Most of these have evaluated the possible formation of casts by fresh medusae, but Adler (2013) carried out controlled decomposition experiments on *Aurelia aurita* (Linnaeus, 1758). These showed that, as decomposition progresses, the medusa sinks to the bottom of the vessel, it loses surface texture, the exumbrella becomes flattened or concave, tentacles and the umbrella disappear, oral arms collapse, and the medusa eventually becomes flattened into a "2-D sticker". Of the various morphologic features, the gastric system retains its form the longest. By the time the medusa is completely flattened, it is unlikely that it could be preserved as a fossil. These observations are specific to *Aurelia,* and the differing features of other medusae are likely to result in preservational variations; for example, some have much more mesoglea and thick, tough ectoderms. Environmental conditions may also cause substantial differences; visible biofilms did not form on Adler's medusae (though there were biofilms on the water surface). Adler (2013) notes that her experimental medusae were not transported at all, and that tentacles and oral arms tend to be lost quickly when transported medusae are abraded by contact with sediment.

As Konservat-Lagerstätten become better understood, it is inevitable that the processes involved in medusan preservation will become clearer. Decay, mineralisation, and the maturation of organic material are all key processes in the preservation of soft tissue (Briggs & McMahon, 2016). Because labile soft tissues such as muscle decay more readily than tough material like cuticle, the latter is much more abundant in the "soft tissue" record (Briggs, 2003). Preservation of labile tissues commonly involves authigenic mineralisation, with the minerals involved varying depending on the ions available, the composition of the microbial community, the presence of oxygen, and the types of carcasses being deposited (Briggs, 2003). Many Konservat-Lagerstätten contain organisms with cuticular preservation, but lack preservation of those with purely labile tissues. Thus, medusae with preserved soft tissue (rather than just mouldic preservation) should only occur in deposits that cross this taphonomic threshold, and those would also have to be in depositional environments where jellyfish were likely to be present in large numbers, hence the rarity of medusa-bearing deposits. Nevertheless, medusae sometimes occur in places where other soft-bodied organisms are absent or extremely rare, such as in Cambrian epicratonic sand flat facies of North America (Hagadorn et al., 2002; Hagadorn & Belt, 2008; Lacelle et al., 2008). This may be due to the substantial robust mesoglea or leathery integument present in certain groups of medusae, and it could be that the taphonomic window or hydraulic energy regime barely allowed these robust forms to pass through, while prohibiting the preservation of more delicate jellyfish along with other soft-bodied organisms. It should also be noted that many medusae have features that may facilitate mouldic preservation, including impressions and/or steinkerns (Adler, 2013).

Chemical composition of the living animals is another factor that may have promoted the preservation of medusae where other soft-bodied fossils are absent. It has been noted that a number of metals occur at enriched levels in modern medusae. In scyphozoan tentacles, bell tissues, and oral arms, metals such as arsenic, cadmium, cobalt, copper, lead, manganese, and zinc can occur in concentrations 100x the ambient levels in seawater, while aluminum and iron can occur at more than 1000x the ambient levels (Cimino et al., 1983; Templeman & Kingsford, 2010). Several of these metals are involved in soft tissue preservation in various medusa-bearing deposits, and it is probable that their pre-existing concentration in medusae may have facilitated that preservation.

Environmental factors that could have inhibited preservation and fossilisation of medusae include but are not limited to: seafloor or shoreline exposure, wave and current action, decomposition, scavenging, disturbance by burrowers in burial sediments, and the activity of grazers on microbial mats. Fossilisation of medusae is often associated with deposition before or shortly after death of the animal, rapid sediment burial, early diagenetic mineralisation, low oxygen and/or elevated salinity, and bioimmuration beneath microbial mats or films. Anoxia or hypoxia will not prohibit decay, but can slow the rate of decay by an order of magnitude, as well as discouraging scavenging, bioturbation, and the grazing of microbial mats (Kristensen et al., 1995; Briggs, 2003; Cotroneo et al., 2016).

In modern oceans, it seems likeliest that appropriate conditions for fossilisation of medusae would be present in restricted lagoons, where there is little wave or current action, where burial can occasionally be rapid (through storm activity or density currents), where microbial mats may be present, and where low oxygen and high salinity related to stratification and limited circulation can inhibit the activity of decomposers, burrowers, scavengers, and grazers. Moreover, the decomposition of dead medusae during blooms could by itself create anoxic or hypoxic conditions in water of various depths, through the effect of their sheer biomass (West et al., 2009; Chelsky et al., 2015). This phenomenon may have been an important factor in deposits where medusan abundance is so high that it reflects a jellyfish bloom or a series of blooms. Fossilisation could have resulted when the local chemical effects of a bloom were associated with other conditions, the most likely of which seem to be the presence of microbial mats and possibly of unusual cations in the porewaters surrounding carcasses. Although most medusae have a density sufficiently low that they will be deposited on shorelines (Titelman et al., 2006), some are denser and have morphologies that allow them to accumulate in deep water (Billett et al., 2006).

OCCURRENCES OF FOSSIL MEDUSAE

The following sections briefly describe each of the 13 verified medusan-bearing deposits or deposit groups, in terms of formation and age, medusan taxa including abundance and sizes, mode of preservation, lithology, depositional environment, and associated biota. Some examples are shown in Pl. 1, and data on facies, size, and abundance are graphically depicted in Fig. 1.

There is not space here to discuss the dozens of described medusoids that do not meet the criteria for recognition as medusae, or where there is not sufficient data to be certain of a medusan attribution (e.g., Hagdorn, 2013; Clemmensen et al., 2016; Sappenfield et al., 2017).

1. Chengjiang Lagerstätte, Kunming, Yunnan Province, China; Yu'anshan Formation, Cambrian (Series 2, Stage 3)

Yunnanoascus haikouensus Hu et al., 2007, formerly considered a ctenophore, was convincingly re-interpreted by Han et al. (2016) as a medusozoan, possibly a scyphozoan. There is a single specimen, with a bell diameter of about 10 mm. Preservation is as a film of organic carbon and pyrite, and the specimen bears rhopalia, lappets, and tentacles. The Chengjiang biota occurs in thin-bedded siltstones and claystones, with most of the exceptional fossils occurring in event beds with sharp bases and gradational tops, which may represent distal mud turbidites (Hou et al., 2017). The diverse associated biota includes algae, sponges, ctenophores, arthropods, brachiopods, worms, and chordates. The depositional setting was a restricted tropical shelf with occasional storm influence (Babcock et al., 2001), and rapid burial in the event beds may have protected carcasses from scavenging. No burrows occur with the soft-bodied fossils (Hou et al., 2017).

2. Qingjiang Lagerstätte, Changyang area, Hubei Province, South China; Shujingtou Formation, Cambrian (Series 2, Stage 3)

Up to five new medusae have been reported in a preliminary publication on this newly discovered biota (Fu et al., 2019). One spectacular example was figured, bearing similarities to semaeostome scyphozoan medusae. Preservation is as a carbonaceous film, with tentacles, a convex bell, manubrium, and other features all clearly visible in the single figured specimen. Unfortunately there is very limited information currently available on abundance, diversity, or sizes of the medusae, as Fu et al. (2019) combine them with polypoid forms in their data tabulation, but the illustrated specimen is very small, with a bell diameter of about 7.5 mm. The Qingjiang biota occurs in calcareous claystones within a succession of laminated black siltstones. The associated biota is of high diversity with more than 100 taxa belonging to algae, ctenophores, arthropods, sponges, priapulids, brachiopods, lobopodians, hyolithids, and other groups. A few taxa are shared with the Chengjiang biota, including the anemone *Xianguangia* (see syntheses in Han et al., 2010; Ou et al., 2017). The depositional setting was on a shelf, distal to the mudstones deposited in the coeval Chengjiang Lagerstätte. Organisms are hypothesised to have been transported downslope by sediment gravity flows, and deposited on an anoxic seafloor below storm wave base. No bioturbation has been reported from the beds that bear soft-bodied fossils.

3. Burgess Shale Lagerstätte, Mount Field, British Columbia, Canada; Burgess Shale Formation, Cambrian (Series 3 [Miaolingian], Stage 5 [Wuliuan])

Medusae, which have not been formally described, were collected by Desmond Collins and earlier Royal Ontario Museum crews and first reported by Devereux (2001; D. Collins, pers. comm.). These specimens, numbering at least 104 individuals, come from multiple horizons (Devereux, 2001; D. Collins, pers. comm.) and appear to be scyphozoans. The medusae exhibit simple, generalised morphology, including fusiform/highly-domed bells and abundant short tentacles that fringe bell margins. Specimens exhibit evidence of shearing, tearing, and folding and some specimens exhibit contracted coronal rings or oral regions. Diameters range from ~45-200 mm and fossils are preserved as organic carbon and aluminosilicate films (Butterfield, 1995, 2003, 2009; Devereux, 2001; Petrovich, 2001). Relief is moderate, suggesting that the medusae had considerable substance, with marked colour contrast from the sediment in fresh specimens (Devereux, 2001). The medusa-bearing facies includes finely layered calcareous shales, mudstones, and siltstones, deposited in deeper water at the foot of a deep escarpment (Briggs et al., 1994; Fletcher & Collins, 2009). The associated fauna is famously diverse and includes many groups such as sponges, arthropods, priapulids, polychaetes, and chordates; these are all generally cuticular forms, and organisms lacking cuticle are largely absent (Butterfield, 2003). The fossils are thought to be preserved as a result of rapid burial by pulses of fine sediment under anoxic conditions, possibly deposited by density currents or turbidity currents (Gabbott & Zalasiewicz, 2009). Microbial structures are known from some intervals in the Burgess Shale, including on surfaces that bear soft-bodied fossils (Gabbott & Zalasiewicz, 2009; see also Mángano et al., 2019), but we do not know whether the medusae are directly associated with these. Although trace fossils are also known from the Burgess (Minter et al., 2011), they do not occur in facies that bear medusae, and when they do occur on beds that bear other soft-bodied fossils, they are often sub-cuticular or cryptic in nature (Mángano et al., 2019).

4. Marjum Formation, Sponge Gully, House Range, Utah, USA; mid Cambrian (Series 3 [Miaolingian], Stage 6 [Drumian])

Varied small medusae were collected by Sue Halgedahl and Richard Jarrard and later documented by Cartwright et al. (2007). These specimens were not formally named but may be allied with narcomedusan hydrozoans, semaeostome scyphozoans, and cubozoans. Specimens were described from at least three horizons. Different specimens exhibit varying suites of morphologic features, including tentacles and bell musculature. Diameters are 7 to 15 mm, and preservation is as largely two-dimensional organic films. They occur in thin-bedded, fine-grained dark grey mudstones alternating with coarser-grained reddish layers. These were deposited below storm wave base in mostly anoxic, quiescent conditions, on a gently sloping ramp. Associated fossils include algae, trilobites, other arthropods, priapulids, echinoderms, brachiopods, sponges, and hyolithids (Briggs & Robison, 1984; Conway Morris & Robison, 1986). Bioturbation is absent in soft-tissue-bearing beds (Gaines et al., 2012), but may be cryptic in nature (Pratt & Kimmig, 2019).

5. Medusae in Cambrian Arenites of North America

5A. Elk Mound Group, Mosinee, Wisconsin, USA; Cambrian (Series 3 [Miaolingian] to Series 4 [Furongian]) - Abundant large medusae have been documented by Hagadorn et al. (2002) and Tarhan (2008), but have not yet been formally described. These fossils, preserved as three-dimensional moulds in medium-grained quartz arenites, probably represent at least two taxa of scyphozoan medusae (Pl. 2, fig. 2). Part-counterpart moulds and steinkerns show features including radial canals, manubria, oral arms, coronal rings, and lappets. The mouldic preservation is somewhat similar to that of Ediacaran fossils. More than 10,000 medusae are known, occurring in more than 20 horizons.

Most diameters range from 80 to 750 mm. The quartz arenites were deposited in shoreface to shallow subtidal marine sands in a barrier island complex, and exhibit features such as raindrop impressions, desiccation cracks, and channels and abundant microbial coating of surfaces (Bottjer & Hagadorn, 2007; Dornbos et al., 2007; MacNaughton et al., 2019). Associated fossils include phyllocarid and euthycarcinoid arthropods (Collette & Hagadorn, 2010) and the trace fossils *Arenicolites*, *Climactichnites*, *Cruziana*, *Diplichnites*, *Planolites*, *Protichnites*, *Rusophycus*, and *Teichichnus* (Getty & Hagadorn, 2008; MacNaughton et al., 2019). The abundant medusae may have been preserved because of a lack of erosional scouring, and limited scavenging and vertically oriented bioturbation (Hagadorn et al., 2002).

5B. Keeseville Formation, Potsdam Group, Ausable Chasm, New York, USA and Havelock, Québec, Canada; Cambrian (Series 3 [Miaolingian]) - Numerous medusae have been documented by Hagadorn & Belt (2008), Lacelle et al. (2008), and Tarhan (2008). These are virtually contemporaneous with the medusae in the Elk Mound Group, and preserved in a very similar depositional setting. The fossils are preserved as moulds in medium-grained quartz arenites, and often appear as simple circular mounds, but some are twisted or folded, exhibit evidence of transport, or have tripartite or quadripartite axial regions (Pl. 1, fig. 1; Pl. 2, fig. 1). They are interpreted as scyphozoan medusae, but have not yet received systematic description. More than 1000 medusae are known, occurring in more than six horizons. Diameters range from about 50 to 660 mm, with an average of just over 200 mm. The depositional environment is interpreted to have been intermittently emergent, and the arenites containing medusae have sedimentary structures indicating deposition in very shallow water less than 2 m deep, with oscillating flow (Hagadorn & Belt, 2008; see also Sanford & Arnott, 2010; Lowe et al., 2017). There is good evidence of microbial mats (Bottjer & Hagadorn, 2007; Landing et al., 2007), and the associated biota includes phyllocarid and euthycarcinoid arthropods (Collette & Hagadorn, 2010) and the trace fossils *Arenicolites*, *Climactichnites*, *Cruziana*, *Diplichnites*, *Planolites*, *Protichnites*, *Rusophycus*, and *Teichichnus* (Getty & Hagadorn, 2008). Deep burrows are absent from medusa-bearing facies.

6. Williams Member, Stony Mountain Formation, William Lake, Manitoba, Canada; Upper Ordovician (Katian)

Thousands of fossil medusae, distributed across more than ten horizons (Pl. 2, figs 3-4), were noted by Young et al. (2007, 2012). Systematic description is in progress, and the fossils include leptomedusan hydrozoans, possible anthomedusan hydrozoans, and possible Scyphozoa. The medusae are three-dimensional moulds and replacement fossils in dolomudstone, preserved as degraded pyrite and as sparry dolomite slightly enriched in iron and silica, surrounded by rusty halos of degraded pyrite. There was apparently substantial pyrite in the fossils as originally preserved, but they were subsequently weathered during exposure near the ground surface over the past several thousand years. Many specimens have a quadrate form and exhibit canals, gonads, and wrinkled bells; features such as tentacles and bell apices are rarely preserved. Diameters range from about 15 to 80 mm. The enclosing dolomudstone is thin bedded, and represents deposition under restricted, shallow, and very low energy marginal marine conditions, possibly in a lagoon. Microbial laminae are observed in some horizons, and some medusae are associated with salt crystal moulds. The associated fauna includes arthropods (eurypterids, xiphosurids, pycnogonids), possible ctenophores, lingulid brachiopods, nautiloid cephalopods, and other groups (Young et al., 2012). Shallow *Chondrites*-like burrows are common or abundant in some horizons.

7. Mazon Creek Lagerstätte, Essex and Astoria, Illinois, USA; Francis Creek Shale, Carbondale Formation, upper Carboniferous, Middle Pennsylvanian (Moscovian)

Several medusan taxa have been described and named (Johnson & Richardson, 1968; Foster, 1979; Sroka, 1997), but these are being re-assessed in a study in progress (see Plotnick et al., 2017), and we only consider two to be valid medusozoans: *Anthracomedusa turnbulli* Johnson & Richardson, 1968, a chirodropid cubozoan (Gershwin, 2003; see Pl. 1, fig. 2), and *Octomedusa pieckorum* Johnson & Richardson, 1968, which may be either a hydrozoan or a scyphozoan (Pl. 1, fig. 5). More than 20 specimens of *A. turnbulli* are known, with bell diameters in the range of 30 to 100 mm, whereas the more than 15 specimens of *O. pieckorum* are much smaller, about 3 to 21 mm. Because most Mazon Creek material was collected from coal mine spoil heaps, it is not possible to determine the number of horizons at which each species occurs - but Baird et al. (1986) documented the presence of nodules across many horizons. The following taxa need reassignment to non-medusan groups (Plotnick et al., 2017): *Essexella asherae* Foster, 1979, *Reticulomedusa greenei* Foster, 1979, and *Lascoa mesostaurata* Foster, 1979. Fossil preservation is as early diagenetic pyrite and siderite moulds and casts, in ironstone concretions (Woodland & Stenstrom, 1979; Baird et al., 1986; Cotroneo et al., 2016). Microbial textures are present, and microbes are considered to have played an important role in Mazon Creek fossilisation (Fernandes, 2012; Cotroneo et al., 2016); the combination of pyrite and siderite is related to a combination of fresh and salt water influences (Cotroneo et al., 2016). The regional environment is interpreted to have been a coastal delta to estuary (Shabica, 1970; Baird et al., 1985), with the Francis Creek Shale being a sediment infill in interdistributary bays or lagoons (Foster, 1979; Baird et al., 1986; Cotroneo et al., 2016). The associated fauna includes many soft-bodied organisms representing brackish, freshwater, and terrestrial settings: plants, arthropods, bivalves, millipedes, vertebrates, and other groups (Johnson & Richardson, 1966; Nitecki, 1979; Wittry, 2012) as well as a diverse array of trace fossils (see synthesis in LoBue, 2006).

8. Mecca Quarry Shale Member, Linton Formation, Carbondale Group, Parke County, Indiana, USA; upper Carboniferous, Middle Pennsylvanian (Moscovian)

A single remarkably preserved medusan is known, representing a chirodropid cubozoan; systematic description is in progress (Young & Hagadorn, 2018). The specimen has a bell diameter of 68 mm; preservation is as a silica sand endocast of the body cavity within the bell, combined with carbon/mineralised films preserving the pedalia, tentacles, and other features (Pl. 1, fig. 4). The Mecca Quarry Shale is a grey to black carbonaceous shale that is enriched in zinc, molybdenum, and other heavy metals (Coveney & Martin, 1983); this unusual composition may be reflected by the occurrence of sphalerite as one of the minerals preserving the medusan. In Indiana, this unit was deposited in nearshore, shallow marine locations adjacent to peat swamps, and anoxic bottom conditions may have been present due to accumulation of plant material and other organics, some of it probably floating at the water surface (Zangerl & Richardson, 1963; Tourtelot, 1979; Coveney & Martin, 1983). The unusual concentration of heavy metals may have resulted from acidic drainage from peat swamps. Associated fauna in the Mecca Quarry Shale includes bivalves, gastropods, ammonoids, bryozoans, corals, crinoids, brachiopods, a variety of fishes, conodonts, annelids, trilobites, phyllocarids, plants including terrestrial logs, sticks and leaves, and forms akin to marine algae. The extreme rarity of trace fossils in the Mecca Quarry Shale beds that contain unusual fossils (Zangerl & Richardson, 1963; Coveney & Martin, 1983) suggests that the body fossils were allochthonous. This deposit represents an open marine facies that was likely deposited offshore from the estuarine-lagoonal Mazon Creek Lagerstätte, a situation akin to the onshore-offshore equivalence of the Chengjiang and Qingjiang Lagerstätten.

9. Stark Shale Member, Dennis Formation, Central United States; upper Carboniferous, Upper Pennsylvanian (Kasimovian)

9A. LIMEKILN HOLLOW, IOWA - The medusan *Prothysanostoma eleanorae* Ossian, 1973 was described on the basis of seven remarkable specimens, occurring together on a single slab. These fossils are considered to represent scyphozoans, possibly members of the Rhizostomeae, with bell diameters of 26 to 51 mm. The medusae are preserved as carbon films and calcium phosphate, and include organs such as oral arms, bells, and rhopalia and lappets on the bell margins.

9B. PAPILLION, NEBRASKA - A single medusan similar to, but larger than *Prothysanostoma eleanorae* is known from this locality (publication in preparation). It is less complete than the type material of *P. eleanorae* but still exhibits features such as the bell, exumbrellar surface, and oral arms; the bell diameter is about 86 mm. Preservation is as carbon and mineralised films rich in silica and aluminum.

In Ossian's publication (1973), *P. eleanorae* is described as occurring in the Wea Shale Member, Cherryvale Formation, but black shales from that area have since been re-assigned to the Kasimovian Stark Shale Member (Heckel & Meacham, 1981; Pope, 2012). The Stark Shale is a buff, grey, or black shale, deposited at intermediate depths in a subtidal mid-shelf setting, possibly during maximum transgression into the midcontinental seaway (Boardman & Heckel, 1989; Watney et al., 1989). The medusae are apparently from the lower half of this unit, in black fissile shale with scarce associated fossils including inarticulate brachiopods, ammonoids, bryozoans, corals, crinoids, bivalves, conodonts, fish, plants, and soft-bodied fossils including a variety of articulated arthropods and coleoids (Schram, 1984; Malinky & Heckel, 1998; Mapes & Doguzhaeva, 2018). Discrete burrows (trace fossils) have not been reported from these localities.

10. Grès à Voltzia Lagerstätte, Vilsberg and Arzviller, Vosges Septentrionales, France; Grès à Voltzia Formation, Middle Triassic (Anisian)

Ten specimens are known from three or more horizons, all of them assigned to *Progonionemus vogesiacus* Grauvogel & Gall, 1962, a limnomedusan hydrozoan similar to the extant *Gonionemus*. Preservation is as calcium phosphate films, which were apparently shielded beneath thin microbial laminae ("veils"; Gall, 1990). The medusae are small, with bell diameters of 8 to 40 mm, and are beautifully preserved with features such as tentacles, gonads, and stinging cells. The enclosing sediment consists of silt and clay laminites which form lensoid bodies, apparently representing deposition in marginal marine ponds, possibly between distributaries on a delta (Gall, 1985; Selden & Nudds, 2004). The ponds were stagnant, and hypersaline at times (Selden & Nudds, 2004). Associated biota includes annelids, lingulid brachiopods, bivalves, crustaceans, xiphosurids, fish, terrestrial arthropods, and plants. Burrows are absent

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EXPLANATION OF PLATE 2

Fossil jellyfish blooms, and modern equivalents (color online).

Fig. 1 - Domical mouldic medusae on bedding plane surface of a Cambrian arenite in the Potsdam Group, Ausable Chasm, New York, USA; width of exposed bedding plane is about 4.5 m.

Fig. 2 - Stranded medusae on oscillation ripple-marked bedding plane, from sand flat facies of a Cambrian arenite of the Elk Mound Group, Blackberry Hill, Wisconsin, USA; rock hammer at top of image is 17.5 cm wide.

Figs 3-4 - Hydrozoan medusae in Upper Ordovician dolomudstones, Stony Mountain Formation, William Lake, Manitoba, Canada;

3 - medusae on the underside of a bedding plane, each of which preserves cross-shaped canals;

4 - line of weathered medusae on a bed top.

Fig. 5 - Modern semaeostome *Aurelia* sp. forming gelatinous mass on the shore of the Baltic Sea, Saaremaa, Estonia; diameters of medusae approximately 100 mm.

Fig. 6 - Stranded bloom of medusae along the Gulf of Mexico; image courtesy of J. Costello.

Figs 7-8 - Bloom of the hydrozoan *Staurophora mertensii* in the Bay of Fundy at Grand Manan Island, New Brunswick, Canada; this taxon is very similar in form and size to the fossil medusae at William Lake.


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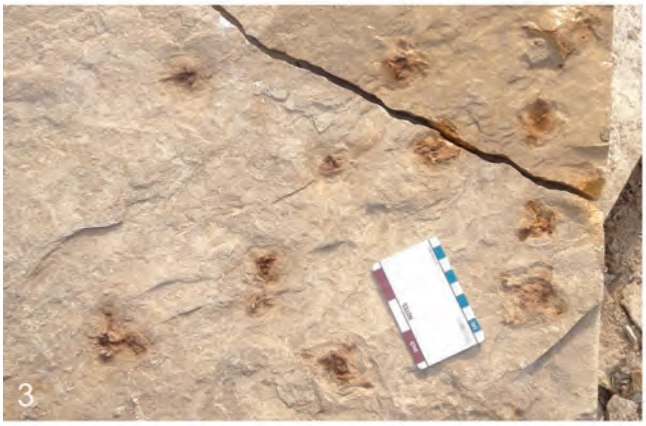
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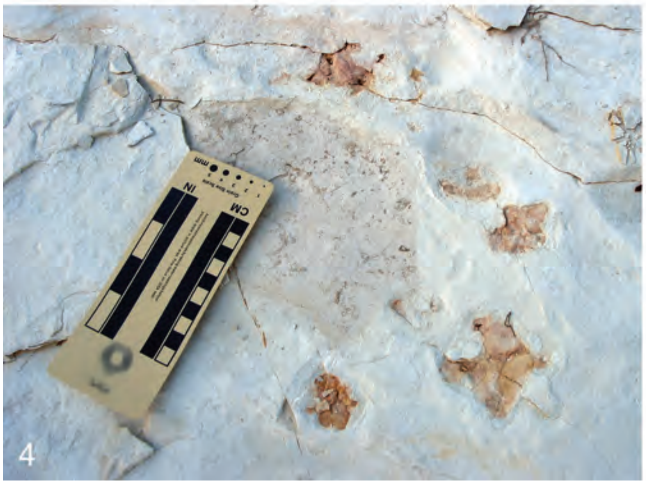
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from most of the horizons containing unusual body fossils (Selden & Nudds, 2004).

11. Cerin lithographic limestone Formation, Cerin, Jura Mountains, France; Upper Jurassic (upper Kimmeridgian)

Four taxa of medusae were described by Gaillard et al. (2006), including two carybdeid cubozoans and two semaeostome scyphozoans. The carybdeids are *Bipedalia cerinensis* Gaillard et al., 2006 (14 specimens in one horizon, bell diameters 45-70 mm) and *Paracarybdea lithographica* Gaillard et al., 2006 (five specimens in one horizon, bell diameters about 50 mm). Semaeostomes are *Paraurelia cerinensis* Gaillard et al., 2006 (more than 1000 specimens in more than six horizons, bell diameters 15 to 105 mm) and *Paraurelia* sp. A (a few specimens in two horizons, diameter 120 mm). Preservation is largely mouldic and details are obscured in most specimens, but it is possible to recognise features such as bell margins, gonads, and tentacles. The lithology consists of lithographic (micritic) limestones that were deposited on the margins of a lagoon that had a marine influence (Gaillard et al., 2006). Laminae in the Cerin are thought to be of microbial origin (Gall, 1990), and preservation may have been due to cover by microbial films and mats. Like the Solnhofen Lagerstätte, the Cerin could be considered an obrution stagnation deposit (Seilacher et al., 1985; Gaillard et al., 2006). The associated biota includes algae, asteroids, echinoids, fishes, and pterosaurs; trace fossils are known from the deposit but absent from the lower medusa-bearing portion of the unit (Gaillard et al., 1994; Audo et al., 2014).

12. Solnhofen Formation, Southern Franconian Alb, Bavaria, Germany; Upper Jurassic (lower Tithonian)

There have been many publications concerning Solnhofen medusae, and numerous taxa have been named, described, and illustrated over the years (Haeckel, 1865, 1866, 1869, 1874; Ammon, 1883, 1906; Walcott, 1898; Maas, 1902, 1906; Kuhn, 1938, 1961; Kieslinger, 1939; Kolb, 1951; Harrington & Moore, 1955, 1956a, b, c; Barthel et al., 1990; Selden & Nudds, 2004; Adler & Roper, 2012). Fortunately, a substantial re-assessment was carried out recently by Adler (2013), and we generally concur with her attributions. Adler recognised four scyphozoan taxa. *Rhizostomites admirandus* Haeckel, 1866, a rhizostome, is very large (diameter 100-540 mm) and is the most abundant Solnhofen medusan, with 194 specimens in collections considered by Adler, and many others elsewhere (Pl. 1, fig. 3). *Myogramma speciosum* Maas, 1902, which is probably a semaeostome, is also large (diameter about 500 mm) but is less common (22 specimens; see Pl. 1, figs 6-8). *Hydrocraspedota mayri* Kolb, 1951, possibly a discomedusan, is smaller (diameter 100-200 mm) and rare (five specimens). *Eulithota fasciculata* Haeckel (1869) is a semaeostome similar to *Cyanea,* with diameters about 55-115 mm and 11 specimens known. A number of other previously described taxa are likely synonyms of the above species, or are discounted because they are unlikely to be medusae. Solnhofen medusae are preserved as moulds, with many of them being a combination of mould and steinkern (Adler, 2013). *Palaequorea rygoli* Adler & Röper, 2012, was considered to be a hydromedusan, but it is likely a sand-volcano-like structure (aka *Astropolithon*) similar to those from the Cambrian of New Brunswick, Canada (Hagadorn & Miller, 2011).

The laminated micritic limestones of the Solnhofen were deposited in hypersaline, stratified, possibly anoxic lagoons, separated from the open sea by bioherms and reefs (Barthel, 1978; Seilacher et al., 1985; Barthel et al., 1990; Viohl, 1996). The fine laminae reflect a microbial influence on sedimentation (Keupp, 1977). Solnhofen medusae occur at three localities, in a total of more than 30 horizons. Some medusae were likely transported live or fresh within suspended sediment loads and deposited with that sediment, whereas others may have been rapidly bio-immured beneath microbial mats (Adler, 2013). The associated biota is rare but highly diverse, with hundreds of species belonging to groups such as plants, crinoids, bivalves, squids, horseshoe crabs, crustaceans, insects, fishes, marine reptiles, dinosaurs, and birds. The benthic life forms were transported from shallow water, possibly by turbidity currents; burrowing trace fossils are absent (Seilacher et al., 1985; Brett & Baird, 1993).

13. Bolca Lagerstätten, Bolca, near Verona, Italy; Eocene (upper Ypresian)

At least two and possibly three medusan taxa are present, including the rhizostome *Simplicibrachia bolcensis* Broglio Loriga & Sala Manservigi, 1973, an as-yet-unnamed probable semaeostome similar to *Aurelia,* and other possible medusae (Pl. 1, figs 9-10; see also Giusberti et al., 2014; Friedman & Carnevale, 2018). The nine mostly incomplete specimens of *S. bolcensis* include examples with bell diameters of 140-150 mm, whereas five of the studied semaeostome medusae have bell diameters of 60-90 mm. The fossils occur as mixed carbonaceous films, with some exquisite preservation of features such as oral arms, gonads, and muscles. The lithology is a finely laminated micritic limestone, which was deposited close to land in a lagoon that was sheltered from an open carbonate platform by a physical barrier (Papazzoni & Trevisani, 2006; Schwark et al., 2009). The lagoon's bottom waters, at a depth of tens of metres, were both anoxic and saline, with microbial biofilms that inhibited decomposition, burrowers, and scavengers (Schwark et al., 2009; Friedman & Carnevale, 2018). Mortality may have been associated with toxic algal blooms (Friedman & Carnevale, 2018). The associated biota is characterised by diverse fishes, along with insects, crustaceans, polychaetes, molluscs, brachiopods, and plants (algae, seagrasses, and land plants). The total diversity is very high, with hundreds of species known.

PATTERNS OF FOSSIL MEDUSAN OCCURRENCE

Medusan-bearing deposits are distributed through the Phanerozoic record, from the lower Cambrian to the Eocene (Fig. 1). Although there is a broad spread, the frequency of occurrences diminishes through time: more than a third of the deposits (five) are of Cambrian age, four are in the post-Cambrian Palaeozoic, the remaining four are Triassic through Eocene, and no verified deposits are known from the past ~40 million years.

Occurrence patterns, described below and in Fig. 1, integrate several potentially relevant factors: depositional setting, medusan size, medusan abundance, presence or absence of microbial structures, mode of preservation, and associated biota. There are currently not sufficient data available for a full detailed comparison of some important aspects such as the relationship to particular sedimentary and microbial structures, the presence of scavengers and scope of their influence, and full taxonomic assignments of medusae and associated biotas.

1. Depositional settings

Although medusae (including hydrozoan, scyphozoan, and cubozoan jellies) thrive in many aquatic environments, all verified medusan-bearing deposits can be assigned to three broad depositional environments: sandy coasts, estuarine-lagoonal settings, and mud-dominated open marine shelves (Fig. 1). In the Cambrian and Ordovician, jellyfish occurrences represent all three types of settings. In the later Palaeozoic, medusae were no longer preserved in coastal sands, but still occur in lagoon/estuary and in restricted subtidal facies. Triassic and Jurassic jellyfish are sometimes splendidly preserved, but only in muddy lagoonal or estuarine settings. The sole post-Jurassic medusan occurrence is in the Eocene Bolca Lagerstätte of northern Italy, which also represents a lagoonal environment.

In total, half of all known occurrences represent lagoonal or estuarine embayments. These can be divided into two groups. The William Lake, Cerin, Solnhofen, and Bolca Lagerstätten are all lagoonal deposits characterised by laminated lithographic carbonates. Each of these was probably deposited in conditions with a substantial degree of stratification and anoxia. The Francis Creek Shale and the Grès à Voltzia Lagerstätte were deposited in the same recurrent facies association, produced by deltaic to marginal marine clastic environments (Baird et al., 1985; Gall, 1985).

2. Size distribution of medusae

The sizes of fossil medusae are extremely variable, both within and between deposits (Fig. 1). Most deposits are dominated by specimens in the intermediate range, with bell diameters in the tens of mm; such deposits include the Burgess Shale, William Lake, Mazon Creek, Mecca Quarry Shale, Stark Shale, Grès à Voltzia, Cerin, and Bolca Lagerstätten. A few deposits contain markedly smaller medusae. For example the single Chengjiang specimen has a diameter of about 10 mm, the illustrated Qingjiang specimen has a diameter of about 7.5 mm, and medusae in the Marjum are 7-15 mm. The Mazon Creek and Grès à Voltzia Lagerstätten also include some minute examples. The presence of such tiny jellyfish is consistent with very quiescent conditions, minimal decomposition, early diagenetic mineralisation, and very fine-grained sediment; such a deposit should provide a good representation of the medusan biota that was present. At the other end of the spectrum are the Cambrian arenites of North America, in which diameters range from 50-750 mm. This strong skew toward larger medusae could be because smaller jellyfish simply would not have been preserved in coarser sediments deposited in these higher energy environments. The Solnhofen assemblage includes some of the largest specimens, with medusae of *Rhizostomites* sp. reaching 500 mm or more in diameter, but it also includes some quite small jellyfish; it is unlikely that there was much size bias to preservation in this very fine-grained deposit because of the remarkable range in size (from tens of mm to nearly a metre) and relief (mm to hundreds of mm) and phenomenal anatomical detail preserved in medusae. The ability of this facies to capture such a range of detail, shapes, and sizes suggests to us that the taphonomic/preservational window was still open at its widest in Solnhofen, and by extension, other Solnhofen-type deposits. Thus, where there are abundant specimens of a given jellyfish taxon in such deposits, the size distribution of those fossils might approach that of the living assemblage of that taxon in that palaeoenvironment, and hence may reflect a portion of its life history/cycle.

3. Medusan abundance within deposits

Abundances range from single specimens in Chengjiang and the Mecca Quarry Shale (although both have onshore/offshore counterpart deposits that also bear medusae), to thousands of medusae in the William Lake dolostones and Cerin lithographic limestones, to tens of thousands of medusae in Cambrian arenites. Considering facies, abundances are greatest in sandy beach deposits (Fig. 1), variable but sometimes very high in lagoonal settings (up to thousands of specimens), and lowest in open marine strata (1-104 specimens).

Possible jellyfish blooms, distinguished by clusters of medusae or large numbers of medusae on a single bedding plane, are recognised in five of the 13 deposits. The most likely examples of true blooms are the abundant medusae distributed across single bedding planes of Cambrian arenites of North America (Pl. 2, figs 1-2), at William Lake (Pl. 2, figs 3-4), and at Cerin (Hagadorn et al., 2002; Gaillard et al., 2006; Hagadorn & Belt, 2008; Lacelle et al., 2008; Tarhan, 2008; Young et al., 2012). Clusters of medusae occasionally occur in the Mazon Creek (Pl. 1, fig. 5), but their relative rarity and preservation in transported concretions precludes assessment of how many of the collected specimens might have come from single horizons. The seven medusae of *Prothysanostoma eleanorae* in the Stark Shale are all packed together on a single slab, indicating that they could also have been part of a jellyfish bloom. Such high-density deposits are thus spread through the Cambrian to Jurassic record, and they occur in all the three known jellyfish-bearing palaeoenvironments (sandy beach, lagoon, and open marine).

4. Microbial structures

At least seven, and possibly eight of the thirteen medusan-bearing deposits show evidence of microbial mats, films, and/or textures. There is a strong facies distinction here: those with such evidence include every deposit from sandy beach and lagoonal settings. Those lacking such evidence on medusa-bearing horizons include all of the deposits from open marine settings.

5. Mode of preservation

Studies of preservation within most of these deposits are still in their infancy, but a generalised comparison indicates an interesting pattern. Although the Qingjiang and Marjum deposits are composed exclusively of carbonaceous or organic films, jellyfish in most other deposits are preserved through a combination of two or more kinds of preservation. These are either carbonaceous films combined with mineral films, or impressions or moulds combined with films. It is notable that the minerals involved in medusan preservation vary tremendously by deposit, and include aluminosilicates, pyrite, sphalerite, dolomite, and calcium phosphate. All of the Cambrian arenites and Cerin contain medusae that are largely mouldic, but also bear microbial structures such as old elephant skin (OES) on the same surfaces where medusae are preserved (e.g., Pl. 1, fig. 1); on some freshly split bed surfaces, these horizons are quite ferruginous, typically bearing a limonitic or hematitic veneer (e.g., fig. 9B in MacNaughton et al., 2019). A similar phenomenon occurs in sandstones that bear Ediacaran fossils, and this veneer is thought to represent a weathering byproduct of pyrite whose original precipitation was fostered by microbial mantling and/or degradation of carcasses (Gehling, 1999; Liu et al., 2019; and synthesis in MacGabhann et al., 2019).

6. Associated biota

The majority of medusan-bearing deposits also contain a variety of other fossils, including both soft-bodied and mineralised forms. These include the renowned and famously diverse Konservat-Lagerstätten such as the Burgess Shale, Mazon Creek, and Solnhofen. Yet with one exception the less well-known medusa-bearing deposits are also moderately to highly diverse, and include some soft-bodied fossils. That exception is in the Cambrian arenites of the North America, where associated body fossils are scarce (Collette & Hagadorn, 2010; Seilacher & Hagadorn, 2010); this lack of body fossils is consistent with the coarser-grained lithologies and higher energies represented by those depositional environments. Associated biotas in the lower Palaeozoic deposits are entirely marine, but from the Carboniferous onward every assemblage includes both marine and terrestrial components.

DISCUSSION

The fossil record of cnidarian medusae is sparse, but their occurrence patterns reveal substantial information about changing processes in the marine realm. Each deposit exhibits unique conditions in terms of depositional environment, taphonomy, and diagenesis. It is notable that deposits are more abundant in the Cambrian than in any subsequent period of the Phanerozoic, a pattern mirrored by Burgess Shale-Type (BST) and Orsten-Type Konservat-Lagerstätten (Conway Morris, 1989; Maas et al., 2006). The youngest documented deposit is the Bolca Lagerstätten, of Eocene age. Many of the environmental factors that affected medusan fossilisation, such as scavenging, burrowing, and the occurrence of microbial mats, have changed dramatically through the Phanerozoic; it is possible that this evolution has resulted in an increasing scarcity of unique or unusual preservational conditions. To assess this possibility, the following discussion considers the "evolution" of key factors that may have affected the fossilisation of medusae.

Scavengers

In modern marine settings, medusae decompose very readily, but scavenging is also a significant factor in the destruction of medusan carcasses. Various groups have been observed to scavenge gelatinous carcasses, including gastropods, fishes, crustaceans, echinoids, starfish, birds, and even dipterans (Kornicker & Conover, 1960; Lebrato & Jones, 2009; Cadée, 2013). Most of these animals had not yet appeared or were of minimal importance in the early Palaeozoic, but shoreline scavengers such as eurypterids, euthycarcinoids, and gastropods had evolved by the later Palaeozoic, and these were joined in the Mesozoic by shore crabs and birds (Bottjer et al., 2000; MacNaughton et al., 2002; Pisani et al., 2004; Collette et al., 2010; Young & Hagadorn, 2010; Mángano et al., 2014). The situation was likely similar in deeper water with the evolution of fishes, crustaceans, and other groups (Ausich & Bottjer, 1982; Bottjer & Ausich, 1986; Crimes & Fedonkin, 1994). Scavengers may thus have played a role in the absence of medusan fossils from beach deposits after the Cambrian, and from open marine settings after the Carboniferous.

Bioturbation

For several of the medusa-bearing deposits, data are limited for factors such as bioturbation. Nevertheless, the majority lack described bioturbation, such as the Chengjiang, Marjum, Burgess Shale, Stark Shale, Grès a Voltzia, Cerin, Solnhofen and Bolca Lagerstätten. Others (e.g., William Lake, Mecca Quarry Shale) have limited bioturbation, and in Cambrian arenites, the majority of bioturbation lacks a vertical (mixing) component.

The geological record of bioturbation documents increased burrowing through time in many different palaeoenvironments, and the restriction of later fossil jellyfish to anoxic lagoon facies is hypothesised to be related to the proliferation of extensive burrowing in most other settings. Infaunal animals developed quickly and were widespread even in the late Cambrian (Bottjer et al., 2000; Tarhan & Droser, 2014; Sappenfield et al., 2017). This was associated with an increase in intensity and depth of burrowing, which continued through the rest of the Phanerozoic in both shallow and deep marine substrates (e.g., Ausich & Bottjer, 1982; Bottjer & Ausich, 1986; Droser & Bottjer, 1989). Cambrian nearshore ichnofaunas were largely limited to the deeper parts of marginal-marine environments, but these moved landward from the Late Ordovician onward (Buatois et al., 2005). Carbonate inner shelf environments were bioturbated in the Cambrian and this increased in the Late Ordovician (Droser & Bottjer, 1993). Nearshore sandstones became heavily bioturbated in post-Palaeozoic rocks (Droser & Bottjer, 1993).

Burrowing will directly disturb medusan carcasses, and the burrowing organisms can be scavengers. Burrowing also greatly increases the oxidation depth of sediment, allowing access by aerobic organisms that can completely oxidize organic carbon and increase the decay capacity (Kristensen, 2000). In modern oceans, low-oxygen seafloor conditions can greatly impede burrowers, resulting in remarkably low species diversity in such settings (Theede et al., 1969). Nevertheless, there are particular infaunal benthic species that are adapted to such conditions; it seems likely that the radiation of life into these hostile environments was gradual and may have occurred well into the Phanerozoic. Their evolution, along with that of microbial decomposers, may have resulted in a substantial increase in the efficiency of organic degradation in environments where medusae may have occasionally been fossilised in previous times. Study of the co-association of oxygen sensitive trace fossils like *Chondrites* (Bromley & Ekdale, 1984) or trace fossil assemblages (Savrda & Bottjer, 1986) with medusae may help test this hypothesis.

Microbial communities

Modern medusae carry their own distinctive microbial communities. For example, the scyphozoans *Chrysaora plocamia* (Lesson, 1830) and *Aurelia aurita* have communities of bacteria associated with cycling of carbon, nitrogen, phosphorus, and sulfur (Lee et al., 2018). If a jellyfish is deposited during or after death, its microbial community will interact with the microbes already present on and in the substrate. It has been observed that only certain bacteria thrive around medusan carcasses, while others are inhibited (Titelman et al., 2006). This inhibition is strongest for the bell of the jellyfish, and weaker for muscle tissues and tentacles; in spite of inhibition, a medusa will break down over an interval ranging from a day to a few days or possibly weeks (Titelman et al., 2006; Adler, 2013). The interaction of microbial communities could be a factor in the unusual ways jellyfish fossilise, often giving them an appearance different from those of associated fossils belonging to groups such as arthropods. This interaction may be enhanced by the presence of various metals, which are concentrated in tissues of living medusae at levels far above those in the surrounding seawater (Cimino et al., 1983; Templeman & Kingsford, 2010).

The record of Konservat-Lagerstätten is consistent with changes in the decomposition of carbon through time. Most notably, the preservation of carbon is hypothesised to have become much more selective after Cambrian Series 3 (Hou et al., 2017). Before that time, in Burgess Shale-type preservation, the seafloor may have been rapidly sealed in calcium carbonate (Gaines et al., 2012), preventing microbes from sourcing the oxidants required for decomposition of organic material.

As described above, the minerals involved in medusan preservation vary by deposit. In some strata, these include unusual fossilising minerals such as sphalerite and siderite, whereas elsewhere there are more typical minerals like pyrite. In each instance, the elements present in the local environment and in the tissues of the medusae affected the microbial community, and in some cases this may have resulted in unusual decomposition pathways and/or authigenic mineralisation of tissues. Medusan fossils are often associated with microbial structures, and about two-thirds of the medusa-bearing deposits show evidence of microbial mats, films, and/or textures, hallmarks of microbial decay-mediated early diagenetic mineralisation by pyrite (see reviews in Canfield & Raiswell, 1991; Schiffbauer et al., 2014; MacGabhann et al., 2019). Those that lack microbial films likely experienced other special fossilising conditions, such as burial by mass flows, seafloor anoxia, or the possible occurrence of a mat of vegetation covering the sea surface (Zangerl & Richardson, 1963).

The occurrence of microbial mats has changed substantially through the Phanerozoic. In the early Cambrian, mats were likely widespread in nearshore marine communities where they are rare today (see reviews in Hagadorn & Bottjer, 1997; Bottjer et al., 2000). Cambrian to Silurian shorelines were substantially different from later ones, as they also lacked land plants and salt marshes; the evolution of mat-grazers and of salt marsh plants has greatly reduced the potential for jellyfish fossilisation in these shoreline settings. In the modern world, microbial mats are characteristic of extreme environments (Gall, 1990): they are supralittoral, in sabkhas, in salt marshes, or in hypersaline or anoxic parts of lagoons. Of these environments, only lagoons have potential as sites for the preservation of medusae.

Jellyfish blooms

There is evidence of jellyfish blooms or bloom-like aggregations in five of the deposits, representing all three basic types of depositional setting: the Cambrian arenites of North America, William Lake (Upper Ordovician), Mazon Creek (upper Carboniferous), Stark Shale (upper Carboniferous), and Cerin (Upper Jurassic) Lagerstätten (see Pl. 2). Jellyfish blooms are thus not an innovation of the modern world; blooms may have been around as long as there have been medusae. Although modern blooms are the subject of widespread and intensive study, their causes seem to vary depending on local or regional conditions. Blooms are most typically associated with conditions of temperature and available hard substrate that are optimal for growth and strobilation of the jellyfish's polyp stage, but other factors that have been proposed include eutrophication and enhanced nutrient supply, changes in freshwater flow, overfishing, and salinity variations (Purcell, 2005; Prieto et al., 2010; Lucas, 2015; Boero et al., 2016). Since the variables that promote blooms are mostly associated with the polyp stage, fossil evidence for a bloom can also be considered as evidence for particular palaeoenvironmental conditions.

It seems that blooming is an adaptation, because some species bloom and others do not (see Jarms & Morandini, 2019). Those that bloom tend to have short life cycles, and their populations can bloom and collapse in a matter of weeks. When a bloom is occurring, the assemblage that washes up on shorelines typically consists of a single species, and there is a huge accumulation of carcasses in the interval of one or two tides (Schäfer, 1972). The effect of blooms on local environments, food chains, fisheries, and people is immense, simply because the numbers of medusae can be mind-boggling - as an example, densities of the rhizostome *Catostylus mosaicus* (Quoy & Gaimard, 1824) on the north and east coasts of Australia can exceed 500 ton/km^2 (Pitt & Kingsford, 2003)! Because these events are very short lived, they are geologically instantaneous.

As a short-lived bloom passes, the environment must absorb an immense number of medusan carcasses. The location of the bloom, and the relative densities of medusae and of the water body and its hydraulic and circulation regime, will greatly affect the postmortem processes. For there to be a chance of fossilisation, the jellyfish carcasses will need to reach the sediment surface rapidly. Medusae that die above deep water may be largely or completely decomposed within the water column (Titelman et al., 2006). Modern carcasses of rhizostome scyphozoans, the coronate scyphozoan *Periphylla,* and some hydromedusae will sink (Billett et al., 2006; Titelman et al., 2006), whereas the semaeostome scyphozoan *Aurelia* floats and will accumulate along shores. We have observed many examples of *Aurelia aurita, Cyanea capillata* (Linnaeus, 1758)*,* the hydromedusan *Staurophora mertensii* Brandt, 1834*,* and other taxa decomposing in clumps near the strandlines of beaches (Pl. 2, figs 5-8). Billett et al. (2006) observed large numbers of the rhizostome *Crambionella orsini* (Vanhöffen, 1888) rolling downslope and accumulating in gelatinous aggregates on the continental rise, so similar clusters of dead and decomposing medusae can form under varied conditions.

It is important to remember that in all of these examples, medusan carcasses behave as clasts. This is true whether they begin transport as intact, pristine specimens, or as sediment-loaded, sediment-coated, or partially degraded bodies. As such, they can accumulate in agglomerations, essentially forming a medusa conglomerate, or "medusaglomerate." Such accumulations locally fill tidal channels in the Elk Mound Group of Wisconsin, and channel- and pool-like depressions in the Stony Mountain Formation at William Lake, Manitoba.

The palaeoenvironmental settings of the richer medusan deposits are generally consistent with known occurrences of dead and dying medusae in modern environments. For example, the Carboniferous *Prothysanostoma eleanorae*, which occurs in a subtidal mid-shelf setting in the Stark Shale, is generally considered to be related to rhizostome scyphozoans. The latter are dense and sink, and thus can be deposited in deeper water. Some of the hydromedusans in the Ordovician William Lake biota, a restricted shallow-water deposit, are very similar to modern *Staurophora,* which is almost neutrally buoyant and may wash up in large numbers along shorelines (Pl. 2, figs 3-4, 7-8).

The seafloor decomposition of jellyfish blooms can cause major changes in the local environment and the relative flux of carbon and nitrogen (Sweetman & Chapman, 2011). In deeper marine environments, the effects of the "jelly-fall" after a bloom may be comparable to those of a whale fall, causing a downward flux of organic carbon that is more than an order of magnitude greater than the annual average (Billett et al., 2006; Sweetman & Chapman, 2011; Chelsky et al., 2015). The biomass of dead and dying medusae can be so large that it overwhelms scavengers, and decomposition can rapidly deplete oxygen in the sediment and surrounding waters (West et al., 2009; Chelsky et al., 2015). In a stratified water body, such as a lagoon, medusan mass mortality can cause hypoxia or anoxia (West et al., 2009). Medusan decomposition may be highly temperature dependent (Lebrato et al., 2011) and is affected by ocean acidity. If a bloom of gelatinous zooplankton is not large enough to cause hypoxia or anoxia, then the jelly-fall may be of great benefit to scavengers (Lebrato & Jones, 2009).

The tissues of medusae are largely composed of lipids, carbohydrates, and proteins. These are readily and rapidly decomposed. As the bloom transfers nutrients from plankton to sediment, the substrate around decaying jellies becomes stained black and enriched in sulfides, with a white layer of sulfur oxidising bacteria (West et al., 2009). Decaying masses of gelatinous zooplankton can contribute to the development of microbial films (Lebrato & Jones, 2009). Microbial veils or mats will form quickly to cover remains as the bacteria create a suitable environment for themselves; certain sulfur bacteria are adapted to operate in this transitional local surface environment, where sediment very low in oxygen may rest below an oxygen-rich water column (Jørgensen & Revsbech, 1983). The abundance of sulfides, anoxic or hypoxic bottom conditions, and presence of microbial veils or mats are all consistent with features observed in most of the medusa-bearing fossil deposits. Microbial degradation of tissue in such conditions, whether it be with a buried jellyfish, log, or shrimp, is an optimal mineralisation catalyst when iron is available, and often leads to pyrite or siderite precipitation, either as a diagenetic halo or crust on the exterior or interior of the organism.

Modern blooms are periodic, with medusan populations oscillating globally in cycles of about 20 years (Condon et al., 2012; Chelsky et al., 2015). It is thus possible that the decomposition of a jellyfish bloom could have created anoxic bottom conditions that enhanced the fossilisation of some late-arriving medusae that were deposited on its surface, but this may have occurred very rarely, and only when there was a particular conjunction of environmental variables.

CONCLUSIONS AND A CHALLENGE

The evolving palaeoenvironmental distribution of fossil jellyfish indicates that they had the potential to be preserved (though rarely) in a variety of environmental settings in the lower Palaeozoic. This range of settings gradually diminished through the Palaeozoic and Mesozoic, with no fossil medusae known after the early Cenozoic. We can thus think of jellyfish fossilisation as a "taphonomic window", which was never open very wide in comparison with the preservation of other groups, but which progressively closed as conditions changed in various marine environments.

Assessment of these deposits raises more questions than it answers. For example, how does each of these deposits fit into the world in which it formed? Is the abundance of medusan-bearing deposits in the Palaeozoic related to the presence of widespread epeiric seas? Given the evidence for jellyfish blooms in several of the deposits, and the carbon inputs to the seafloor from medusan mass falls, is it possible that at times medusae were significant but episodic carbon burial engines that impacted global carbon cycles? Can ancient jellyfish blooms be considered as indicators of particular sets of environmental conditions? If we can answer more of these questions, we will know more about the world, and we may also know much more about where fossil jellyfish could be found in the future.

Finally, a challenge from us to you: is there anywhere on Earth where medusae are being fossilised right now?

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REFERENCES

Adler L. & Röper M. (2012). Description of a new potential fossil hydromedusa *Palaequorea rygoli* and revision of the fossil medusa *Hydrocraspedota mayri* from the plattenkalks of the Franconian Alb, southern Germany. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 264: 249-262.

Adler L.B. (2013). The Taphonomy of Soft-Bodied Cnidarians. 270 pp. Ph.D. Thesis, University College, Dublin.

Alpert S. (1973). *Bergaueria* Prantl (Cambrian and Ordovician), a Probable Actinian Trace Fossil. *Journal of Paleontology*, 47: 919-924.

Ammon L. von (1883). Ueber neue Exemplare von jurassischen Medusen. *Abhandlungen der Königlich Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse*, 15: 103-168.

Ammon L. von (1906). Ueber eine coronate qualle (*Ephyropsites jurassicus*) aus dem Kalkschiefer. *Sonderdruck aus dem Geognostischen Jahrescheften 1906,* 19: 169-186.

Audo D., Charbonnier S., Schweigert G. & Saint Martin J.-P. (2014). New eryonid crustaceans from the Late Jurassic Lagerstätten of Cerin (France), Canjuers (France), Wattendorf (Germany) and Zandt (Germany). *Journal of Systematic Palaeontology*, 12: 459-479.

Ausich W.I. & Bottjer D.J. (1982). Tiering in suspension-feeding communities on soft substrata throughout the Phanerozoic. *Science*, 216: 173-174.

Babcock L.E., Zhang W. & Leslie S. (2001). The Chengjiang biota: record of the early Cambrian diversification of life and clues to exceptional preservation of fossils. *GSA Today,* February 2001: 4-9.

Baird G.C., Sroka S.D., Shabica C.W. & Beard T.L. (1985). Mazon Creek-type fossil assemblages in the U.S. midcontinent Pennsylvanian: their recurrent character and palaeoenvironmental significance. *Philosophical Transactions of the Royal Society of London*, B 311: 87-99.

Baird G.C., Sroka S.D., Shabica C.W. & Kuecher G. (1986). Taphonomy of Middle Pennsylvanian Mazon Creek area fossil localities, northeast Illinois: Significance of exceptional fossil preservation in syngenetic concretions. *Palaios*, 1: 271-285.

Barthel K.W. (1978). Solnhofen. Ein Blick in die Erdgeschichte. 393 pp. Ott-Verlag, Thun, Switzerland.

Barthel K.W., Swinburne N.H.M. & Conway Morris S. (1990). Solnhofen: A Study in Mesozoic Palaeontology. 236 pp. Cambridge University Press, Cambridge.

Billett D.S.M., Bett B.J., Jacobs C.L., Rouse I.P. & Wigham B.D. (2006). Mass deposition of jellyfish in the deep Arabian Sea. *Limnology and Oceanography,* 51: 2077-2083.

Boardman D.R. & Heckel P.H. (1989). Glacial-eustatic sea-level curve for early Upper Pennsylvanian sequence in north-central Texas and biostratigraphic correlation with curve for midcontinent North America. *Geology*, 17: 802-805.

Boero F., Brotz L., Gibbons M.J., Piraino S. & Zampardi S. (2016). 3.10 Impacts and effects of ocean warming on jellyfish. *In* Lagïffoley D. & Baxter J.M. (eds), Explaining Ocean Warming: Causes, scale, effects and consequences. Gland, Switzerland, IUCN: 213-237.

Bottjer D.J. & Ausich W.I. (1986). Phanerozoic development of tiering in soft substrata suspension-feeding communities. *Paleobiology*, 12: 400-420.

Bottjer D.J. & Hagadorn J.W. (2007). Mat growth features. *In* Schieber J., Bose P.K., Ericksson P.G., Banerjee S., Sarkar S., Altermann W. & Catuneanu O. (eds), Atlas of Microbial Mat Features Preserved Within the Siliciclastic Rock Record. Elsevier, Amsterdam: 53-71.

Bottjer D.J., Hagadorn J.W. & Dornbos S. (2000). The Cambrian substrate revolution. *GSA Today*, 10: 1-7.

Brandt J.F. (1834). Prodromus descriptionis animalium ab H. Mertensio in orbis terrarum circumnavigatione observatorum. Fascicule 1. *Recueil des Actes de la Séance Publique de l'Académie Imperiale des Sciences de St. Pétersbourg*: 201-275 (A part: 1835).

Brett C.E. & Baird G.C. (1993). Taphonomic approaches to temporal resolution in stratigraphy. *In* Kidwell S.M. & Behrensmeyer A.K. (eds), Taphonomic Approaches to Time Resolution in Fossil Assemblages. *Paleontological Society Short Course*, 6*:* 250-274.

Briggs D.E.G. (2003). The role of decay and mineralization in the preservation of soft-bodied fossils. *Annual Reviews of Earth and Planetary Science*, 31: 275-301.

Briggs D.E.G., Erwin D.H. & Collier F.J. (1994). The fossils of the Burgess Shale. 238 pp. Smithsonian Institution Press, Washington.

Briggs D.E.G. & McMahon S. (2016). The role of experiments in investigating the taphonomy of exceptional preservation. *Palaeontology*, 59: 1-11.

Briggs D.E.G. & Robison R.A. (1984). Exceptionally preserved nontrilobite arthropods and *Anomalocaris* from the Middle Cambrian of Utah. 23 pp. *University of Kansas Paleontological Contributions*, Paper 111.

Broglio Loriga C. & Sala Manservigi A. (1973). Minor unpublished fossils of the "Pesciara" of Bolca (Verona, Italy). *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 2. Museo Civico di Storia Naturale di Verona: 157-176.

Bromley R.G. & Ekdale A.A. (1984). *Chondrites*: a trace fossil indicator of anoxia in sediments. *Science*, 224: 872-874.

Brusca R.C. & Brusca G.J. (2003). Invertebrates. 2nd ed. 183 pp. Sinauer Associates, Sunderland, Massachusetts.

Bruton D.L. (1991). Beach and laboratory experiments with the jellyfish *Aurelia* and remarks on some fossil "medusoid" traces. *In* Simonetta A.M. & Conway Morris S. (eds), The Early Evolution of Metazoa and the Significance of Problematic Taxa. Cambridge University Press, Cambridge: 125-129.

Buatois L.A., Gingras M.K., MacEachern J., Mángano M.G., Zonneveld J.P., Pemberton S.G., Netto R.G. & Martin A. (2005). Colonization of brackish-water systems through time: evidence from the trace-fossil record. *Palaios*, 20: 321-347.

Butterfield N.J. (1995). Secular distribution of Burgess-Shale-type preservation. *Lethaia*, 28: 1-13.

Butterfield N.J. (2003). Exceptional fossil preservation and the Cambrian Explosion. *Integrative and Comparative Biology*, 43: 166-177.

Butterfield N.J. (2009). Fossil preservation in the Burgess Shale. *In* Caron J.B. & Rudkin D.M. (eds), A Burgess Shale Primer: History Geology and Research Highlights. International conference on the Cambrian explosion (ICCE, August 3-8th, 2009: Banff, Alberta, Canada): 63-69.

Cadée G.C. (2013). Can Recent traces help in recognising probable jellyfish remains from the Muschelkalk of Winterswijk? A comment. *Netherlands Journal of Geosciences*, 92: 301-302.

Canfield D.E. & Raiswell R. (1991). Pyrite formation and fossil preservation. *In* Allison P. & Briggs D.E.G. (eds), Taphonomy: Releasing the Data Locked in the Fossil Record. New York, NY: Plenum: 337-387.

Cartwright P., Halgedahl S.L., Hendricks J.R., Jarrard R.D., Marques A.C., Collins A.G. & Lieberman B.S. (2007). Exceptionally preserved jellyfishes from the Middle Cambrian. *PLoS ONE* 2: e1121.

Chelsky A., Pitt K.A. & Welsh D.T. (2015). Biogeochemical implications of decomposing jellyfish blooms in a changing climate. *Estuarine, Coastal and Shelf Science*, 154: 77-83.

Cimino G., Alfa M. & La Spada G. (1983). Trace elements in tentacles from the jellyfish *Pelagia noctiluca. Marine Pollution Bulletin*, 14: 197-198.

Clemmensen L.B., Glad A.C. & Pedersen G.K. (2016). Early Cambrian wave-formed shoreline deposits: the Hardeberga Formation, Bornholm, Denmark. *International Journal of Earth Sciences*, 106: 1889-1903.

Collette J.H. & Hagadorn J.W. (2010). Three-dimensionally preserved arthropods from Cambrian Lagerstätten of Quebec and Wisconsin. *Journal of Paleontology*, 84: 646-667.

Collette J.H., Hagadorn J.W. & Lacelle M.M. (2010). Dead in their tracks: Cambrian arthropods and their traces from intertidal sandstones of Quebec and Wisconsin. *Palaios*, 25: 475-486.

Condon R.H., Duarte C.M., Pitt K.A., Robinson K.L., Lucas C.H., Sutherland K.R., Mianzan H.W., Bogeberg M., Purcell J.E., Decker M.B., Uye S.-I., Madin L.P., Brodeur R.D., Haddock S.H.D., Malej A., Parry G.D., Eriksen E., Quiñones J., Acha M., Harvey M., Arthur J.M. & Graham W.M. (2012). Recurrent jellyfish blooms are a consequence of global oscillations. *Proceedings of the National Academy of Sciences (PNAS)*, 110: 1000-1005.

Conway Morris S. (1989). Burgess Shale faunas and the Cambrian Explosion. *Science*, 246: 339-346.

Conway Morris S. & Robison R.A. (1986). Middle Cambrian priapulids and other soft-bodied fossils from Utah and Spain. 22 pp. *University of Kansas Paleontological Contributions,* Paper 117.

Cotroneo S., Schiffbauer J.D., McCoy V.E., Wortmann U.G., Darroch S.A.F., Peng Y. & Laflamme M. (2016). A new model of the formation of Pennsylvanian iron carbonate concretions hosting exceptional soft-bodied fossils in Mazon Creek, Illinois. *Geobiology*, 14: 543-555.

Coveney R.M. & Martin S.P. (1983). Molybdenum and other heavy metals of the Mecca Quarry and Logan Quarry Shales. *Economic Geology*, 78: 132-149.

Crimes P. & Fedonkin M.A. (1994). Evolution and dispersal of deepsea traces. *Palaios*, 9: 74-83.

Devereux M.G. (2001). Palaeoecology of the Middle Cambrian Raymond Quarry Fauna, Burgess Shale, British Columbia. 196 pp. M.Sc. Thesis, University of Western Ontario, London, Canada.

Dornbos S.Q., Noffke N. & Hagadorn J.W. (2007). Mat-decay features. *In* Schieber J., Bose P.K., Ericksson P.G., Banerjee S., Sarkar S., Altermann W. & Catuneanu O. (eds), Atlas of Microbial Mat Features Preserved Within the Siliciclastic Rock Record. Elsevier, Amsterdam: 106-110.

Droser M.L. & Bottjer D.J. (1989). Ordovician increase in extent and depth of bioturbation: Implications for understanding early Paleozoic ecospace utilization. *Geology*, 17: 850-852.

Droser M.L. & Bottjer D.J. (1993). Trends and patterns of Phanerozoic Ichnofabrics. *Annual Review of Earth and Planetary Sciences*, 21: 205-225.

Fernandes A.S. (2012). A geobiological investigation of the Mazon Creek concretions of northeastern Illinois, mechanisms of formation and diagenesis. M.Sc. Thesis, Western University, London, Ontario. 176 pp. *Electronic Thesis and Dissertation Repository,* Paper 398.

Fernandez-Lopez S.R. (2013). Postulates of the evolutionary taphonomy. *In* Chacaltana C., Tejada L.M. & Morales M.C. (eds), I Simposio Internacional Paleontological del Perú. Instituto Geológico Minero y Metalúrgico, Lima: 119-122.

Fletcher T.P. & Collins D. (2009). Geology and stratigraphy of the Burgess Shale Formation on Mount Stephen and Fossil Ridge. *In* Caron J.B. & Rudkin D.M. (eds), A Burgess Shale Primer: History Geology and Research Highlights. International conference on the Cambrian explosion (ICCE, August 3-8th, 2009: Banff, Alberta, Canada): 33-53.

Foster M.W. (1979). Soft-bodied coelenterates in the Pennsylvanian of Illinois. *In* Nitecki M.H. (ed.), Mazon Creek Fossils. Academic Press, New York: 191-267.

Friedman M. & Carnevale G. (2018). The Bolca Lagerstätten: shallow marine life in the Eocene. *Journal of the Geological Society*, 175: 569-579.

Fryer G. & Stanley G.D. Jr (2004). A Silurian porpitoid hydrozoan from Cumbria, England and a note on porpitoid relationships. *Palaeontology*, 47: 1109-1120.

Fu D., Tong G., Dai T., Liu W., Yang Y., Zhang Y., Cui L., Li L., Yun H. & Wu Y. (2019). The Qingjiang biota - A Burgess Shale-type fossil Lagerstätte from the early Cambrian of South China. *Science*, 363: 1338-1342.

Gabbott S. & Zalasiewicz J. (2009). Sedimentation of the Phyllopod Bed within the Cambrian Burgess Shale Formation. *In* Caron J.B. & Rudkin D.M. (eds), A Burgess Shale Primer: History Geology and Research Highlights. International conference on the Cambrian explosion (ICCE, August 3-8th, 2009: Banff, Alberta, Canada): 55-61.

Gaillard C., Bernier P., Gall J.-C., Gruet G., Barale G., Bourseau J.-P., Buffetaut E. & Wenz S. (1994). Ichnofabric from the Upper Jurassic lithographic limestone of Cerin, southeast France. *Palaeontology*, 37: 285-304.

Gaillard C., Goy J., Bernier P., Bourseau J.P., Gall J.C., Barale G., Buffetaut E. & Wenz S. (2006). New jellyfish taxa from the Upper Jurassic lithographic limestone of Cerin (France): taphonomy and ecology. *Palaeontology*, 49: 1287-1302.

Gaines R.R., Hammarlund E.U., Hou X., Qi C., Gabbott S.E., Zhao Y., Peng J. & Canfield D.E. (2012). Mechanism for Burgess Shale-type preservation. *Proceedings of the National Academy of Sciences (PNAS)*, 109: 5180-5184.

Gall J.C. (1985). Fluvial depositional environment evolving into deltaic setting with marine influences in the Buntsandstein of northern Vosges (France). *In* Mader D. (ed.), Aspects of fluvial sedimentation in the Lower Triassic Buntsandstein of Europe. *Lecture Notes in Earth Sciences*, 4: 449-477.

Gall J.C. (1990). Les voiles microbiens. Leur contribution à la fossilization des organisms au corps mou. *Lethaia*, 23: 21-28.

Gehling J.G. (1999). Microbial mats in terminal Proterozoic siliciclastics; Ediacaran death masks. *Palaios*, 14: 40-57.

Gershwin L.A. (2003). Cubozoa: Systematics. University of California Museum of Paleontology website. http://www.ucmp.berkeley.edu/cnidaria/cubozoasy.html.

Getty P.R. & Hagadorn J.W. (2008). Reinterpretation of *Climactichnites* Logan 1860 to include subsurface burrows, and erection of *Musculopodus* for resting traces of the trackmaker. *Journal of Paleontology*, 82: 1161-1172.

Giusberti L., Fornasiero M. & Zorzin R. (2014). 7. The Pesciara-Monte Postale Fossil-Lagerstätte: 4. The “minor fauna” of the laminites. *In* Papazzoni C.A., Giusberti L., Carnevale G., Roghi G., Bassi D. & Zorzin R. (eds), The Bolca *Fossil-Lagerstätten:* A window into the Eocene World. *Rendiconti della Società Paleontologica Italiana,* 4: 73-87.

Grauvogel L. & Gall J.C. (1962). *Progonionemus vogesiacus* nov. gen. nov. sp., une méduse du Grès à Voltzia des Vosges Septentrionales. *Bulletin de la Service Carte géologique Alsace et Lorraine*, 15: 17-27.

Haeckel E. (1865). Ueber fossile medusen. *Zeitschrift für wissenschaftliche Zoologie*, 15: 504-514.

Haeckel E. (1866). Über zwei neue fossile medusen aus der familie der Rhizostomiden. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*, 1866: 257-282.

Haeckel E. (1869). Ueber die fossilen medusen der Jura-Zeit. *Zeitschrift für Wissenschaftliche Zoologie*, 19: 538-562.

Haeckel E. (1874). Ueber eine sechszählige fossile Semaeostomee. *Jennaische Zeitschrift für Naturwissenschaft*, 8: 308-330.

Hagadorn J.W. & Belt E.S. (2008). Stranded in upstate New York: Cambrian medusae from the Potsdam Sandstone. *Palaios*, 23: 424-441.

Hagadorn J.W. & Bottjer D.J. (1997). Wrinkle structures: microbially mediated sedimentary structures common in subtidal siliciclastic settings at the Proterozoic-Phanerozoic transition. *Geology*, 25: 1047-1050.

Hagadorn J.W., Dott R.H. Jr & Damrow D. (2002). Stranded on a Late Cambrian shoreline: medusae from central Wisconsin. *Geology*, 30: 147-150.

Hagadorn J.W. & Miller R.F. (2011). Hypothesized Cambrian medusae from Saint John, New Brunswick, reinterpreted as sedimentary structures. *Atlantic Geology*, 47: 66-80.

Hagdorn H. (2013). Medusen aus dem Lettenkeuper (Mittlere Trias, Ladinium) von Schwäbisch Hall. *Gesellschaft für Naturkunde in Württemberg, Sonderbände*, 3: 271-290.

Hamada T. (1977). Medusae and their conditions to be fossilized. *Fossils*, 27: 61-75.

Han J., Hu S., Cartwright P., Zhao F., Ou Q., Kubota S., Wang X. & Yang X. (2016). The earliest pelagic jellyfish with rhopalia from Cambrian Chengjiang Lagerstätte. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 449:166-173.

Han J., Kubota S., Uchida H.-o., Stanley G.D. Jr, Yao X., Shu D., Li Y. & Yasui K. (2010). Tiny Sea Anemone from the Lower Cambrian of China. *PLoS ONE*, 5: e13276.

Harrington H.J. & Moore R.C. (1955). Fossil jellyfishes from Kansas Pennsylvanian rocks and elsewhere. *Kansas Geological Survey Bulletin*, 114: 156-163.

Harrington H.J. & Moore R.C. (1956a). Scyphomedusae. *In* Moore R.C. (ed.), Treatise on Invertebrate Paleontology, Part F, Coelenterata. Geological Society of America and University of Kansas Press, Lawrence: 38-53.

Harrington H.J. & Moore R.C. (1956b). Trachylinida. *In* Moore R.C. (ed.), Treatise on Invertebrate Paleontology, Part F, Coelenterata. Geological Society of America and University of Kansas Press, Lawrence: 68-76.

Harrington H.J. & Moore R.C. (1956c). Medusae incertae sedis and unrecognizable forms. *In* Moore R.C. (ed.), Treatise on Invertebrate Paleontology, Part F, Coelenterata. Geological Society of America and University of Kansas Press, Lawrence: 153-161.

Heckel P.H. & Meacham J.F. (1981). New data on Missourian (upper Pennsylvanian) stratigraphy of the Forest City basin, southwestern Iowa and adjacent Nebraska. *Geological Society of America, Abstracts with Programs*, 13: 280.

Hou X.-G., Siveter D.J., Siveter D.J., Aldridge R.J., Cong P.-Y., Gabbott S.E., Ma X.-Y., Purnell M.A. & Williams M. (2017). The Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal Life, 2nd Edition. 328 pp. Wiley-Blackwell.

Hu S., Steiner M., Zhu M., Erdtmann B.-D., Luo H., Chen L. & Weber B. (2007). Diverse pelagic predators from the Chengjiang Lagerstätte and the establishment of modern-style pelagic ecosystems in the early Cambrian. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 254: 307-316.

Jarms G. & Morandini A.C. (eds) (2019). World Atlas of Jellyfish. 815 pp. Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg, Special Volume | 2019. Dölling und Galitz Verlag, München - Hamburg.

Johnson R.G. & Richardson E.S. Jr (1966). A remarkable Pennsylvanian fauna from the Mazon Creek area, Illinois. *Journal of Geology*, 74: 626-631.

Johnson R.G. & Richardson E.S. (1968). The Essex Fauna and medusae. *Fieldiana: Geology*, 12: 109-115.

Jørgensen B.B. & Revsbech N.P. (1983). Colorless Sulfur Bacteria, *Beggiatoa* spp. and *Thiovulum* spp., in O_2 and H_2S Microgradients. *Applied and Environmental Microbiology*, 45: 1261-1270.

Keupp H. (1977). Ultrafazies und Genese der Solnhofener Plattenkalke (Oberer Malm, siidliche Frankenalb). *Abhandlungen der Naturhistorischen Gesellschaft Nürnberg*, 37: 1-128.

Kieslinger A. (1939). Revision der Solnhofener medusen. *Paläontologische Zeitschrift*, 21: 287-296.

Kolb A. (1951). *Hydrocraspedota mayri* n. g. n. sp., eine Hydromeduse aus den Plattenkalken von Pfalzpaint. *Geologische Blätter für Nordost-Bayern*, 1: 113-127.

Kornicker L.S. & Conover J.T. (1960). Effect of high storm tide levels on beach burial of jellyfish (Scyphozoa) and other organisms. *Internationale Revue der Gesamten Hydrobiologie*, 45: 203-214.

Kristensen E. (2000). Organic matter diagenesis at the oxic/anoxic interface in coastal marine sediments, with emphasis on the role of burrowing animals. *Hydrobiologia*, 426: 1-24.

Kristensen E., Ahmed S.I. & Devol A.H. (1995). Aerobic and Anaerobic Decomposition of Organic Matter in Marine Sediment: Which is Fastest? *Limnology and Oceanography*, 40: 1430-1437.

Kuhn O. (1938). Eine neue meduse (hydromeduse) aus dem Oberjura von Solnhofen. *Zoologischer Anzeiger*, 122: 307-312.

Kuhn O. (1961). Die Tier- und Pflanzenwelt des Solnhofener Schiefers. 68 pp. *Geologica Bavarica,* 48.

Lacelle M.A., Hagadorn J.W. & Groulx P. (2008). The widespread distribution of Cambrian medusae: Scyphomedusae strandings in the Potsdam Group of southwestern Quebec. *Geological Society of America Abstracts with Programs*, 40: 369.

Landing E., Franzi D.A., Hagadorn J.A., Westrop S.R., Kroger B. & Dawson J.C. (2007). Cambrian of east Laurentia. *In* Landing E. (ed.), Field workshop in eastern New York and western Vermont, Ediacaran-Ordovician of East Laurentia: S.W. Ford Memorial Volume. 94 pp. *New York State Museum Bulletin*, 50.

Lebrato M. & Jones D.O.B. (2009). Mass deposition event of *Pyrosoma atlanticum* carcasses off Ivory Coast (West Africa). *Limnology and Oceanography*, 54: 1197-1209.

Lebrato M., Pahlow M., Oschlies A., Pitt K.A., Jones D.O.B., Molinero J.C. & Condon R.H. (2011). Depth attenuation of organic matter export associated with jelly falls. *Limnology and Oceanography*, 56: 1917-1928.

Lee M.D., Kling J.D., Araya R. & Ceh J. (2018). Jellyfish life stages shape associated microbial communities, while a core microbiome is maintained across all. *Frontiers in Microbiology*, 9: 1534.

Lesson R.P. (1830). Centurie zoologique, ou, Choix d'animaux rares, nouveaux ou imparfaitement connus. 244 pp. F.G. Levrault, Paris & Strasbourg.

Linnaeus C. (1758). Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. 824 pp. Editio decima, reformata. Stockholm.

Liu A.G., McMahon S., Matthews J.J., Still J.W. & Brasier A.T. (2019). Petrological evidence supports the death mask model for the preservation of Ediacaran soft-bodied organisms in South Australia. *Geology*, 47: 215-218.

LoBue D.J. (2006). Ichnotaxonomic Assessment of Mazon Creek Area Trace Fossils, Illinois, USA. 128 pp. M.S. Thesis, University of Kansas.

Lowe D.G., Arnott R.W.C., Nowlan G.S. & McCracken A.D. (2017). Lithostratigraphic and allostratigraphic framework of the Cambrian-Ordovician Potsdam Group and correlations across Early Paleozoic southern Laurentia. *Canadian Journal of Earth Sciences*, 54: 550-585.

Lucas C.H. (2015). Towards a mechanistic understanding of population-scale variability in scyphozoan jellyfish. PERSEUS International Jellyfish Workshop, Cadiz (Spain), 2-3 March 2015: 9-10.

Lynam C.P., Hay S.J. & Brierley A.S. (2005). Jellyfish abundance and climatic variation: contrasting responses in oceanographically distinct regions of the North Sea, and possible implications for fisheries. *Journal of the Marine Biological Association of the United Kingdom*, 85: 435-450.

Maas A., Braun A., Dong X.-P., Donoghue P.C.J., Müller K.J., Olempska E., Repetski J.E., Siveter D.J., Stein M. & Waloszek D. (2006). The 'Orsten'-More than a Cambrian Konservat-Lagerstätte yielding exceptional preservation. *Palaeoworld*, 15: 266-282.

Maas O. (1902). Über Medusen aus dem Solenhofer Schiefer und der unteren Kreide der Karpathen. *Palaeontographica*, 48: 293-315.

Maas O. (1906). Ueber eine neue Medusengattung aus dem lithographischen Schiefer. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*, 2: 90-99.

MacGabhann B.A., Schiffbauer J.D., Hagadorn J.W., Van Roy P., Lynch E.P., Morrison L. & Murray J. (2019). Resolution of the earliest metazoan record: Differential taphonomy of Ediacaran and Paleozoic fossil molds and casts. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 513: 146-165.

MacNaughton R.B., Cole J.M., Dalrymple R.W., Braddy S.J., Briggs D.E.G. & Lukie T.D. (2002). First steps on land: Arthropod trackways in Cambrian-Ordovician eolian sandstone, southeastern Ontario, Canada. *Geology*, 30: 391-394.

MacNaughton R.B., Hagadorn J.W. & Dott R.H. Jr (2019). Cambrian wave-dominated tidal-flat deposits, central Wisconsin, USA. *Sedimentology*, 66: 1643-1672.

Malinky J. & Heckel P. (1998). Paleoecology and Taphonomy of Faunal Assemblages in gray "core" (offshore) shales in midcontinent Pennsylvanian cyclothems. *Palaios*, 13: 311-334.

Mángano M.G., Buatois L.A., Astini R. & Rindsberg A.K. (2014). Trilobites in early Cambrian tidal flats and the landward expansion of the Cambrian explosion. *Geology*, 42: 143-146.

Mángano M.G., Hawkes C.D. & Caron J.-B. (2019). Trace fossils associated with Burgess Shale non-biomineralized carapaces: bringing taphonomic and ecological controls into focus. *Royal Society Open Science*, 6: 172074.

Mapes R.H. & Doguzhaeva L.A. (2018). New Pennsylvanian coleoids (Cephalopoda) from Nebraska and Iowa, USA. *Journal of Paleontology*, 92: 146-156.

Minter N.J., Mángano M.G. & Caron J.-B. (2011). Skimming the surface with Burgess Shale arthropod locomotion. *Proceedings of the Royal Society B*, *Biological Sciences*, 279: 1613-1620.

Müller A.H. (1984). Aktualistische beiträge zur taphonomie fossiler Quallen. *Freiberger Forschungsheft*, C395: 82-95.

Müller A.H. (1985). Aktualistische beiträge zur taphonomie fossiler Quallen, Teil II. *Freiberger Forschungsheft*, C400: 80-89.

Muscente A.D., Allmon W.D. & Xiao S. (2016). The hydroid fossil record and analytical techniques for assessing the affinities of putative hydrozoans and possible hemichordates. *Palaeontology*, 59: 71-87.

Nathorst A.G. (1881). Om aftryck af medusor I sveriges kambriska lager. *Kongliga Svenska Vetenskaps-Akademiens Handlingar*, 19: 3-34.

Nitecki M.H. (ed.) (1979). Mazon Creek Fossils. 600 pp. Academic Press, New York.

Norris R.D. (1989). Cnidarian taphonomy and affinities of the Ediacara biota. *Lethaia*, 22: 381-393.

Ossian C.R. (1973). New Pennsylvanian scyphomedusan from western Iowa. *Journal of Paleontology*, 47: 990-995.

Ou Q., Han J., Zhang Z., Shu D., Sun G. & Mayer G. (2017). Three Cambrian fossils assembled into an extinct body plan of cnidarian affinity. *Proceedings of the National Academy of Sciences (PNAS)*, 114: 8835-8840.

Papazzoni C.A. & Trevisani E. (2006). Facies analysis, palaeoenvironmental reconstruction, and biostratigraphy of the "Pesciara di Bolca" (Verona, northern Italy): an early Eocene *Fossil-Lagerstätte*. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 242: 21-35.

Parry L.A., Smithwick F., Nordén K.K., Saitta E.T., Lozano-Fernandez J., Tanner A.R., Caron J.-B., Edgecombe G.D., Briggs D.E.G. & Vinther J. (2018). Soft-Bodied Fossils Are Not Simply Rotten Carcasses - Toward a Holistic Understanding of Exceptional Fossil Preservation. *BioEssays*, 40: 1700167.

Pemberton G., Frey R.W. & Bromley R.G. (2011). The ichnotaxonomy of *Conostichus* and other plug-shaped ichnofossils. *Canadian Journal of Earth Sciences*, 25: 866-892.

Petrovich R. (2001). Mechanisms of fossilization of the soft-bodied and lightly-armored faunas of the Burgess Shale and of some other classical localities. *American Journal of Science*, 301: 683-726.

Pisani D., Poling L.L., Lyons-Weiler M. & Hedges S.B. (2004). The colonization of land by animals: molecular phylogeny and divergence times among arthropods. *BMC Biology,* 2004, 2: 1.

Pitt K.A. & Kingsford M. (2003). Temporal variation in the virgin biomass of the edible jellyfish, *Catostylus mosaicus* (Scyphozoa, Rhizostomeae). *Fisheries Research*, 63: 303-313.

Plotnick R.E., Hagadorn J.W. & Young G.A. (2017). The Mazon Creek cnidarian *Essexella:* the world turned upside down. *Geological Society of America Annual Meeting*, Paper No. 1-10. October 2017, Seattle.

Pope J.P. (2012). Description of Pennsylvanian units, revision of stratigraphic nomenclature, and reclassification of the Morrowan, Atokan, Desmoinesian, Missourian, and Virgilian stages in Iowa. 140 pp. Iowa Geological and Water Survey, Special Report SR-5.

Pratt B.R. & Kimmig J. (2019). Extensive bioturbation in a middle Cambrian Burgess Shale-type fossil Lagerstätte in northwestern Canada. *Geology*, 47: 231-234.

Prieto L., Astorga D., Navarro G. & Ruiz J. (2010). Environmental control of phase transition and polyp survival of a massive-outbreaker jellyfish. *PLoS ONE*, 5: e13793.

Purcell J.E. (2005). Climate effects on formation of jellyfish and ctenophore blooms: a review. *Journal of the Marine Biological Association of the United Kingdom*, 85: 461-476.

Quoy J.R.C. & Gaimard J.P. (1824). Des zoophytes ou animaux rayonnés. *In* Voyage autour du monde, entrepis par ordre du Roi, sous le ministère et conformément aux instructions de S. Exc. M. Le Vicomte de Bouchage, secrétaire d'état au départment de la Marine, exécuté sur les corvettes de S.M. l'Uranie et la Physicienne, pendant les années 1817, 1818, 1819 et 1820 (Vol. Zoologie). Chez Pillet Ainé, Paris: 559-571.

Rozhnov S.V. (1998). Results of burial experiments on the Scyphomedusa *Cyanea capillata* L., 1758. *Palaeontological Journal*, 32: 226-228.

Sanford B.V. & Arnott R.W.C. (2010). Stratigraphic and structural framework of the Potsdam Group in eastern Ontario, western Quebec, and northern New York. *Geological Survey of Canada, Bulletin*, 597: 1-242.

Sappenfield A.D., Tarhan L.G. & Droser M.L. (2017). Earth's oldest jellyfish strandings: a unique taphonomic window or just another day at the beach? *Geological Magazine*, 154: 859-874.

Savrda C.E. & Bottjer D.J. (1986). Trace-fossil model for reconstruction of paleo-oxygenation in bottom waters. *Geology*, 14: 3-6.

Schäfer W. (1941). Fossilisations-Bedingungen von Quallen und Laichen. *Senckenbergiana*, 23: 189-216.

Schäfer W. (1972). Ecology and Palaeoecology of Marine Environments. 568 pp. University of Chicago Press, Chicago.

Schiffbauer J.D., Xiao S., Cai Y., Wallace A.F., Hua H., Hunter J., Xu H., Peng Y. & Kaufman A.J. (2014). A unifying model for Neoproterozoic-Palaeozoic exceptional fossil preservation through pyritization and carbonaceous compression. *Nature Communications*, 5: 5754.

Schnedler-Meyer N.A., Kiørboe T. & Mariani P. (2018). Boom and Bust: Life History, Environmental Noise, and the (un) Predictability of Jellyfish Blooms. *Frontiers in Marine Science*, 5: 1-10.

Schram F.R. (1984). Upper Pennsylvanian arthropods from black shales of Iowa and Nebraska. *Journal of Paleontology*, 58: 197-209.

Schwark L., Ferretti A., Papazzoni C.A. & Trevisani E. (2009). Organic geochemistry and paleoenvironment of the Early Eocene "Pesciara di Bolca" Konservat-Lagerstätte, Italy. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 273: 272-285.

Seilacher A. & Hagadorn J.W. (2010). Early molluscan evolution: Evidence from the trace fossil record: *Palaios*, 25: 565-575.

Seilacher A., Reif W.-E. & Westphal F. (1985). Sedimentological, ecological and temporal patterns of fossil Lagerstätten. *Philosophical Transactions of the Royal Society of London B*, 311: 5-23.

Selden P.A. & Nudds J.R. (2004). Evolution of Fossil Ecosystems. 160 pp. Manson Publishing and University of Chicago Press, Chicago.

Shabica C.W. (1970). Depositional environments in the Francis Creek Shale. *In* Depositional Environments in Parts of the Carbondale Formation - Western and Northern Illinois. *Illinois State Geological Survey Guidebook Series*, 8: 43-52.

Sroka S.D. (1997). Cnidaria. *In* Shabica C.W. & Hay A.A. (eds), Richardson's Guide to the Fossil Fauna of Mazon Creek. Northeastern Illinois University, Chicago: 57-63.

Sweetman A.K. & Chapman A. (2011). First observations of jelly-falls at the seafloor in a deep-sea fjord. *Deep-Sea Research I*, 58: 1206-1211.

Tarhan L.G. (2008). Taphonomy and classification of Late Cambrian medusae of central Wisconsin and northeastern New York: Problems of preservation. 113 pp. B.A. Thesis, Amherst College, Amherst, MA, USA.

Tarhan L.G. & Droser M.L. (2014). Widespread delayed mixing in early to middle Cambrian marine shelfal settings. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 399: 310-322.

Templeman M.A. & Kingsford M.J. (2010). Trace element accumulation in *Cassiopea* sp. (Scyphozoa) from urban marine environments in Australia. *Marine Environmental Research*, 69: 63-72.

Theede H., Ponat A., Hiroki K. & Schlieper C. (1969). Studies on the resistance of marine bottom invertebrates to oxygen-deficiency and hydrogen sulphide. *Marine Biology*, 2: 325-337.

Thiel H. (1971). Erhaltungsfähige abdrücke von der ohrenqualle *Aurelia aurita* Lam. (Scyphomedusae) an einem sandstrand der Ostsee. *Senckenbergiana Maritima*, 3: 79-91.

Titelman J., Riemann L., Sørnes T.A., Nilsen T., Griekspoor P. & Båmstedt U. (2006). Turnover of dead jellyfish: stimulation and retardation of microbial activity. *Marine Ecology Progress Series*, 325: 43-58.

Tourtelot H.A. (1979). Black shale - its deposition and diagenesis. *Clays and Clay Minerals*, 27: 313-321.

Vanhöffen E. (1888). Untersuchungen über semäostome und rhizostome Medusen. *Bibliotheca Zoologica*, 1: 5-52.

Van Iten H., de Moraes Leme J., Guimarães Simões M., Marques A.C. & Collins A.G. (2006). Reassessment of the phylogenetic position of conularids (?Ediacaran-Triassic) within the Subphylum Medusozoa (Phylum Cnidaria). *Journal of Systematic Palaeontology*, 4: 109-118.

Viohl G. (1996). The paleoenvironment of the Late Jurassic fishes from the southern Franconian Alb (Bavaria, Germany). *In* Arratia G. & Viohl G. (eds), Mesozoic Fishes - Systematics and Paleoecology. Proceedings of the International Meeting, Eichstätt, 1993. Dr. Friedrich Pfeil Verlag, Munich: 513-528.

Walcott C.D. (1898). Fossil Medusae. 201 pp. *Monographs of the United States Geological Survey, Washington*, 30.

Wang X., Han J., Vannier J., Ou Q., Yang X., Uesugi K., Sasaki O. & Komiya T. (2017). Anatomy and affinities of a new 535-million-year-old medusozoan from the Kuanchuanpu Formation, South China. *Palaeontology*, 60: 853-867.

Watney W.L., French J.A. & Franseen E.K. (1989). Sequence stratigraphic interpretations and modeling of cyclothems. 211 pp. Kansas Geological Society Guidebook, 41st Annual Field Conference.

West E.J., Welsh D.T. & Pitt K.A. (2009). Influence of decomposing jellyfish on the sediment oxygen demand and nutrient dynamics. *Hydrobiologia*, 616: 151-160.

Wittry J. (2012). The Mazon Creek Fossil Fauna. 202 pp. ESCONI, Chicago, Illinois.

Woodland B. & Stenstrom R. (1979). The occurrence and origin of siderite concretions in the Francis Creek Shale (Pennsylvanian) of northeastern Illinois. *In* Nitecki M.H. (ed.), Mazon Creek Fossils. Academic Press, New York: 69-103.

Young G.A. & Hagadorn J.W. (2010). The fossil record of cnidarian medusae. *Palaeoworld*, 19: 212-221.

Young G.A. & Hagadorn J.W. (2018). Midwestern medusae: cubozoan and scyphozoan jellyfish from Pennsylvanian cyclothems of the central United States. Canadian Paleontology Conference, Saskatoon, Proceedings Volume No. 15 (unpaginated).

Young G.A., Rudkin D.M., Dobrzanski E.P., Robson S.P., Cuggy M.B., Demski M.W. & Thompson D.P. (2012). Late Ordovician Konservat-Lagerstätten in Manitoba. *Geoscience Canada*, 39: 201-213.

Young G.A., Rudkin D.M., Dobrzanski E.P., Robson S.P. & Nowlan G.S. (2007). Exceptionally preserved Late Ordovician biotas from Manitoba, Canada. *Geology*, 35: 883-886.

Zangerl R. & Richardson E.S. Jr (1963). The paleoecological history of two Pennsylvanian black shales. 352 pp. *Fieldiana Geology Memoirs,* Volume 4.

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Tournaisian (Carboniferous) rugose corals of the Donets Basin, Ukraine

Viktor Ohar

V. Ohar, Institute of Geology, Taras Shevchenko National University of Kyiv, 90 Vasylkivska str., 03022 Kyiv, Ukraine; ogar_victor@ukr.net

KEY WORDS - Rugosa, taxonomy, Dinantian.

ABSTRACT - The results of the study of a rugose coral collection from the southern part of the Donets Basin are presented herein. Some species that were only mentioned in previous Donets Basin faunal lists are described and illustrated. The genera Aulokoninckophyllum *Sando, 1976 and* Merlewoodia *Pickett, 1967 are reported for the first time from the Donets Basin. The stratigraphic distribution of the studied species is analysed. The uneven distribution of corals in the Tournaisian of the Donets Basin is explained by a complex combination of regional paleogeographic conditions and global events. The studied stratigraphic levels with corals are compared with the coral zones and third-order sequences of the Belgian Namur-Dinant Basin.*

INTRODUCTION

Tournaisian sedimentary rocks are exposed in the southern part of the Donets Basin (Ukraine), where they are dominated by shallow-water platform limestone. It is the only area in Ukraine where Tournaisian and Visean strata are easily accessible. They crop out in narrow bands through the towns of Novotroitske, Dokuchaevsk, Styla and Kalmiuske (Donetsk region), where numerous natural sections along the Kalmius, Mokra Volnovakha and Sukha Volnovakha rivers have been studied since the 19th century. Most of these sections were unfortunately destroyed by anthropogenic activities. However, Tournaisian rocks were exposed in this area by numerous active and inactive flux quarries. Brief information about the location of the study area, lithology and stratigraphy of the Tournaisian within the Donets Basin was presented earlier (Ogar, 2016). Therefore, in this paper only a brief reference to some important points regarding the lithology and stratigraphy of the study area is made. In the most recently defined stratigraphic scheme of the Donets Basin, some changes were made to the indexing of the lower Carboniferous complex biostratigraphic zones and subzones (Gozhyk, 2013). For the Tournaisian, the following simplified indexes have been proposed: Tb_1, Tb_2, Tc (Tc_1, Tc_2), Td (Td_1, Td_2) and Te (= Va). The Ta zone was previously defined according to the results of biostratigraphic studies and assigned to the Upper Devonian (Famennian Stage). It is possible that the position of the Devonian/Carboniferous boundary in the Donets Basin was not completely established due to new data obtained as a result of a detailed study of the boundary stratotype in southern France (Aretz & Corradini, 2019).

A stratigraphic gap was recorded in the uppermost part of the Ta zone. It is marked in the section along the Mokra Volnovakha River by a thin iron oolitic layer. Index Te was proposed instead of Va. The Va zone has been related to the lower Visean for a long time. Only after stabilisation of the Tournaisian and Visean boundary (T/V) in the Pengchong section (South China) according to changes in the foraminiferal evolutionary lineage *Eoparastaffella* (Devuyst et al., 2003), the assignment of the T/V boundary in the Donets Basin to the basal part of the Vb zone has been accepted. Thus, the Va zone is assigned now to the top of the Tournaisian. To avoid confusion, parallel indexing for this Te (Va) zone is made. A stratigraphic gap is also supposed at the base of this zone during correlation with a more complete section of the Dnieper-Donets depression located to the northwest of the Donets Basin. Simultaneously, a stratigraphic gap in the basal part of the Vb zone where lithology and faunistic associations sharply changed, has not been reliably established.

PREVIOUS STUDIES

The lower Carboniferous corals of the Donets Basin were studied in detail by Vassiljuk (1959, 1960). From the Tournaisian she described *Campophyllum caninoides* Sibly, 1906 (Tb zone), *Cyathoclisia modavensis* (Salée, 1913) (Tc zone) and *Calmiussiphyllum calmiussi* Vassiljuk, 1959 (Va zone). Moreover, Vassiljuk (1960) listed corals previously reported (unpublished date) from the lower Carboniferous of the Donets Basin by I.I. Gorsky, V.D. Fomichev and other researchers. The Tournaisian rugose coral studies by Gorsky and Fomichev were not finished; no images or descriptions of these corals have been published and their collections were irretrievably lost. Later, in a joint publication on zonal framework of the lower Carboniferous of the Donets Basin, Vassiljuk (in Poletaev et al., 1990) has added to the Tournaisian rugose corals list in this area two species - *Cyathoclisia tabernaculum uralensis* Sayutina, 1970 and *Amplexus* aff. *A. cornuformis* Ludwig, 1965. Recently, Ogar (2010) published images of *Keyserlingophyllum obliquum* (Keyserling, 1846) from the Tournaisian of the Donets Basin whereas *Conilophyllum priscum* (Münster, 1840) and *Corphalia simplex* (Perna, 1923) were documented for the first time by Ogar (2016). Images of other collected taxa are published in this paper.

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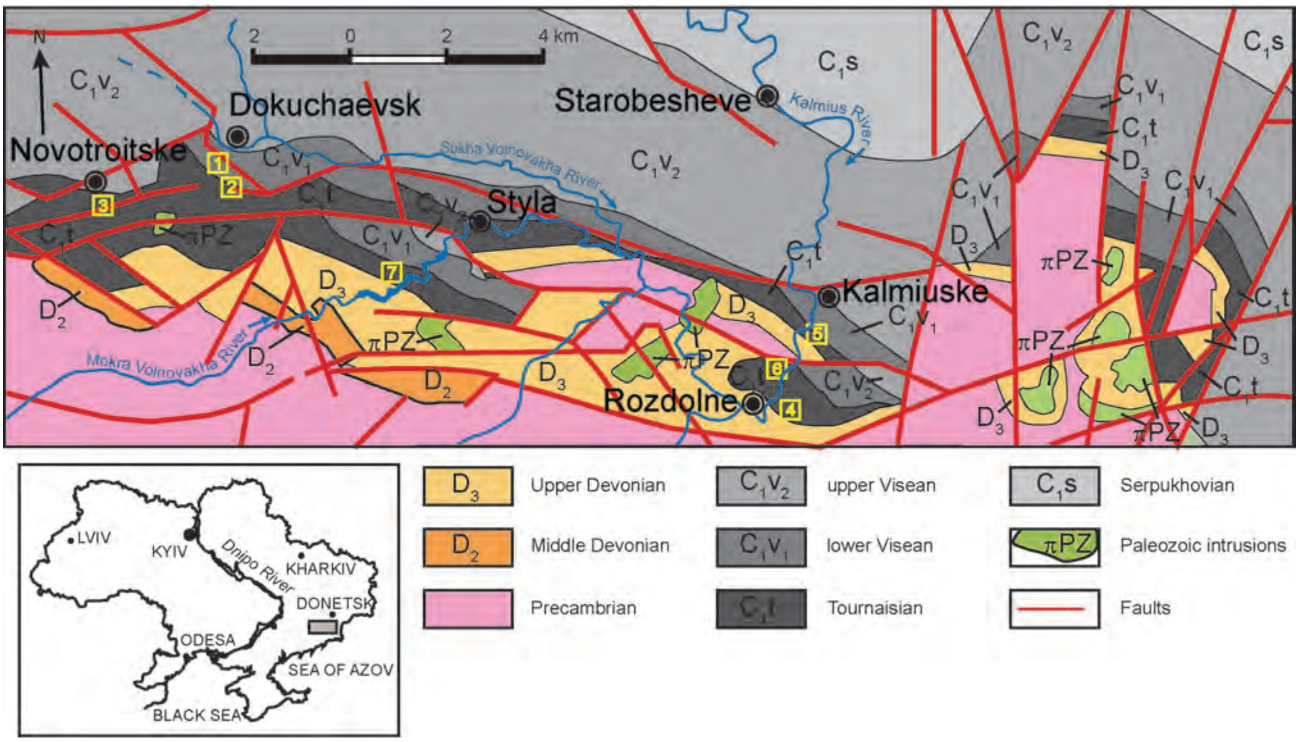

Fig. 1 - (color online) Simplified geological map of the South Donbas (modified after Aizenverg et al., 1975) with location of coral localities: 1: Central Quarry and 2: Dolomite Quarry near Dokuchaevsk town; 3: Eastern Quarry near Novotroitske town; 4: Karakuba Quarry and 6: Southern Quarry near Rozdolne town, 5: Northern Quarry near Kalmiuske town; 7: left bank of the Mokra Volnovakha River.

MATERIALS AND METHODS

The Tournaisian rugose corals were collected for this study in the southern part of the Donets Basin during 2004-2011. A key section of the lower Carboniferous along the left bank of the Mokra Volnovakha River was examined. This section was partially flooded by the Styla reservoir in the 1960s. In addition, a number of quarries for the extraction of limestone has been investigated, which revealed the section of Tournaisian deposits in whole or in part. The Dolomite, Central, Eastern, Southern, Northern and Karakuba quarries (Fig. 1) were investigated. As a result, the entire section of the Tournaisian, from the Upper Devonian (Ta zone) to the lower Visean (Vb-c zones), was studied. The collection of Tournaisian rugose corals comprises over 73 specimens. Not all corals are well preserved, most of them are fragments, often intensively altered by secondary dolomitisation, silicification, and leaching. Therefore, the fine microstructure of septa was studied only in a few specimens. Traditional techniques with thin sections, polished surfaces and acetate peels were used for the study of corals. The studied material is housed in the Museum of Paleontology of Taras Shevchenko National University of Kyiv (Acronyms TSNUK, 2P264 and 2P267).

SYSTEMATIC NOTES

Subclass Rugosa Milne-Edwards & Haime, 1850
Order Stauriida Verrill, 1865
Suborder Stereolasmatina Wedekind, 1927
Family Amplexidae Chapman, 1893

Genus *Amplexus* Sowerby, 1814

Type species *Amplexus coralloides* Sowerby, 1814; lower Carboniferous of Ireland.

Diagnosis - See Poty (1981).

Amplexus coralloides Sowerby, 1814
(Fig. 2a-c)

1814 *Amplexus coralloides* Sowerby, p. 165, Pl. 72.
2014 *Amplexus coralloides* Sowerby - Denayer, Fig. 4e-f (cum syn.).

Lectotype - B.M. 44115, chosen by Smith & Thomas (1963, p. 163-166, pl. 7, fig. 5): specimen figured by Sowerby (1814, pl. 72, fig. 1). Upper Tournaisian or lower Visean (*Syringothyris* Zone C, Waulsortian facies) of Limerick, Ireland.

Diagnosis - *Amplexus* variable in size (up to 50 mm in diameter) having up to 62 septa (after Poty, 1981).

Material - One specimen enclosed in a rock without proximal edge and calice, 2P264-A/c3-1, Southern Quarry. Two thin sections and five polished surfaces available for study.

Remarks - The Donets specimen is represented by the early growth stages and therefore it is difficult to compare it with the lectotype. However, it is close to the specimen described by Smith & Thomas (1963)

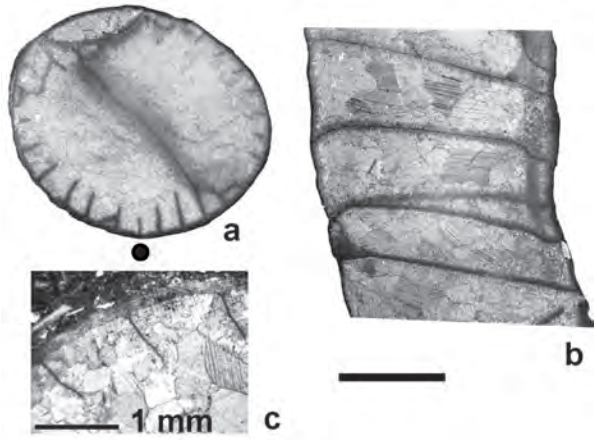

Fig. 2 - *Amplexus coralloides* Sowerby, 1814. Specimen 2P264-A/c3-1 in transverse section (a); detail of transverse section showing the septa and outer wall (c) and longitudinal section (b); Southern Quarry near Rozdolne town, Tc_2 subzone. Scale bar is 5 mm, except of specially indicated in c. Here and in subsequent figures with transverse sections of corals, the position of the cardinal septum is marked by a dot.

which has a slender form with diameter about 10-25 mm, approximately 2 mm long and with 25 septa. *Amplexus* sp. described in the Kuznetsk Basin (Dobrolyubova & Kabakovitch, 1966) is also very similar to the Donets specimen.

Note that, due to the morphological similarity of *Amplexus coralloides* mature growth stages, in this species was included a large number of occurrences in different regions of the world. They possibly belong to separate species differing by their early growth stages. These stages are rarely preserved, so an additional study of specimens originating from the *A. coralloides* type locality is required to stabilise the species.

Occurrence - Upper Tournaisian of the Omolon Massif (Poty & Onoprienko, 1984) and north-western Turkey (Denayer, 2014); upper Tournaisian and upper Visean of Belgium (Poty, 1981; Denayer et al., 2011), Brittany (Vuillemin, 1990), Scotland (Hill, 1938-1941), Ireland (Somerville, 1994), Wales (Somerville et al., 1986) and the Kuznetsk Basin (Dobrolyubova & Kabakovitch, 1966). In the Donets Basin this species is present from the upper Tournaisian, Tc_2 subzone of the Southern Quarry near Rozdolne town.

Family Antiphyllidae Ilina, 1970

Genus *Proheterelasma* Cotton, 1973

Type species *Hadrophyllum edwardsianum* De Koninck, 1872 = *Proheterelasma omaliusi* (Milne-Edwards & Haime, 1850); Tournaisian of Tournai, Belgium.

Diagnosis - See Cotton (1973).

Proheterelasma omaliusi (Milne-Edwards & Haime, 1851) (Fig. 3g-h)

1851 *Zaphrentis omaliusi* Milne-Edwards & Haime, p. 377, Pl. 5, fig. 3.
2015 *Proheterelasma omaliusi* (Milne-Edwards & Haime) - Denayer, p. 375, Fig. 3A1-A2 (cum syn.).

Holotype - Specimen figured by Milne-Edwards & Haime (1851, pl. 5, fig. 3), from the upper Tournaisian of Tournai, Belgium; Syntype MNHN.F.A29688, National Museum of Natural History, Paris.

Diagnosis - Small *Proheterelasma*, maximum 13 mm in diameter. Maximum 32 major septa joined in four groups around the fossulae and united in an axial column. Septa withdrawn and rhopaloid in counter quadrants. Minor septa very short. Tabulae complete, downturned toward the periphery (after Cotton, 1973).

Material - One specimen 2P264/1 without proximal edge and calice. Central Quarry near Dokuchaevsk town. One thin section and three peels.

Remarks - The features of the presented specimen correspond to the diagnosis of the species. It differs from occurrences in other regions by the relatively smaller diameter of the stereocolumn. At the same time, specimens described from Northern Germany demonstrate the variable thickness of a stereocolumn even in the same specimen (Weyer, 1993, pl. 4, fig. 3a-c).

Occurrence - Upper Tournaisian (Ivorian) of Belgium, England and Turkey (Vaughan, 1906; biozone RC3α of Poty et al., 2006; Denayer, 2015). In the Tournaisian this species was described in the Kuznetsk Basin (Dobrolyubova & Kabakovitch, 1966) and northern Iran (Flügel, 1991). The species is known in the Moliniacian (lower Visean) in France (Vuillemin, 1990; Poty & Hannay, 1994), Belgium (Poty, 2007; Denayer et al., 2011), Britain (Mitchell, 1981; Mitchell et al., 1986), and Ireland (Somerville & Jones, 1985). In the Donets Basin *Proheterelasma omaliusi* is found in black rocks of the Dokuchaevsky Horizon, Te (Va). Approximately at the same stratigraphic level (Chadian) this species is known from northern Germany (Weyer, 1993).

Family Hapsiphyllidae Grabau, 1928

Genus *Zaphrentites* Hudson, 1941

Type species *Zaphrentis parallela* Carruthers, 1910; Tournaisian of England.

Diagnosis - See Carruthers (1910).

Zaphrentites parallela (Carruthers, 1910) (Fig. 3a-c)

1910 *Zaphrentis parallela* Carruthers, p. 533, Pl. 37, fig. 4.
non 1967 *Zaphrentites parallela* (Carruthers) - Ivanowski, p. 41, Pl. 2, fig. 2.
2005 *Zaphrentites parallela* (Carruthers) - Chwieduk, p. 427, Pl. 15, fig. 6 (cum syn.).

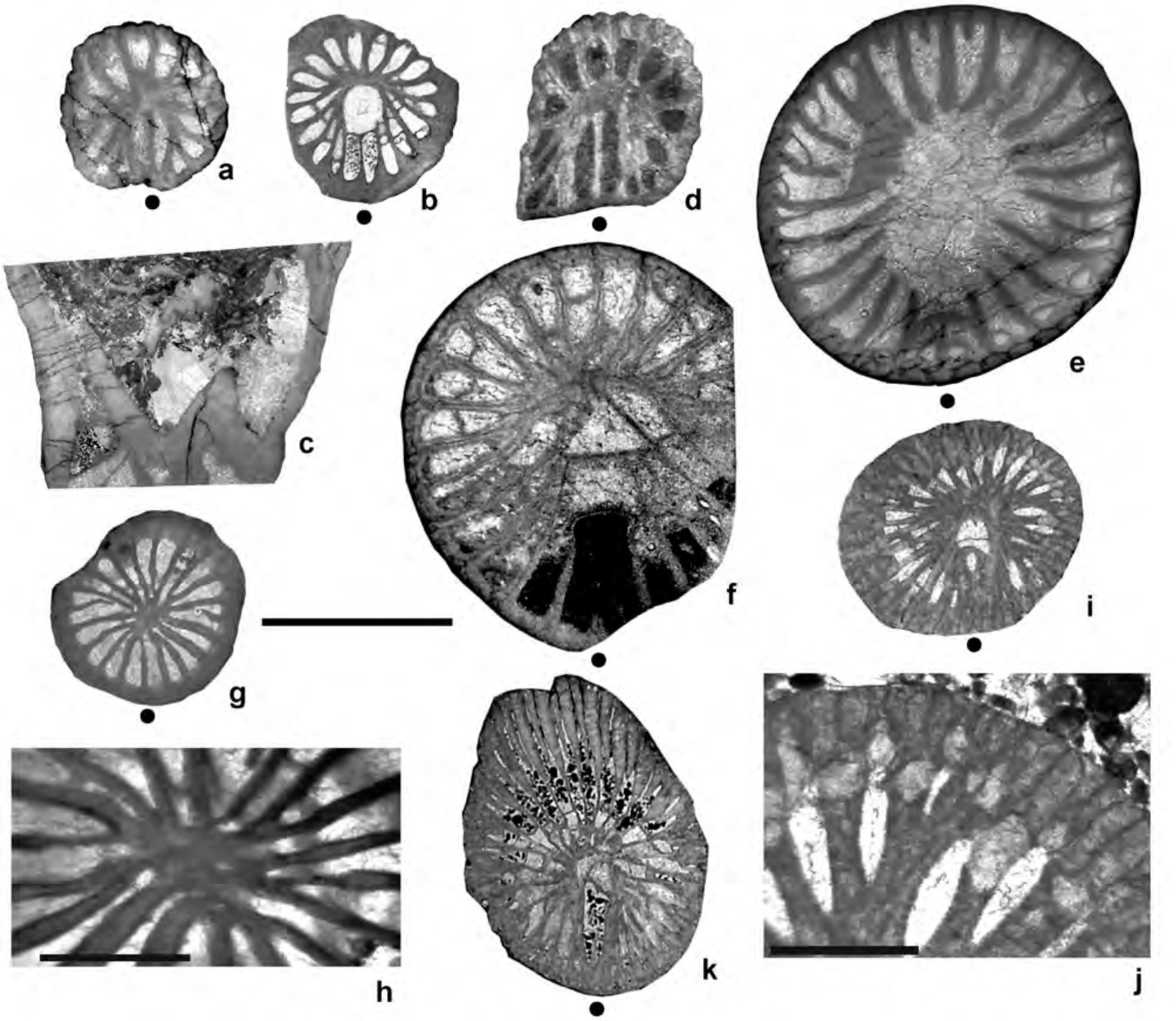

Fig. 3 - a-c) *Zaphrentites parallela* (Carruthers, 1910). Specimen 2P267A/c-8.1 in transverse sections (a-b) and longitudinal section (c); Dolomite Quarry, Tc zone. d-f) *Zaphrentites* cf. *delanouei* Milne-Edwards & Haime, 1851. Specimen 2P267A/c-6.10 in transverse sections (d-e); specimen 2P267A/c-c-1.1 in transverse section (f); Central Quarry near Dokuchaevsk town; Tc zone. g-h) *Proheterelasma omaliusi* (Milne-Edwards & Haime, 1851). Specimen 2P264/1 in transverse section (g) and detail of transverse section showing stereocolumn structure (h); Central Quarry, uppermost Tournaisian, Te (Va) zone. i-k) *Sychnoelasma konincki* (Milne-Edwards & Haime, 1851). Specimen 2P267A/c8-4 in transverse section (i) and detail of transverse section showing septotheca (j); Dolomite Quarry; specimen 2P264A/c2-6 in transverse section (k); Southern Quarry; Tc zone. Scale bar is 5 mm for all figures except for h and j (1 mm).

Holotype - Specimen PF1256 (56567), figured by Hill (1981, fig. 207.6), Tournaisian, the Larriston Quarry, Liddesdale, Scotland; Institute of Geological Sciences, Leeds.

Diagnosis - *Zaphrentites* maximum 10 mm in diameter and having 25 major septa. Cardinal fossula parallel-sides. Cardinal septum reaches ½ of the fossula length. Minor septa poorly developed (after Carruthers, 1910).

Material - Seventeen specimens enclosed in rock: Byzynova Valley (2P264A/c-2.2); Central Quarry (2P267A/c-1.6-1.14; 1.7-1.9) and Dolomite Quarry (2P267A/c-8.1-8.3); Southern Quarry (2P264A/c-3.1). Three thin sections.

Remarks - This species is very similar to *Zaphrentites delanouei* (Milne-Edwards & Haime, 1851). According to Dobrolyubova & Kabakovitch (1966), *Z. delanouei* has a pear-shaped fossula, intersecting throughout and at all stages of growth cardinal septum including the mature growth stages. In contrast, *Z. parallela* has parallel walls and the cardinal septum is half the length of the fossula. These differences can be added to the large sizes of *Z. delanouei*, whose diameter reaches 13 mm, while the diameter of *Z. parallela* does not exceed 10 mm. According to this study of Donets material *Z. parallela* does not exceed 8 mm with a cardinal septum, which is about half the fossula length. However, in juvenile stages the cardinal septum like that of *Z. delanouei* completely crosses the fossula and so cannot be used as a criterion for the difference between these species. In our opinion, the main differences appear at mature growth stages. The amplexoid stage in *Z. parallela* occurs with a diameter of 5-6 mm, whereas in *Z. delanouei* much later, with a diameter of 10 mm.

Occurrence - Western Europe, Tournaisian (Carruthers, 1910; Chwieduk, 2005), Kuznetsk Basin (Dobrolyubova & Kabakovitch, 1966), Armenia (Papoyan & Tchudinova, 1974) and northern Iran (Heravi & Khaksar, 1999). Upper Tournaisian - lower Visean of Sinai (Kora & Jux, 1986) and Turkey (Denayer, 2014). Donets Basin: Byzynova Valley; Central Quarry and Dolomite Quarry near Dokuchaevsk town; Southern Quarry near Rozdolne town, Tc zone.

Zaphrentites cf. *delanouei*
(Milne-Edwards & Haime, 1851)
(Fig. 3d-f)

Material - Two specimens enclosed in a rock: Central Quarry (2P267A/c-6.10 and c-1.1). Four thin sections.

Remarks - Unlike typical *Zaphrentites delanouei* one specimen has a fossula with parallel walls and indistinct alar pseudofossulae. Another specimen with conspicuous alar pseudofossulae has a shortened cardinal septum. In addition, *Z. delanouei* with a septal index of 25-30:9 mm is larger than these specimens (Denayer, 2015, fig. 3B-C).

Occurrence - Central Quarry near Dokuchaevsk town; upper Tournaisian, Tc_2 subzone.

Genus *Sychnoelasma* Lang, Smith & Thomas, 1940

Type species *Verneuilia urbanowitschi* Stuckenberg, 1895; lower Carboniferous of the Ural Mountains.

Diagnosis - See Cotton (1973).

Sychnoelasma konincki (Milne-Edwards & Haime, 1851)
(Fig. 3i-k)

1851 *Zaphrentis konincki* Milne-Edwards & Haime, p. 331, Pl. 5, fig. 5.
2005 *Sychnoelasma konincki* (Milne-Edwards & Haime) - Chwieduk, p. 429, Pl. 16, fig. 1 (cum syn.).

Holotype - Specimen figured by Milne-Edwards & Haime (1851, pl. 5, fig. 5-5a). Tournaisian of Belgium.

Diagnosis - Small ceratoid *Sychnoelasma*, 9-10 mm in diameter. Major septa pinnately arranged in the cardinal quadrants but radially arranged in counter quadrants. Minor septa usually short to one-third as long as the major septa. Cardinal septum shorter. Cardinal fossula long and closed. Outer wall thick. Tabulae numerous, irregular and vesicular (after Cotton, 1973).

Material - Four specimens: two from Southern Quarry (2P264A/c2-6 and 2-7), one from Eastern Quarry (2P267A/c3-7), one from Dolomite Quarry (2P267A/c8-4). All corals are enclosed in rock, early growth stages and calices not preserved. Two thin sections and one polished surface.

Remarks - The variety *S. konincki* var. *calmisia* (Lissitzin) in Vassiljuk (1960, p. 48-49, pl. 12, fig. 2-2c) described in the Donets Basin from the lower Visean differs from *S. konincki* by its large size and, accordingly, by its higher number of septa (septal index 34-35:12 mm; 36-38:16 mm). *S. hawbankense* Mitchell & Somerville, 1988 (p. 158-160, fig. 3a-g) also has a large size and number of septa (septal index 38-43:14-21 mm) but it displays longer minor septa, which are half the major septa in length. The type species *S. urbanowitschi* reaches even larger diameters (up to 20 mm). Mitchell & Somerville (1988) indicated that the species *S. konincki*, *S. hawbankense* and *S. urbanowitschi* are phylogenetically related.

Occurrence - Tournaisian of Western Europe: Armorican Massif (Vuillemin, 1990), Great Britain (Mitchell & Somerville, 1988), France (Poty & Hannay, 1994), Belgium (Denayer et al., 2011), Poland (Chwieduk, 2005), Urals (Gorsky et al., 1975; Sayutina, 1976; Simakova et al., 1978), and Kuznetsk Basin (Dobrolyubova & Kabakovitch, 1966). Donets Basin (Southern, Eastern and Dolomite quarries), Tc zone. This species is listed by I.I. Gorsky (in Vassiljuk, 1960).

Suborder Caniniina Wang, 1950
Family Cyathopsidae Dybowski, 1873

Genus *Siphonophyllia* Scouler in McCoy, 1844

Type species *Siphonophyllia cylindrica* Scouler in McCoy, 1844; lower Visean of Ireland.

Diagnosis - See Poty & Boland (1994).

Siphonophyllia cylindrica Scouler in McCoy, 1844
(Fig. 4a-b)

1844 *Siphonophyllia cylindrica* Scouler in McCoy, p. 187, Pl. 27, fig. 5.
1994 *Siphonophyllia cylindrica* Scouler in McCoy - Poty & Boland, p. 207 (cum syn.).

Holotype - Specimen 80-1925, Griffith collection, Museum of Natural History of Dublin (Ireland), lower Carboniferous, Ardsallagh, Drumguin (Ireland), single specimen figured by McCoy (1844, pl. 27, fig. 5) and Lewis (1927, p. 16, fig. 1a-b).

Diagnosis - Large ceratoid or cylindrical *Siphonophyllia*, maximum 70 mm in diameter and having 72 major septa. Major septa thickened in the tabularium, especially in the cardinal quadrants. Minor septa short or as septal crests on the dissepiments. Cardinal and counter septa are shorter. Cardinal and counter fossulae developed. Dissepimentarium wide, made of simple interseptal and lonsdaleoid dissepiments. Tabulae dispersed, slightly

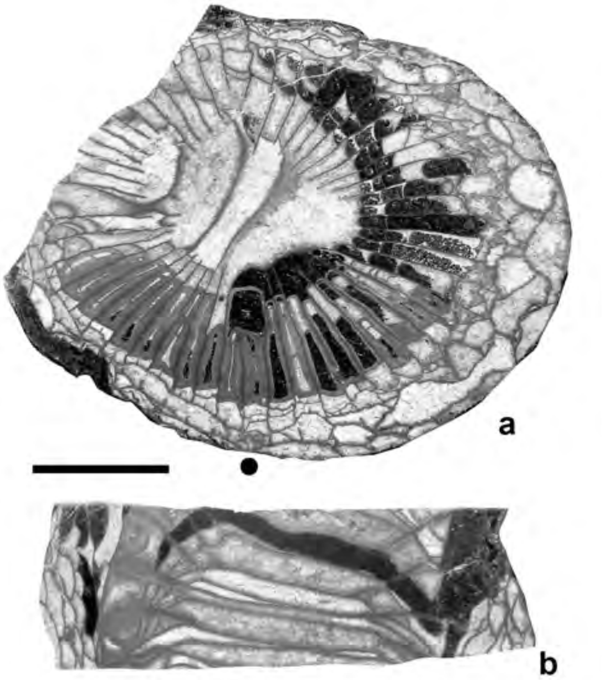

Fig. 4 - *Siphonophyllia cylindrica* Scouler in McCoy, 1844. Specimen 2P264-A/c-1in transverse (a) and longitudinal (b) sections; Southern Quarry near Rozdolne town; Tc_1 subzone. Scale bar is 10 mm.

divided and downturned towards the cardinal fossula (after Poty & Boland, 1994).

Material - Three specimens, 2P264A/c-1, Southern Quarry, 2P267A/c-9 and c-10, Karakuba Quarry near Rozdolne town. Two thin sections.

Remarks - "*Caninia*" *cylindrica* in the lower Carboniferous of the Donets Basin was first discovered by Lebedev (in Vassiljuk, 1960). Later, its presence was confirmed by I.I. Gorsky (in Vassiljuk, 1960). The fragments of rugose corals similar to "*Caninia*" *cylindrica* from the horizon with "*Spirifer*" *desinuatus* (i.e., *Paleochoristites cinctus desinuatus*, Tc zone; Poletaev et al., 2011), were indicated by Fomichev (1953) but the description and image of these corals are published here for the first time. *S. cylindrica* differs from other species of the genus *Siphonophyllia* mainly by the poor development of minor septa. In the Donets Basin, Te (Va) zone, *S. caninoides* was initially described as a *Campophyllum* (Vassiljuk, 1960, p. 63, pl. 14, fig. 1c-d) and differs from *S. cylindrica* by thin short septa and large homogeneous lonsdaleoid dissepiments. This is clearly seen in the descriptions and images of the paralectotype of this species (Somerville et al., 1986, p. 68-69, fig. 6d-g).

Occurrence - Widespread species, described from the Tournaisian of Western Europe (Poty & Boland, 1994), Urals (Gorsky et al., 1975; Simakova et al., 1978), Omolon Massif (Poty & Onoprienko, 1984), Kuznetsk Basin (Dobrolyubova & Kabakovitch, 1966), and Kazakhstan (Volkova, 1941). Donets Basin (Central and Karakuba quarries), upper Tournaisian, Tc_1 subzone.

Genus *Uralinia* Stuckenberg, 1895

Type species *Heliophyllum multiplex*
Ludwig, 1862; Tournaisian of the Ural Mountains.

Diagnosis - See Poty & Boland (1994).

Uralinia cf. *multiplex* (Ludwig, 1862)
(Fig. 5a)

Material - Two deformed specimens, 2P267-A/c-6-4, Central Quarry, 2P267-A/c-1d, Dolomite Quarry. Three thin sections.

Remarks - Donets specimens are most similar to *Uralinia multiplex* described in many regions of the world (see Denayer, 2015 and references therein) but present only as fragment of corals. The similar species *U. lobata* Poty & Boland, 1994 has septa thickened in cardinal and counter quadrants. Only Fomichev (1953) indicated the presence of *Uralina*-like corals in the Donets Basin.

Occurrence - Central and Dolomite quarries near Dokuchaevsk town, upper Tournaisian, Tc_2 subzone.

Genus *Keyserlingophyllum* Stuckenberg, 1895

Type species *Cystiphyllum obliquum* Keyserling, 1846;
Tournaisian of the Ural Mountains.

Diagnosis - See Poty & Xu (1996).

Keyserlingophyllum obliquum (Keyserling, 1846)
(Fig. 5b)

1846 *Cystiphyllum obliquum* KEYSERLING, p. 160, Pl. 1, fig. 5a-d.
1895 *Keyserlingophyllum obliquum* (Keyserling) - STUCKENBERG, p. 102, Pl. 5, fig. 8; Pl. 6, fig. 3; Pl. 20, fig. 2.
1987 *Keyserlingophyllum obliquum* (Keyserling) - IVANOWSKI, p. 24, Pl. 6, fig. 4.
2010 *Keyserlingophyllum obliquum* (Keyserling) - OGAR, fig. 6 N-O.
2015 *Keyserlingophyllum obliquum* (Keyserling) - DENAYER, p. 383, fig. 7 B1-B2, C1-C2, D, and E (cum syn.).

Holotype - Specimen 4/46, Museum of Saint Petersburg Mining University, Tournaisian of the Sopleska River, left tributary of the Pechora River, Russia; Keyserling collection. Figured by Stuckenberg (1895, pl. 6, fig. 8) and Ivanowski (1987, p. 24, pl. 6, fig. 4).

Diagnosis - *Keyserlingophyllum* up to 50 mm in diameter and having up to 68 major septa. Major septa very thickened and coalescent in the cardinal quadrants. Minor septa absent. Tabularium as wide as half of the radius. Axis of the coral eccentric toward the cardinal fossula. Cardinal fossula closed by the curved end of the septa, enclosing one or several septa. Dissepiments small, simple interseptal and lonsdaleoid (after Poty & Xu, 1996).

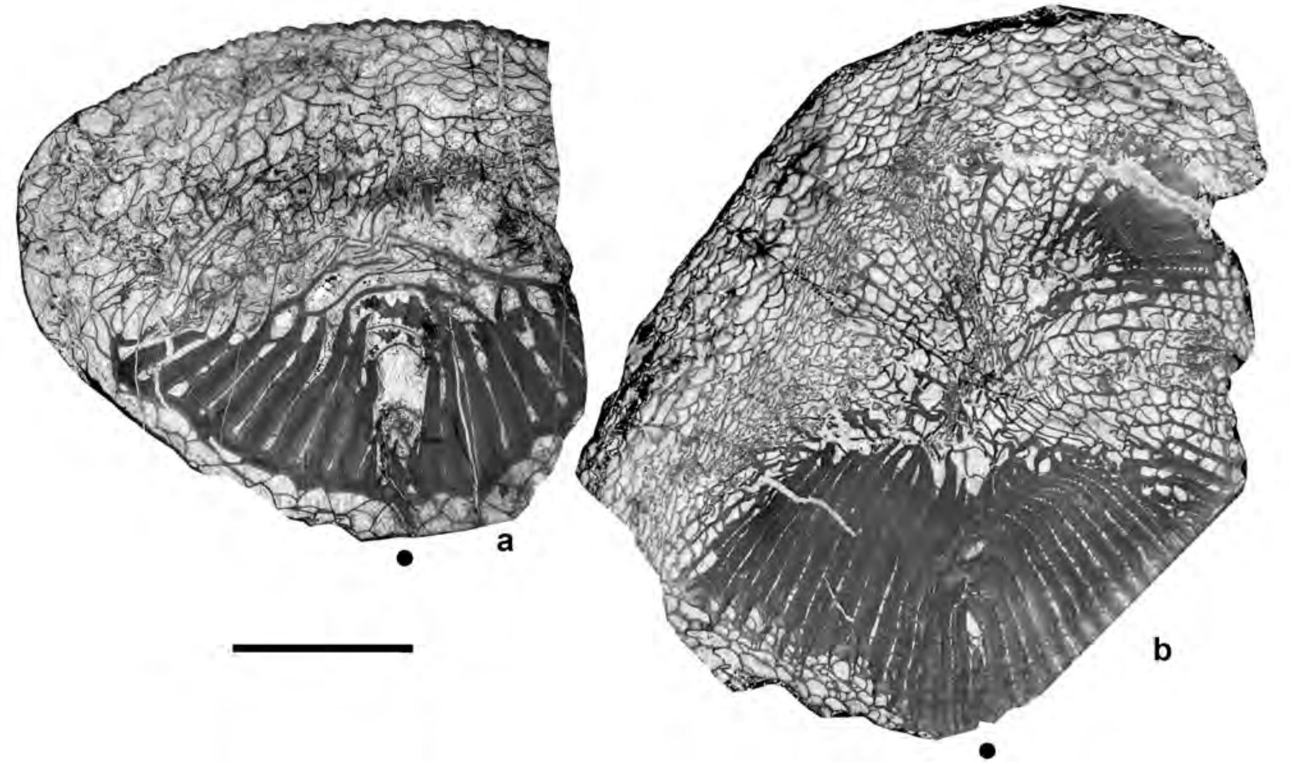

Fig. 5 - a) *Uralinia* cf. *multiplex* (Ludwig, 1862). Specimen 2P267-A/c-6-4 in transverse section; Central Quarry, Tc_2 subzone. b) *Keyserlingophyllum obliquum* (Keyserling, 1846). Specimen 2P264-A/c-2-2 in transverse section; Southern Quarry, Tc_2 subzone. Scale bar is 10 mm.

Material - Fragments of three large corals enclosed in rock with weathered external surface: 2P264-A/62, Central Quarry, 2P264-A/c-2-2, Southern Quarry and 2P267-A/c-9, Karakuba Quarry. The image of one of them (2P264-A/62) was figured by Ogar (2010, p. 291, fig. 6 N-O). Three thin sections.

Remarks - According to Stuckenberg's description, the number of septa in the type species are 64 in a diameter of 30 mm. It is close to that in the specimens studied by the author. The main difference is the presence of minor septa in the type specimens depicted by both Stuckenberg (1895, pl. 6, fig. 3) and Ivanowski (1987, pl. 6, fig. 4a). It is considered here that this feature is not decisive for determination of the species.

Distribution - Upper Tournaisian of Belgium (Denayer et al., 2011), Urals (Gorsky et al., 1975; Simakova et al., 1978), Pechora basin (Soshkina, 1960), South China (Poty & Xu, 1996), South Turkey (Denayer, 2015), and Armenia (Papoyan & Tchudinova, 1974). Donets Basin (Central, Southern and Karakuba quarries), upper Tournaisian, Tc_2 subzone.

Family Bothrophyllidae Fomichev, 1953

Genus *Caninophyllum* Lewis, 1929

Type species *Cyathophyllum archiaci* Milne-Edwards & Haime, 1852; Visean of England.

Diagnosis - See Poty (1981).

Caninophyllum tomiense (Tolmatchev, 1931)
(Fig. 6a-f)

1931 *Caninia tomiense* Tolmatchev, p. 329, Pl. 20, figs 3-8, 11.
1931 *Caninia patula* Michelin - Tolmatchev, p. 329, Pl. 19, figs 16-19; Pl. 20, figs 1-2.
1970 *Caninophyllum tomiense* (Tolmatchev) - Von Shouppé, p. 10, Pl. 1, figs 12-13; Pl. 2, figs 1-7 (cum syn.)

Lectotype - Specimen in collection No. 2555, CNIGR Museum, St. Petersburg, Russia; Kuznetsk Basin, Tom' River, Roiskaya village, lower Carboniferous, Tournaisian; figured by Tolmatchev (1931, p. 329, pl. 19, figs 16-18). Selected by Dobrolyubova & Kabakovitch (1966).

Material - Three specimens: 2P267A/c-3d with preservation of the corallite form; 2P267A/cd-9.1, 2P267A/c-1-4, without calices and proximal ends in dolomitic limestone. Three thin sections.

Diagnosis - Trochoid to cylindrical coral, up to 55 mm in diameter. Major septa extending rarely to the axis and thickened in the tabularium in the cardinal quadrants. Minor septa short or rudimentary. Cardinal septum short and placed in fossula. Dissepimentarium wider in the counter quadrants made of simple small dissepiments and occasionally second order lonsdaleoid dissepiments. Tabulae complete sub-horizontal or slightly sagging

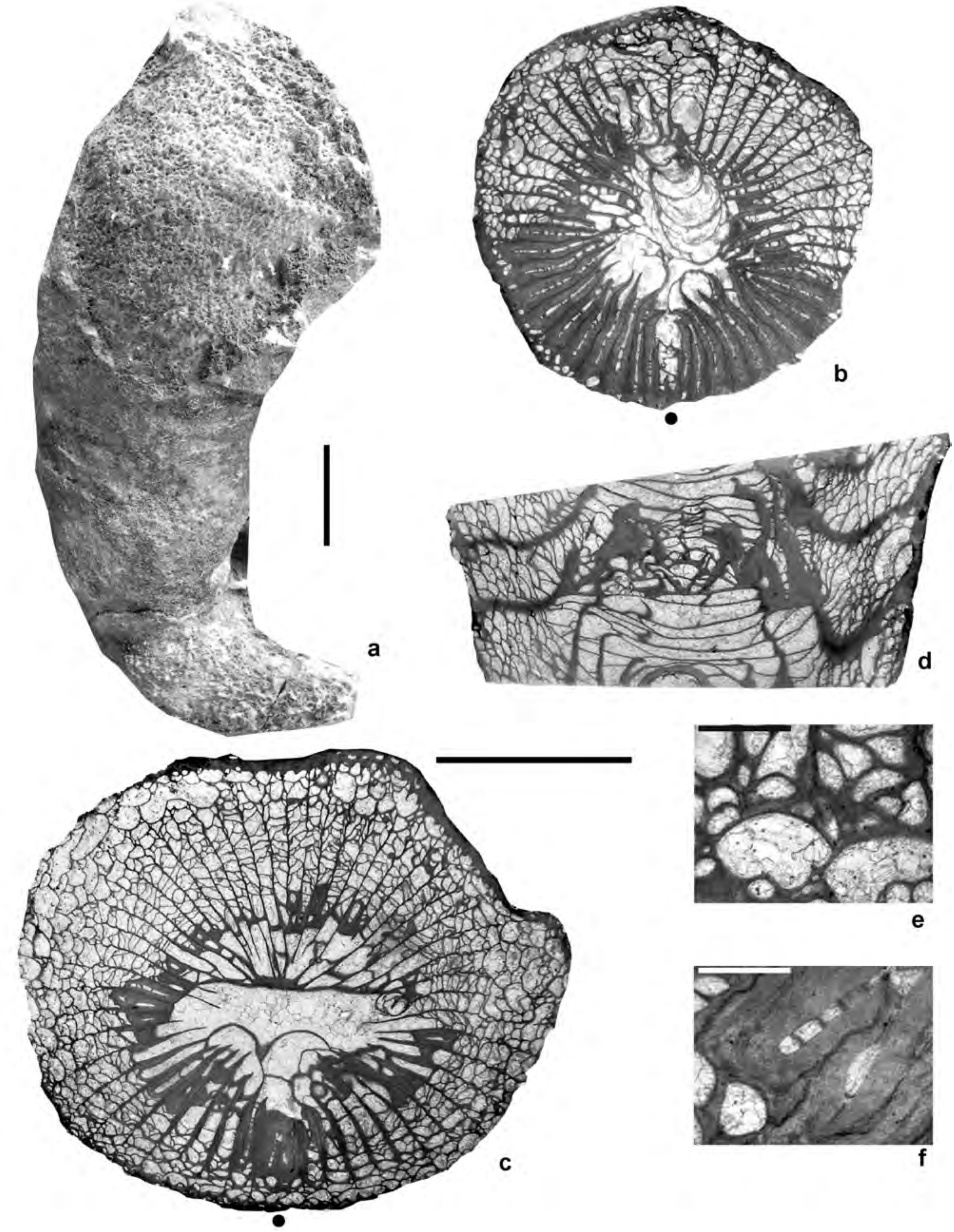

Fig. 6 - *Caninophyllum tomiense* (Tolmatchev, 1931). Specimen 2P267A/cd-9.1 in external view showing trochoid habitus of coral (a); transverse sections (b-c); longitudinal section (d); detail of transverse section showing lonsdaleoid dissepiment development (e-f); Dolomite Quarry near Dokuchaevsk town, Td_1 subzone. Scale bars are 10 mm in all the figures, except in e and f (1 mm).

in axial part of the tabularium (after Dobrolyubova & Kabakovitch, 1966).

Remarks - This species is most similar to *Caninophyllum patulum* (Michelin, 1846) and differs by its large size and somewhat higher number of septa (50:30 mm *C. patulum* and 54:25 mm in Donets specimens). The main feature considered here is the greater width of the dissepimentarium in the counter quadrants compared to the cardinal quadrants. It was the main difference of *Caninia patula* var. *tomiensis* Tolmatchev (Fomichev, 1931).

Occurrence - Upper Tournaisian of the Kuznetz Basin (Dobrolyubova & Kabakovitch, 1966), Urals (Gorsky et al., 1975; Simakova et al., 1978), Russian platform and Pechora area (Soshkina, 1960; Ivanowski, 1987), Omolon (Poty & Onoprienko, 1984), Armenia (Papoyan & Tchudinova, 1974), and Afghanistan (Shouppé, 1970). The Donets Basin, Dolomite Quarry near Dokuchaevsk town, upper Tournaisian, Tc_2 and Td_1 subzones (2P267A/c-3d and 2P267A/cd-9-1); Central Quarry, Tc_2 subzone (2P267A/c-1-4).

Caninophyllum kosvensis (Degtjarev, 1972)
(Fig. 7a-b)

1972 *Caninia kosvaensis* DEGTJAREV, p. 105, Pl. 30, fig. 2.
1978 *Caninia kosvensis* Degtjarev - SIMAKOVA, DEGTJAREV & RAKSHYN, Pl. 17, fig. 2.

Holotype - No. 5/70913, Uralian Geological Museum, Yekaterinburg, Russia. Figured by Degtjarev, 1972, p. 105-106, pl. 30, fig. 2. Western slope of the Middle Urals, Kosva River, Shirokovsky town, upper Tournaisian, Kosvinsky Horizon.

Diagnosis - *Caninophyllum*, 30 mm in diameter and 56 septa with a thin external wall. Cardinal and two neighbouring septa shortened and located in open fossula. Septa thickened in cardinal quadrants, long in juvenile growth stages and reach half of major septa length in mature growth stages. Minor septa not developed. Dissepimentarium concentric, wider in counter quadrants, composed of rectangular interseptal dissepiments. Tabulae complete, horizontal or slightly wavy in the tabularium, incomplete and vesicular near the dissepimentarium (after Degtjarev, 1972).

Material - Two fragments, one of which is rock-free, recrystallised with poorly preserved juvenile growth stages (2P267Va-41), the other specimen is cylindrical and enclosed in rock (2P264Va-4). Two thin sections.

Remarks - In the holotype, the cardinal septum is not cut by the thin section. In the specimen 757/601 VNIGRI Museum (St. Petersburg) from the Usuili River (Simakova et al., 1978; pl. 17, fig. 2) the cardinal septum is short. The thickening of the major septa is similar to our specimens. It differs from *Caninophyllum tomiense* by the development of rectangular dissepiments and a smaller number of septa with equal diameters.

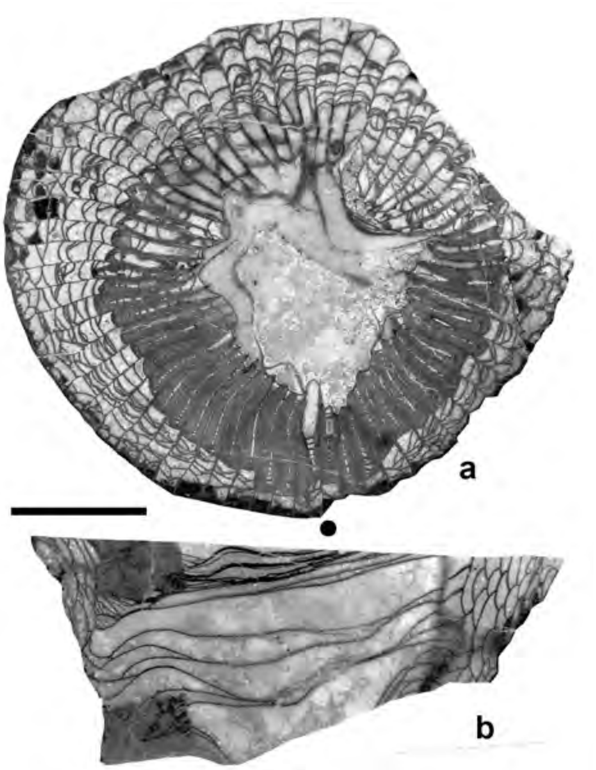

Fig. 7 - *Caninophyllum kosvensis* (Degtjarev, 1972) Specimen 2P264Va-4 in transverse (a) and longitudinal (b) sections; Northern Quarry near Kalmiuske town, Te (Va) zone. Scale bar is 10 mm.

Occurrence - Upper Tournaisian, Kosvinsky Horizon in the Western slope of the South Urals. In the Donets Basin, Central Quarry near Dokuchaevsk town and Northern Quarry near Kalmiuske town, Te (Va) zone.

Genus *Calmiussiphyllum* Vassiljuk, 1959

Type species *Calmiussiphyllum calmiussi* Vassiljuk, 1959; uppermost Tournaisian, Te (Va) zone of the Donets Basin.

Diagnosis - Large solitary coral. Major septa numerous, extending almost to the axis, except the cardinal septum and its neighbouring septa. Cardinal septum at the early growth stages long and shortened at the mature growth stages. Minor septa half as long as the majors, contratingent. Septa thickened in juvenile stages. Thickening decreasing in mature stages, firstly in counter quadrants then in the cardinal parts of the dissepimentarium. Dissepimentarium wide, made of simple interseptal and rare lonsdaleoid dissepiments in mature stages. Tabulae incomplete, domal (Poty & Xu, 1996; slightly supplemented).

Calmiussiphyllum calmiussi Vassiljuk, 1959
(Figs 8a-h, 9)

1959 *Calmiussiphyllum calmiussi* VASSILJUK, p. 87, Pl. 3, figs 2-3.
1960 *Calmiussiphyllum calmiussi* Vassiljuk - VASSILJUK, p. 67, Pl. 14, fig. 3, 3a; Pl. 15, fig. 1-1e.

Holotype - National Museum of Natural History of Ukraine (Kyiv), No. 1405/7, Donets Basin, Kalmius River near Kalmiuske (Komsomolske) town, Donkhushi-Tukhaya Valley, Uppermost Tournaisian, Te (Va) zone, figured by Vassiljuk (1959, pl. 3, fig. 2; 1960, pl. 14, fig. 1-1e).

Diagnosis - As for the genus.

Material - Many crushed and fragmented specimens were collected in the quarries. Only fourteen of them to some extent allow to study the early growth stages of these corals. From the preserved specimen (2P267Va-8.4, Southern Quarry) eight thin sections were made. Other specimens from Central Quarry (2P267Va-40-49) show trochoid parts of corals and in the Eastern Quarry (2P267Va-1) three cylindrical fragments were collected from the dolomitic limestone.

Description - Long trochoid corals (more than 9 cm), covered with growth striae and conspicuous septal furrows (Fig. 8a). The major septa are long, thickened in the early growth stages in all quadrants. Trabecular microstructure of the septa is recognised (Fig. 8h). Most septa almost reach the axis of the coral. Some specimens (2P268Va-44) have rhopaloid septa. In mature specimens, thick septa remain only in the cardinal quadrants tabularium. The cardinal septum in the early growth stages is long and thick. It reaches the corallite axis where it bends or connects to the counter septum (Fig. 8c). In mature growth stages it is shortened and placed in a fossula (Fig. 8d). The cardinal-lateral septa are shortened. The alar pseudofossulae are conspicuous. The minor septa appear where the diameter reaches 13-14 mm. They are very short and thickened (Fig. 8c). With the growth of the coral, they become thin and lengthen, penetrating far into the tabularium. The septal index of the studied specimen: 25:9-10 mm; 28:13-14 mm; 36:20 mm; 38:25 mm; 43:27 mm. The first interseptal rectangular dissepiments appear where the corallum reaches a diameter of 20 mm (Fig. 8d-f). Their morphology is more complicated at large corallite diameters (Fig. 9). The number of rows of interseptal dissepiments increases to eight-nine. A narrow outer zone consists of lonsdaleoid dissepiments. The tabulae are thin, complete or not, sub-horizontal, distant of 5 mm from each other. The outer wall is thin, 0.4-0.5 mm.

Remarks - In the specimen that was studied in detail, only the early growth stages are preserved, the mature stages being eroded. It displays a high similarity with the transverse section of the paratype figured by Vassiljuk (1960, pl. 15, fig. 1c) with close diameter (20-25 mm). Therefore, the figured specimen is confidently included in the species *C. calmiussi*.

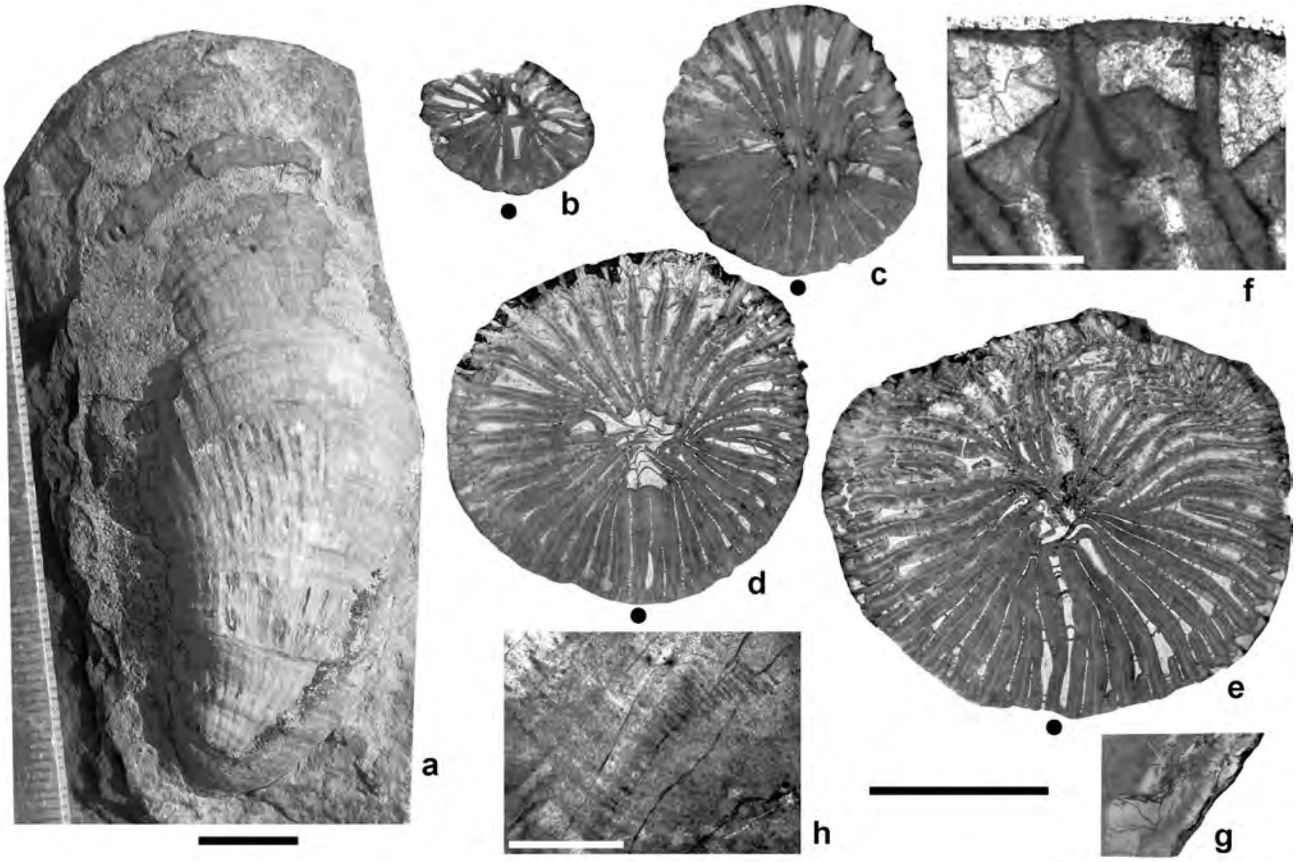

Fig. 8 - *Calmiussiphyllum calmiussi* Vassiljuk, 1959. Specimen 2P267Va-8.4 with view of the specimen showing trochoid habitus, growth striae and conspicuous septal furrows (a); transverse sections (b-e); detail of transverse section showing of septa, dissepiments and outer wall (f); longitudinal section (g); detail of longitudinal section showing trabecular microstructure of the septum (h); Southern Quarry near Rozdolne town, Te (Va) zone. Scale bars are 10 mm in all the figures, except in h and f (1 mm).

Fig. 9 - *Calmiussiphyllum calmiussi* Vassiljuk, 1959. Specimen MNH 1405/240, figured by Vassiljuk (1959, p. 3, fig. 3a; 1960, pl. 14, fig. 3): transverse section of the adult growth stage; Right bank of the Kalmius River near Kalmiuske town, Te (Va) zone. Scale bar is 10 mm.

Calmiussiphyllum calmiussi is possibly present in the Urals (Degtjarev, 1973) and in Belgium (Denayer et al., 2011, pl. 2, fig. J), where it is described in open nomenclature. From South Turkey, Denayer (2015) assigned to *Calmiussiphyllum* the species *C.* cf. *dobroljubovae* (Flügel, 1963). It should be noticed that *Bothrophyllum dobroljubovae* Flügel, 1963 has a long counter septum reaching the centre, which is not characteristic of the genus *Calmiussiphyllum*. *C.* cf. *dobroljubovae* (Flügel, 1963) from Turkey and the Donets Basin have more similar features. Both of them have a long cardinal septum at early growth stages. But the septa of *C.* cf. *dobroljubovae* are pinnately arranged in the cardinal quadrants with distinct lateral fossulae. In addition, the dissepiments in this species appear very early (at a diameter of 8 mm). A wide dissepimentarium in counter quadrants also makes it easy to distinguish this species from *C. calmiussi*. Denayer (2015) compares his species with similar corals described by Ivanowski (1967) as *Caninia ussovi* Gabunia, 1919 but these corals do not have thick septa in the cardinal quadrants with radial arrangement of septa and have an inconspicuous fossula.

Occurrence - Donets Basin. Dokuchaevsk, Novotroitske, Rozdolne, and Kalmiuske towns area, Te (Va) zone.

Family Aulophyllidae Dybowski, 1873
Subfamily Amygdalophyllinae Grabau in Chi, 1935

Genus *Cyathoclisia* Dingwall, 1926

Type species *Cyathoclisia tabernaculum* Dingwall, 1926; Tournaisian of England.

Diagnosis - See Poty (1981).

Cyathoclisia soshkinae Sayutina, 1973
(Fig. 10a-h)

p. 1960 *Cyathoclisia modavense* (Saleé) - Vassiljuk, Pl. 30, fig. 1c.
p. 1970 *Cyathoclisia modavensis* Soshkina, 1960, Pl. 1, figs 1-4.
1973 *Cyathoclisia soshkinae* Sayutina, p. 70, Text-figs 13-14; Pl. 6, figs 7-8.

Holotype - Specimen 703/5102, Paleontological Institute (PIN), Russia, selected by Sayutina, 1973, East European Platform, Moscow Basin, Cherepet railway station, Cherepet River, Tula region; Tournaisian, Cherepet horizon; figured by Soshkina (1960, pl. 1, fig. 4a-b).

Diagnosis - *Cyathoclisia* reaching a diameter of 25 mm and having up to 40 septa of each order. Major septa thin, reach the axial structure, where their ends slightly twist. Minor septa short, appearing where diameter reaches 6-7 mm; 1/3 of the length of the major septa, often contratingent. Axial structure compact, monolithic, up to 2 mm-thick, composed of a short and thick axial plate and septal lamellae, immersed in a stereoplasm. Tabulae rare, often complete, upturned towards the axis with an angle of 50-60°. Dissepimentarium narrow, appearing late in ontogeny, composed of 1-2 rows of interseptal dissepiments (after Sayutina, 1973).

Material - Nineteen specimens: four specimens from the Buzynova Valley (left bank of the Mokra Volnovakha River), (2P264A/2.1; 2.3 - 2.5); two specimens from the Karakuba Quarry (2P267A/c-31 and c-32); one specimen from the Central Quarry (2P267A/c-6-9); four specimens from the Southern Quarry (2P264A/c-2.3 - 2.5 and c-2.8); eight specimens from the Eastern Quarry (22P267A/c-3.1-3.6; c-4.1, 4.2). Most of the specimens are enclosed in rock; only a single specimen free of rock. Early growth stages are often preserved; one specimen (2P267A/cd-9.2, Dolomite Quarry) has partially preserved calice.

Remarks - The Donets specimens differ from the holotype in slightly larger size and higher number of septa. The diameter of the calice reaches 30 mm, whereas in the species of the Moscow Basin it is no more than 25 mm. *Cyathoclisia soshkinae* differs from the closest species *C. uralensis* by its smaller size and fewer septa, that are thinner, and a narrow dissepimentarium (one-two rows compared to four-five rows in *C. uralensis*). At a diameter of 15 mm the number of major septa in *C. soshkinae* is 39-40, whereas in *C. uralensis*, at the same diameter, there are 44-46 septa.

Note that, as pointed out by Sayutina (1973), and then noted by Weyer (2006), the name *uralensis* was used by Stuckenberg for another closely related species (*Clisiophyllum uralense* Stuckenberg, 1895) and therefore is a homonym.

From the similar species *C. modavensis*, the Donets specimens from Tc zone differ by a simpler and compact axial structure, much smaller size and more scattered slightly upturned tabulae, as well as the absence of a diplosepta. Already at early growth stages (4 mm in diameter) the axial structure of *C. modavensis* from Te (Va) zone of the Donets Basin (Vassiljuk, 1960, p. 124,

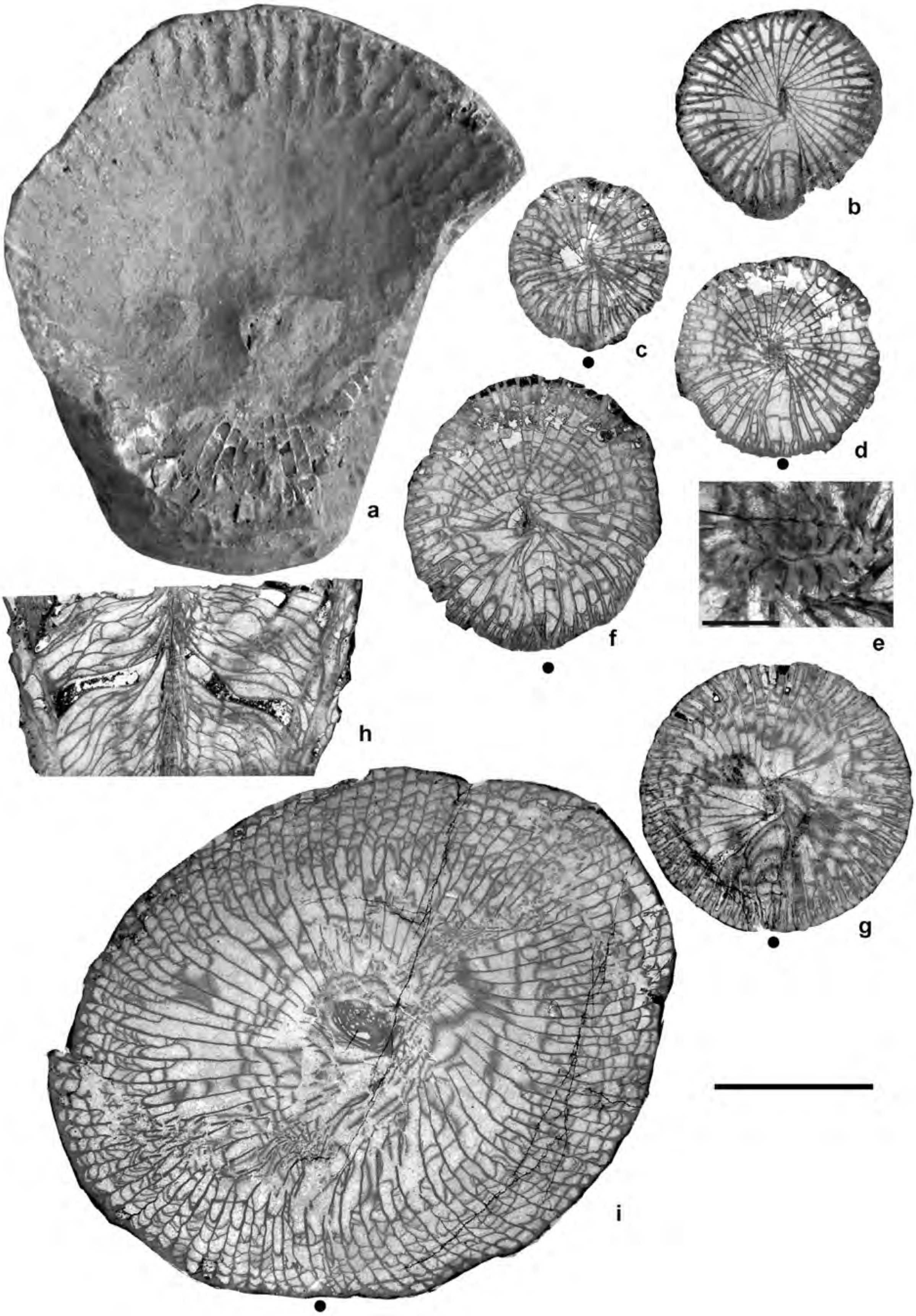

Fig. 10 - a-h) *Cyathoclisia soshkinae* Sayutina, 1973. Specimen 2P267A/c-d-9 with view of the specimen showing trochoid habitus and fragmentarily preserved calice (a), Dolomite Quarry, Tc_2 subzone and in transverse section (b). Specimen 2P267A/c-31 in transverse sections (c-d, f-g); detail of transverse section showing axial structure (e) as enlargement of (d); longitudinal section (h); Karakuba Quarry, Tc_2 subzone. i) *Cyathoclisia* cf. *modavensis* (Salée, 1913). Specimen 2P267A/d-9-2 in transverse section; Dolomite Quarry, Tc_2 subzone. Scale bar is 10 mm for all figures except for e (1 mm).

pl. 30, fig. 1-1b) is built of numerous radial lamellae connected to major septa.

Occurrence - Moscow Syneclise, Tournaisian, Cherepet horizon (Soshkina, 1960); the North Urals (Sayutina, 1973), Tournaisian, Kiselovian horizon. In Donets Basin this species is abundant from middle part of Tournaisian (Tc$_2$ subzone), Buzynova Valley, Central, Dolomite, Southern, Eastern, and Karakuba quarries.

Cyathoclisia cf. *modavensis* (Salée, 1913)
(Fig. 10i)

Material - Three deformed cylindrical and sub-cylindrical fragments without early growth stages. 2P267A/d9-1, 9-2 and 9-8.

Remarks - This species differs from *Cyathoclisia soshkinae* by its large size, thinness of septa and the development of a dissepimentarium. It is similar to *C. modavensis* but distinguished by having fewer septa (72:30 mm in *C. modavensis* and 56:35 mm in *C.* cf. *modavensis*) and by less complex axial structure. *Cyathoclisia densum* Gorsky (1935) is described in detail by Dobrolyubova & Kabakovitch (1966, p. 44, pl. 3, figs 1-5; pl. 4, fig. 1; pl. 5, fig. 1) from the Kuznetsk Basin and was originally described by Gorsky (1935, p. 42, pl. 7, figs 10-14 and pl. 8, fig. 1) as *Lophophyllum caninoides* var. *densa* from zone Etroeungt of Nowaya Zemlya; it has a wider dissepimentarium, smaller size, higher number of septa with equal diameters, thickened major septa and thin minor septa. In the Donets specimens major and minor septa do not differ in thickness.

Occurrence - Dolomite Quarry near Dokuchaevsk town; upper Tournaisian, Tc$_2$ subzone.

Family PALAEOSMILIDAE Hill, 1940
Subfamily PALAEOSMILINAE Hill, 1940

Genus *Aulokoninckophyllum* Sando, 1976

Type species *Campophyllum carinatum* Carruthers, 1909 (p. 150, pl. 1, figs 3-6), Russia, Novaya Zemlya, uppermost Visean.

Diagnosis - See Sando (1976).

Remarks - In the diagnosis proposed by Somerville et al. (2016) the presence of long carinate major septa is indicated. Such carinate major septa are not observed in the Donets specimen.

Aulokoninckophyllum sp.
(Fig. 11a-c)

Material - One fragment 2P267-A/c-1-3 of coral recrystallised and enclosed in rock. Three thin sections.

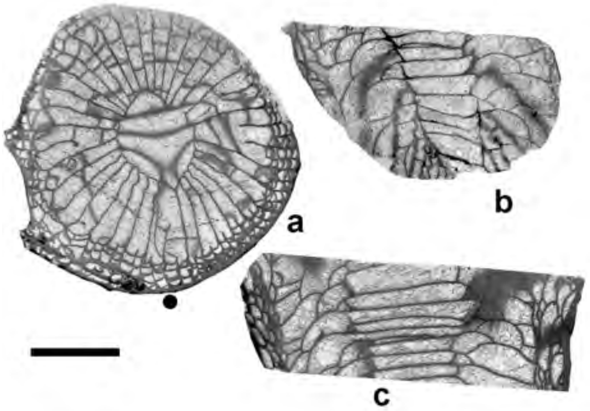

Fig. 11 - *Aulokoninckophyllum* sp. Specimen 2P267-A/c-1-3 in transverse (a) and longitudinal (b-c) sections; Central Quarry, near Dokuchaevsk town, Tc$_2$ subzone. Scale bar is 5 mm.

Remarks - The most similar to illustrated species are *Aulokoninckophyllum* cf. *ngakoi* Vuillemin, 1990 from the upper Tournaisian, RC4α-β$_1$ (Denayer et al., 2011, p. 162, pl. 4, fig. N), and *Aulokoninckophyllum* sp. (Denayer et al., 2011, p. 162, pl. 3, fig. M), RC3β of Belgium. *Aulokoninckophyllum ngakoi* Vuillemin from the lower Visean of the Armorican Massif has a much larger number of septa 45:10-12 mm. Donets species, as well as *A.* cf. *ngakoi* and *Aulokoninckophyllum* sp. from Belgium occurrence in the upper Tournasian. A study of the aulate corals (Somerville et al., 2016) shows that they are probably the oldest species of the genus and the most ancestral in the phylogenetic lineage of *Aulokoninckophyllum*.

Occurrence - Central Quarry near Dokuchaevsk town, upper Tournaisian, Tc$_2$ subzone.

Suborder LONSDALEIINA Spassky, 1974
Family APHROPHYLLIDAE Hill, 1973

Genus *Merlewoodia* Pickett, 1967

Type species *Merlewoodia bensoni* Pickett, 1967; upper Tournaisian or lower Visean Namoi Fm., Babbinboon, New South Wales, Australia.

Diagnosis - See Poty (2007).

Remarks - The initial diagnosis of *Merlewoodia* (Pickett, 1967), as well as the emended diagnosis proposed by Poty (2007), indicates a long counter septum. The presence of a shortened counter septum in our species does not correspond to the proposed diagnoses of the genus. These and other differences may be sufficient to establish a separate new genus widespread in Europe.

Merlewoodia sp. 1
(Fig. 12 f-m)

Materials - Two specimens (2P267-A/c-1-2; 2P267-A/c-1-5) from the same location (Central Quarry) completely enclosed in rock. One of the specimens preserved early growth stages. Six thin sections and three polished surfaces are available for study.

Description - Solitary corals with the largest diameter of 20 mm. At the earliest growth stages, at a diameter of 3.5-4 mm there are 19 thickened septa. They do not reach the axis, but their inner ends fuse, leaving a free space 1.2-1.5 mm wide. With a maximum observed diameter of 20 mm, major septa are long, but have unequal lengths. In the cardinal parts of the dissepimentarium they are thinned. The longest of them reach the axis, where they are connected with stereoplasm. The cardinal septum is shortened, located in the open fossula. In some sections it is clear that the cardinal septum is shorter than the neighbouring two septa. The alar pseudofossulae are conspicuous. The counter septum is somewhat shorter than the others. One of the lateral septa is notably lengthened. At large corallite diameters, the septa are thickened with a clear dark median line. Their pinnate arrangement is observed in some asymmetrical corals. This asymmetry is visible in the different lengths of the lateral septa, as well as in the ends of major septa, some of which having their inner ends fused, whereas some remain free (Fig. 12g). Septal index: 28-30:7-8 mm; 35:9.5-10 mm; 40:13.5mm; 45:20 mm. The minor septa are unstable, very short, the first of them appear in counter quadrants where the corallite diameter reaches 8 mm. They are completely enclosed in the stereoplasm of the wall. At the same diameter, the first dissepiments appear in counter quadrants (Fig. 12g). At mature stages the dissepimentarium is better developed in counter quadrants. It consists of small irregular dissepiments, grouped in seven-eight rows. The outer wall disintegrates with the emergence of a naotic structure in the periphery (Fig. 12i-k). The tabulae are incomplete and are rarely located and depressed in the axial part. Near the dissepimentarium densely packed concave interstitial tabellae (Poty, 2002) develop (Fig. 12l-m).

Remarks - The presence of naotic dissepiments at the mature growth stages in the Donets specimens is a characteristic feature of the genus *Merlewoodia* (Webb, 1990; Poty, 2007). Slight development of minor septa, a thick outer wall, are important diagnostic features of *Merlewoodia* sp. 1. The Donets specimens are very similar to those reported from Belgium (Denayer et al., 2011): *Merlewoodia* sp. nov. C (Denayer et al., 2011, p. 170, pl. 5, fig. R) and *Merlewoodia* sp. nov. B (pl. 5, fig. T). The limited number of specimens precludes describing the Donets coral as a new species.

Occurrence - Central Quarry near Dokuchaevsk town, Tc_2 subzone.

Merlewoodia sp. 2
(Fig. 12a-e)

Material - One specimen, 2P267/Va-40 from the Central Quarry. A fragment of calice is preserved. Four thin sections are available.

Description - Trochoid coral with a destroyed surface about 5 mm long and maximum diameter of 28 mm. A fragment of calice with recess 5 mm depth extended along from cardinal to counter septa, major septa are thick with a clear median line, pinnate arrangement and varying in length. Cardinal septum is placed on the convex side of the coral and located in an open fossula. The cardinal and neighbouring septa are shortened. The counter septum is also shortened. Two alar pseudofossulae are conspicuous. The others septa reach the axis or are slightly withdrawn from the axis, retaining stereoplasmic thickening. They are thinner in the counter quadrants at mature growth stages. The minor septa are rudimentary (Fig. 12d). They occur together with dissepiments at a corallite diameter of about 15 mm. Septal index 27:9-10 mm; 34:13-15 mm; 42:17.5 mm; 50:28 mm. The tabulae are incomplete, depressed in the axial part and inclined towards the wall. Densely packed interstitial tabellae are developed near the outer wall between thickened septa (Fig. 12c, e).

Remarks - *Merlewoodia* sp. 2 differs from the species described above by smaller number of septa with equal diameter and of the delayed appearance of a dissepimentarium. There is no doubt that both of them belong to the same genus.

Occurrence - Central Quarry near Dokuchaevsk town, Te (Va) zone.

TAXONOMICAL COMPOSITION

In addition to the previously described (Ogar, 2016) *Conilophyllum priscum* and *Corphalia simplex*, this paper provides refined and supplemented data on the systematic composition of rugose corals of the Tournaisian within the Donets Basin. The species and systematics of some rugose corals previously described or indicated by Vassiljuk were revised by the author. *Cyathoclisia tabernaculum uralensis* (Poletaev et al., 1990) and partly *C. modavensis* (Vassiljuk, 1960, pl. 30, fig. 1c) with a simplified axial structure is considered as a species of *Cyathoclisia soshkinae*. The basis for this revision was the results of a study of 19 specimens of this species that was collected. The specimen illustrated by Vassiljuk (1960, pl. 14, fig. 1c-d) as *Campophyllum caninoides* is assigned to the genus *Siphonophyllia* Scouler in McCoy, 1844.

A detailed study of the early stage development of *Calmiussiphyllum calmiussi* was performed. Despite the large number of specimens, their poor preservation did not allow to study its early stages of growth. It was established that the cardinal septum in this species is prolongated in the early growth stages. The septa have a trabecular microstructure.

The presence of undissepimented rugose genera in the Tournaisian of the Donets Basin was established previously (Vassiljuk, 1960) but illustrations of the genera *Amplexus* Sowerby, 1814, *Sychnoelasma* Lang, Smith & Thomas, 1940, *Zaphrentites* Hudson, 1941, *Proheterelasma* Cotton, 1973 are published here for the first time.

The presence of large caninoid rugosans *Siphonophyllia* Scouler in McCoy, 1844 and *Uralinia* Stuckenberg, 1895, as well as *Caninophyllum* Lewis, 1929 is confirmed, and their brief characteristics and illustrations are given.

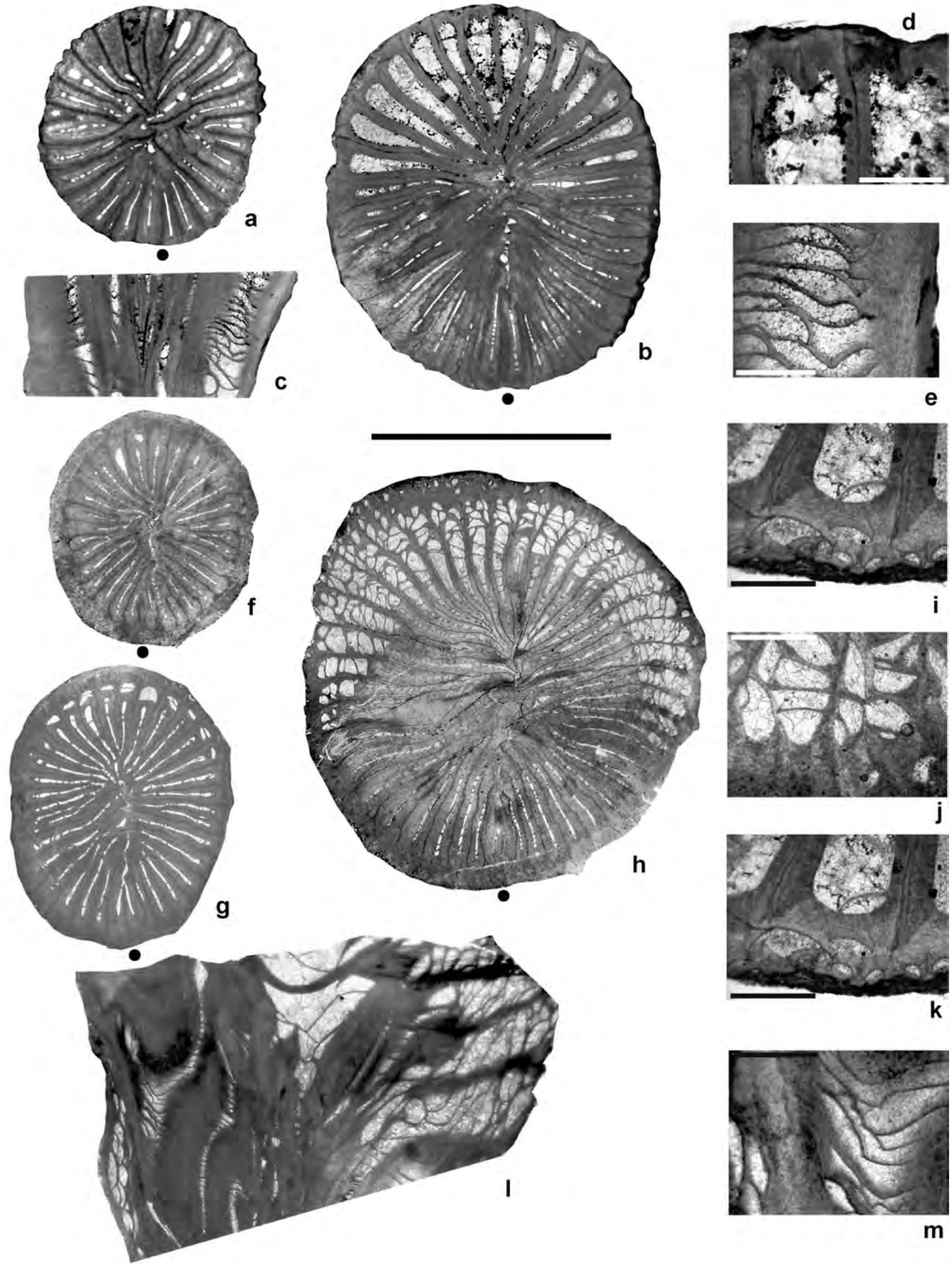

Fig. 12 - a-e) *Merlewoodia* sp. 2. Specimen 2P267/Va-40 in transverse (a-b) and longitudinal (c) sections; detail of transverse section showing minor septa (d) as enlargement of (b); detail of longitudinal section showing densely packed interstitial tabellae (e) as enlargement of (c); Central Quarry, Te (Va) zone. f-m) *Merlewoodia* sp. 1. Specimen 2P267-A/c-1-2 in transverse sections (f-h); details of transverse sections showing minor and major septa, lonsdaleoid dissepiments and naotic structure development (i-k); longitudinal section (l); detail of longitudinal section showing densely packed interstitial tabellae (m) as enlargement of (l); Central Quarry, Tc_2 subzone. Scale bar is 10 mm, except in d, e, i, j, k and m (1 mm).

Keyserlingophyllum Stuckenberg 1895, the presence of which in the Donets Basin was previously indicated (Ogar, 2010), is also illustrated in this paper.

Aulokoninckophyllum Sando, 1976 and *Merlewoodia* Pickett, 1967 were found in the Donets Basin for the first time. The insufficient numbers of specimens do not allow to describe them as new species.

STRATIGRAPHIC DISTRIBUTION AND CORRELATION

The rugose coral species established in the Donets Basin are irregularly distributed in the section (Fig. 13). In the lower part of the Tournaisian only one species, *Conilophyllum priscum,* was found. The correlation of this stratigraphic level has been given earlier (Ogar, 2016).

In the Tc zone twelve species of rugose corals were identified. Large caninoid rugose corals *Siphonophyllia* occur in Tb_2 zone and in Tc_1 subzone. This stratigraphical interval approximately equals the RC2 zone of Belgium. *Keyserlingophyllum* and *Uralinia* occur in the Tc_2 subzone. The rugose corals *Zaphrentites* and *Cyathoclisia soshkinae* are dominant here. This part of the section corresponds to subzones RC3α-β in Belgium (Poty et al., 2006; Denayer et al., 2011) and to the Cherepet horizon of the East European Platform or to the lower part of the Rugose coral zone III (Hecker, 2001).

Only two species, *Caninophyllum tomiense* and *Corphalia simplex,* were found in the Td zone (Fig. 13). The correlation of layers with *Corphalia* was reported earlier (Ogar, 2016).

A new episode of taxon diversity occurs at the top of the Tournaisian, Te (Va) zone, where they are concentrated in a thin stratum of black mudstones interbedded with limestones. *Calmiussiphyllum calmiussi* dominates here. A few specimens belong to the genera *Proheterelasma*, *Caninophyllum*, *Cyathoclisia*, and *Siphonophyllia.* This horizon compares to the rather narrow stratigraphic interval with $RC4\beta_1$ rugose corals subzone in Belgium (Poty et al., 2006; Denayer et al., 2011).

Only one species of *Sychnoelasma* (*S. konincki*) typical of the Tournaisian was found in the Visean basal strata (Vb-c zones) possibly unconformably overlapping the Te (Va) zone sediment.

PALEOENVIRONMENTAL CONDITIONS AND PALEOBIOGEOGRAPHY

The irregular stratigraphic distribution of rugose corals in the Donets Basin is explained by a complex combination of regional and global factors that influenced the paleogeographic position and changes in the conditions of the sedimentation. They were the main constraints on the existence and migration of rugose corals. The beginning of the Tournaisian in the Donets Basin was marked by a significant shallowing caused by the global Hangenberg event, corresponding to a sea-level fall and marked by a stratigraphic gap. With the deepening of the basin paleogeographic relations arose with other basins, as recorded by the occurrence of *Conilophyllum*. This stratigraphic level roughly corresponds to the boundary 1 to 2 of the third-order sequences of the Belgian Dinantian (Denayer et al., 2011; Poty, 2016) (Fig. 13). The middle of the Tournaisian time was marked by a maximum transgression. An extensive shallow shelf was located within the Donets Basin, in which large caninoid rugoses inhabited, as in many other regions of the Paleotethys. The maximum deepening of the basin occurs during the second half of the Tc interval when black limestones with numerous *Zaphrentites* and *Cyathoclisia soshkinae* were formed. This level corresponds to the boundary of 2 to 3 sequences. A gradual shallowing of the basin ended with a short gap that occurred during Td. Only two species of rugose corals in the Donets Basin were identified and only limited paleogeographic communications with the Kuznetsk Basin, the Urals Ocean and Dinant Basin existed at that time.

The lithology of the Te (Va) zone is sharply different from lithology of other zones. It is characterised by high clay and organic matter content in the rocks. The composition of the rugose coral assemblages indicates unstable conditions in a relatively deep basin. This stratum reflects the global eustatic “Avins event” (Poty, 2007). The subsequent regression and shallowing with discontinuity in the sedimentation corresponds to the sequences 4 to 5 boundary of Belgium (Poty, 2016).

At the beginning of the Visean, shallow-water sedimentation was established in the Donets Basin, which was a gulf in the Paleotethys Ocean. Colonial rugose corals appear in the Donets Basin only from Visean time. The composition of solitary and colonial corals indicates wide paleogeographic relationships with remote basins. The T/V boundary on the Donets Basin is compared with the boundary of sequences 4 to 5 of the Namur-Dinant Basin.

CONCLUSIONS

Many previously unknown solitary rugose corals in the Tournaisian of the Donets Basin have been documented for the first time. Colonial rugose corals appear in this basin only from the early Visean.

Some newly discovered genera, including *Merlewoodia* and *Aulokoninckophyllum*, are very similar to those found earlier in Belgium and surrounding areas and should be described as new species in accordance with the results of joint studies. They are possibly relevant for further phylogenetic and paleogeographic reconstructions.

The composition of corals assemblages indicates wide paleobiogeographic relationship between the shelf seas of the Paleoasiatic, Paleotethys, Ural and Rheic oceans in separate episodes of Tournaisian time.

Significant changes in the composition of coral fauna near the Tournaisian - Visean boundary of the Donets Basin are considered as a result of a global “Avins event.”

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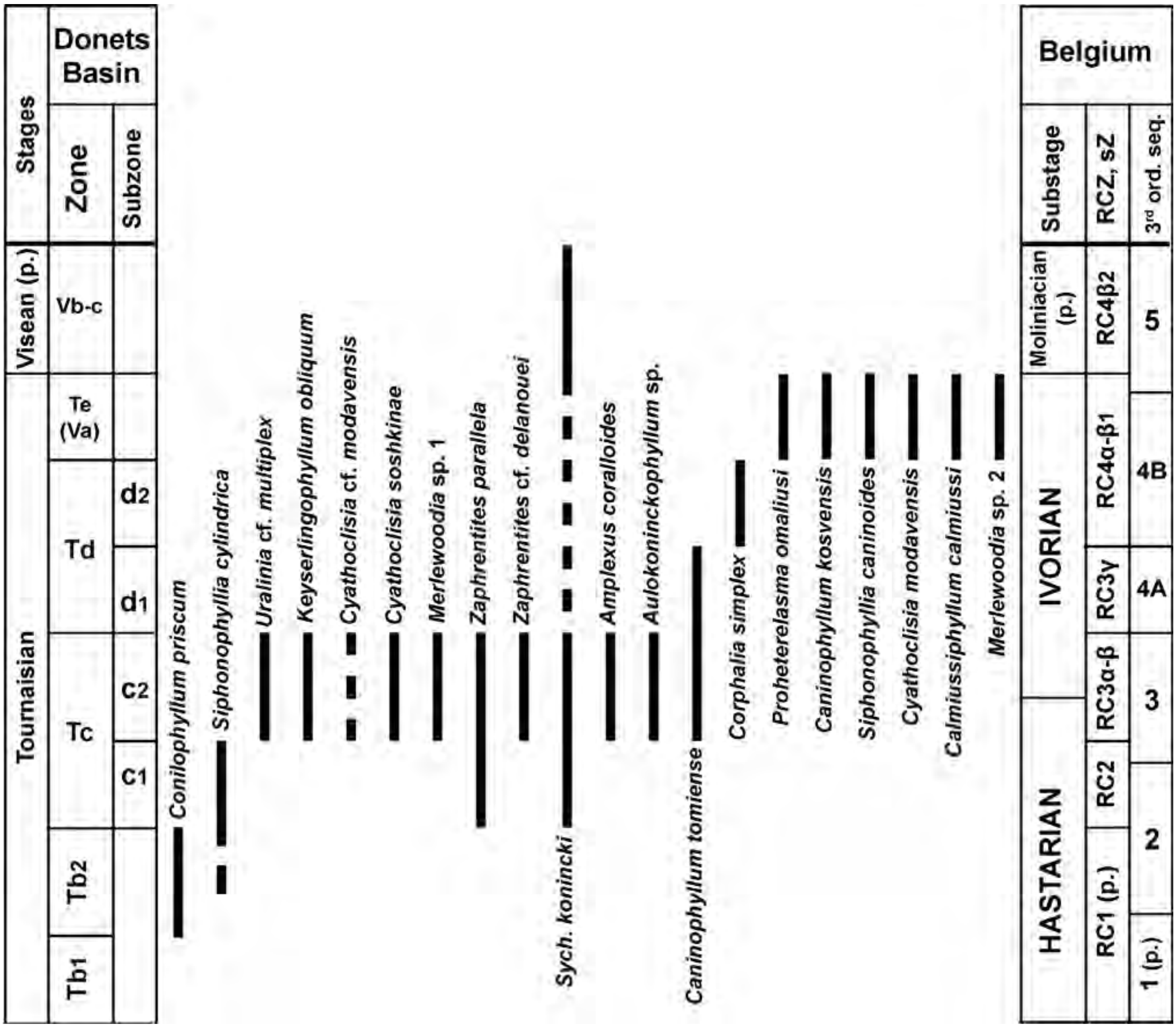

Fig. 13 - Stratigraphical distribution of rugose corals in the Tournaisian of the Donets Basin. Stratigraphic frameworks: Donets Basin (Poletaev et al., 2011; Gozhyk, 2013); Belgian Namur-Dinant Basin (Poty, 2016); 3rd ord. seq. = third-order sequences; RCZ, sZ = Rugose coral zones and subzones.

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REFERENCES

Aizenverg D.E., Lagutina V.V., Levenshtein M.L. & Popov V.S. (1975). Field excursion guidebook for the Donets Basin. VIII International Congress on Carboniferous Stratigraphy and Geology, 306 pp. Nauka, Moscow. [in Russian and English]

Aretz M. & Corradini C. (2019). The redefinition of the Devonian/Carboniferous Boundary: state of the art. *In* Hartenfels S., Herbig H.-G., Amler M.R.W. & Aretz M. (eds), Abstracts, 19th International Congress on the Carboniferous and Permian, Cologne, July 29 - August 2, 2019. *Kölner Forum für Geologie und Paläontologie*, 23: 31-32.

Carruthers R.G. (1909). Notes on corals. *In* Lee G.W. (ed.), A Carboniferous fauna from Novaja Semlja, collected by W. S. Bruce. *Royal Society of Edinburgh Transactions*, 47: 143-186.

Carruthers R.G. (1910). On the evolution of *Zaphrentis delanouei* in lower Carboniferous times. *Quarterly Journal of the Geological Society of London*, 64: 523-538.

Chapman E.J. (1893). On the corals and coralliform types of Paleozoic strata. *Proceedings and Transactions of the Royal Society of Canada,* 10: 39-48.

Chi Y.S. (1935). Additional fossil corals from the Weiningian limestone of Hunan, Yunnan and the Kwangsi provinces, in SW China. *Palaeontologia Sinica*, *B*, 12: 1-38.

Chwieduk E. (2005). Late Devonian and early Carboniferous Rugosa from Western Pomerania, northern Poland. *Acta Geologica Polonica*, 55: 393-443.

Cotton G. (1973). The Rugose Coral Genera. 358 pp. Elsevier, Amsterdam.

Degtjarev D.D. (1972). Suborder Caniniina. *In* Goryainov V.B., Degtjarev D.D., Zhavoronkova Z.A. & Kaplan A.A. (eds), Novye vidy odinochnykh korallov Rugosa of USSR. Moscow, Nauka: 105-106. [in Russian]

Degtjarev D.D. (1973). Distribution of corals in the Lower Carboniferous section of the Urals. *Trudy Instituta geologii i* *geokhimii Ural'skogo Nauchnogo Tsentra AN SSSR*, 82: 206-228. [in Russian]

De Koninck L.-G. (1872). Nouvelles recherches sur les animaux fossiles du terrain carbonifère de la Belgique. *Mémoire de l'Academie des Sciences du Belgique,* 39: 1-78.

Denayer J. (2014). Taxonomy, Biostratigraphy and Palaeobiogeography of the Late Tournaisian rugose corals of north-western Turkey. *Paläontologische Zeitschrift,* 89: 313-333.

Denayer J. (2015). Rugose corals at the Tournaisian-Viséan transition in the Central Taurides (S Turkey) - Palaeobiogeography and palaeoceanography of the Asian Gondwana margin. *Journal of Asian Earth Sciences*, 98: 371-398.

Denayer J., Poty E. & Aretz M. (2011). Uppermost Devonian and Dinantian rugose corals from Southern Belgium and surrounding areas. *In* Aretz M. & Poty E. (eds), 11th International Symposium on Fossil Cnidaria and Porifera, Liège, 2011, Field Guide. *Kölner Forum für Geologie und Palaöntologie*, 20: 151-201.

Devuyst F.X., Hance L., Hou H.-F., Wu X., Tian S., Coen M. & Sevastopulo G. (2003). A proposed Global Stratotype Section and Point for the base of the Visean Stage (Carboniferous): the Pengchong section, Guangxi, South China. *Episodes*, 26: 105-115.

Dingwall J. 1926. *Cyathoclisia*, a new genus of Carboniferous coral. *Quarterly Journal of the Geological Society of London*, 82: 12-21.

Dobrolyubova T.A & Kabakovitch N.V. (1966). Rugose corals from Lower Carboniferous of Kuznetsk Basin. *Trudy Paleontologicheskogo Instituta Akademiya Nauk SSSR,* 111: 7-203. [in Russian]

Dybowski W.N. (1873). Monographie der Zoantharia Sclerodermata Rugosa aus der Silurformation Estlands, Nord-Livland und der Insel Gotland. *Archiv für Naturkunde der Livlands-Estlands, Kurlands*, 5: 257-414.

Flügel H. (1963). Korallen aus der oberen Vise-Stufe (Kueichouphyllum-zone) Nord-Irans. *Jahrbuch der Geologischen Bundesanstalt,* 106: 365-404.

Flügel H. (1991). Rugosa aus dem Karbon der Ozbak-Kuh-Gruppe Ost-Iran. *Jahrbuch der Geologischen Bundesanstalt,* 134: 657-688.

Fomichev V.D. (1931). New data on Lower Carboniferous corals of the Kuznetsk Basin. *Transactions of the Geological and Prospecting Service of USSR*, 49: 1-80. [in Russian]

Fomichev V.D. (1953). Rugose corals and stratigraphy of Middle and Upper Carboniferous and Permian deposits of the Donets Basin. *Trudy VSEGEI*, 662 pp. Gosgeolizdat, Moscow. [in Russian]

Gabunia K.E. (1919). Materials on corals fauna from Lower Carboniferous deposits near v. Rojki along R. Tom'. *Izvestia Sibirskogo Nauchno-Issledovatelskogo Instituta Geologii, Geofiziki i Mineralnogo Syr'ya*, 1: 1-48. [in Russian]

Gorsky I.I. (1935). Some Coelenterata from the Lower Carboniferous beds of the Nowaya Zemlya. *Transactions of the Arctic Institute*, 28: 6-122. [in Russian]

Gorsky I.I., Degtyarev D.D., Katchanov E.I., Rakshyn P. & Simakova M.A. (1975). Tetracoralla (Rugosa). *In* Stephanov D.L., Krylova A.K., Gorozdilova L.P., Pozner V.M. & Soultanaev A.A. (eds), Paleontologitcheskiy Atlas Kamennougol'nykh Otlozheniy Urala. Nedra, Leningrad: 73-89. [in Russian]

Gozhyk P.F., ed. (2013). Stratigraphy of Upper Proterozoic and Phanerozoic of Ukraine. 1. Stratigraphy of Upper Proterozoic, Paleozoic and Mesozoic of Ukraine. 637 pp. National Academy of Sciences of Ukraine, Institute of Geological Sciences; Kyiv. [in Ukrainian]

Grabau A.W. (1928). Palaeozoic corals of China: part 1, Tetraseptata, second contribution. *Acta Palaeontologica Sinica*, 2: 1-175.

Hecker M. (2001). Lower Carboniferous (Dinantian and Serpukhovian) rugose coral zonation of East European Platform and Urals, and correlation with Western Europe. *Bulletin of the Tohoku University Museum*, 1: 298-310.

Heravi M.A. & Khaksar K. (1999). An assemblage of corals of Iran. *Geological Survey of Iran, Mahshad*: 357.

Hill D. (1938-1941). A monograph on the Carboniferous rugose corals of Scotland. *Palaeontographical Society*, 91, 92, 94: 1-204.

Hill D. (1973). Lower Carboniferous Corals. *In* Hallam A. (ed.), Atlas of Palaeobiogeography. Elsevier Scientific Publishing Company: 133-142.

Hill D. (1981). Coelenterata; supplement 1, Rugosa and Tabulata. *In* Teichert C. (ed.), Treatise on Invertebrate Paleontology. 762 pp. The Geological Society of America and the University of Kansas, Boulder, Colorado, Lawrence, Kansas.

Hudson R.G.S. (1941). On the Carboniferous corals: *Zaphrentis carruthersi* sp. nov. from the Mirk Fell Beds and its relation to the *Z. delanouei* species-group. *Proceedings of the Yorkshire Geological Society,* 24: 290-311.

Ilina T.G. (1970). Some new Permian Rugosa from South-eastern Pamir. *In* Astrova G.G. & Chudinova I.I. (eds), New species of Paleozoic bryozoans and corals, Nauka, Moscow: 146-151. [in Russian]

Ivanowski A.B. (1967). Etyudy o rannekamennougolnykh rugozakh. 97 pp. Nauka, Moscow. [in Russian]

Ivanowski A.B. (1987). Rugosy opisannye A. A. Stukenbergom (1888-1905). 45 pp. Nauka, Moscow. [in Russian]

Keyserling A. von (1846). Geognostische Beobachtungenin. Wissenschaftliche Beobachtungen auf einer Reise in das Petschora-Land im Jahre 1843, St.-Petersburg: 149-336.

Kora M. & Jux U. (1986). On the early Carboniferous macrofauna from the Um Bogma Formation, Sinai. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 2: 85-98.

Lang W.D., Smith S. & Thomas H.D. (1940). Index of Palaeozoic Coral Genera. 231 pp. British Museum of Natural History, London.

Lewis H.P. (1927). *Caninia cylindrica* Scouler and other large Caninias from the Carboniferous Limestone of Ireland. *Scientific Proceedings of the Royal Dublin Society*, 30: 373-382.

Lewis H.P. (1929). On the Avonian Coral *Caninophyllum*, gen. nov. and *C. archiaci* (Edwards and Haime). *Annals and Magazine of Natural History*, 10: 456-468.

Ludwig R. (1862). Zur Palaeontologie des Urals: Actinozoen und Bryozoen aus dem Carbon-Kalkstein im Gouvernement Perm. *Palaeontographica,* 10: 179-226.

Ludwig R. (1865). Corallen aus palaolithischen Formationen. *Palaeontographica*, 14: 133-172.

McCoy F. (1844). A Synopsis of the Characters of the Carboniferous Limestone Fossils of Ireland. 207 pp. University Press, Dublin.

Michelin H. (1841-1848). Iconographie zoophytologique, description par localités et terrains des Polypiers fossiles de France et pays environnants. 348 pp. Fain et Thunot, Paris.

Milne-Edwards H. & Haime J. (1850-1855). A monograph of the British corals. *Palaeontographical Society of London*, Monograph, part. 1 (1850), 1-71, part. 2 (1852), 147-210, part. 3 (1853), 211-244, part. 4 (1855): 245-299.

Mitchell M. (1981). The distribution of Tournaisian and early Visean (Carboniferous) coral faunas from the Bristol and South Wales area of Britain. *Acta Palaeontologica Polonica*, 25: 577-585.

Mitchell M. & Somerville I.D. (1988): A new species of *Sychnoelasma* (Rugosa) from the Dinantian of the British Isles: its phylogeny and biostratigraphical significance. *Proceedings of the Yorkshire Geological Society*, 47: 155-162.

Mitchell M., Strank A.R.E., Thornbury B.M. & Sevastopulo G. (1986). The distribution of platform conodonts, corals and foraminifera from the Black Rock Limestone (late Tournaisian and early Visean) of Tears Point, Gower, South Wales. *Proceedings of the Yorkshire Geological Society*, 46: 11-14.

Münster G. (1840). Die Versteinerungen des Uebergangkalkes mit Clymenien und Orthoceratiten von Oberfranken. *Beiträge zur Petrefacten-Kunde*, Bayreuth, 3: 33-121.

Ogar V. (2010). New data on the Carboniferous corals of the Donets Basin. *In* Kossovaya O. & Somerville I. (eds), 10th International

Symposium on Fossil Cnidaria and Porifera, Saint-Petersburg, 2007. *Palaeoworld*, 19: 284-293.

Ogar V.V. (2016). New Rugose corals and refinements of the Tournaisian biostratigraphy of the Donets Basin (Ukraine). *Geologica Belgica*, 19: 21-28.

Papoyan A.S. & Tchudiniva I.I. (1974). Coral polyps. *In* Akopyan V.T. (ed.), Atlas of fossil fauna of the Armenian SSR. Yerevan, Academy of Sciences of the Armenian SSR: 69-76.

Perna A.Y. (1923). Rugose corals from the Lower Carboniferous on the southern slope of the South Urals. *Trudy Geologicheskjgo Komiteta, Novaya seria*, 175: 3-34. [in Russian]

Pickett J. (1967). Lower Carboniferous coral faunas from the New England District of New South Wales. *Memoirs of the Geological Survey of New South Wales, Palaeontology*, 15 (1966): 1-38.

Poletaev V.I., Brazhnikova N.E., Vasilyuk N.P. & Vdovenko M.V. (1990). Local zones and major Lower Carboniferous biostratigraphic boundaries of the Donets Basin (Donbass), Ukraine. U.S.S.R. *Courier Forschungsinstitut Senckenberg,* 130: 47-59.

Poletaev V.I., Vdovenko M.V., Shchoglev O.K., Boyarina N.I. & Makarov I.A. (2011). The stratotypes of the regional subdivisions of Carboniferous and Lower Permian Don-Dnieper Depression and their biostratigraphy, 236 pp. Logos, Kyiv. [in Ukrainian]

Poty E. (1981). Recherches sur les Tétracoralliaires et les Hétérocoralliaires du Viséen de la Belgique. *Mededelingen Rijks Geologische Dienst*, 35: 1-161.

Poty E. (2002). Interstitial tabellae: a new type of tabellae developed between highly thickened septa in Rugosa. *Coral Research Bulletin*, 7: 167-173.

Poty E. (2007). The Avins event: a remarkable worldwide spread of corals at the end of the Tournaisian (Lower Carboniferous). *In* Hubmann B. & Piller W.E. (eds), Fossil Corals and Sponges. Proceedings of the 9th International Symposium on Fossil Cnidaria and Porifera, Graz, 2003. Schriftenreihe der Erdwissenschaftlichen Kommissionen. *Österreichische Akademie der Wissenschaften*, 17: 231-249.

Poty E. (2016). The Dinantian (Mississippian) succession of southern Belgium and surrounding areas: stratigraphy improvement and inferred climate reconstruction. *Geologica Belgica*, 19: 177-200.

Poty E. & Boland K. (1994). Révision des Tétracoralliaires Caninomorphes de l'Hastatien (Tournaisien) Belge. *Annales de la Société Géologique de Belgique*, 117: 221-225.

Poty, E., Devuyst F.-X. & Hance L. (2006). Upper Devonian and Mississippian foraminiferal and rugose coral zonations of Belgium and northern France: a tool for Eurasian correlations. *Geological Magazine*, 143: 829-857.

Poty E. & Hanney D. (1994). Stratigraphy of Rugose corals in the Dinantian of the Boulonnais (France). *Mémoires Institut Géologique de l'Université Catholique de Louvain*, 35: 51-82.

Poty E. & Onoprienko Y. (1984). Rugose corals. *In* Shilo N.A., Bouckaert J., Afanasieva M.J.M., Bless M.J.M., Conil R., Erlanger O.A., Gagiev M.H., Lazarev S.S., Onoprienko Y., Poty E., Razina T.P., Simakov K.V., Smirnova L.V., Streel M. & Swennen R. (eds), Sedimentological and Palaeontological Atlas of the Late Famennian and Tournaisian Deposits in the Omolon Region (NE USSR). *Annales de la Société géologique de Belgique,* 107: 200-213.

Poty E. & Xu S. (1996). Rugosa from the Devonian-Carboniferous transition in Hunan, China. *Mémoires de l'Institut de Géologie de l'Université de Louvain,* 36: 89-139.

Salée A. (1913). Contribution à l'étude des Polypiers du Calcaire Carbonifère de la Belgique, II, Le groupe des Clisiophyllides. *Mémoires de l'Institut de Géologie de l'Université de Louvain,* 1: 179-293.

Sando W. J. (1976). Revision of the Carboniferous genus *Aulina* Smith (Coelenterata, Anthozoa). *U.S. Geological Survey Research Journal*, 4: 421-435.

Sayutina T.A. (1970). On the variability of some Clisiophyllid corals (Rugosa). *Paleontolojischeskiy Zhurnal*, 2: 33-42. [in Russian]

Sayutina T.A. (1973). Lower Carboniferous corals from the Northern Urals, suborder Acrophyllina. *Akademiya Nauk SSR, Trudy Paleontologicheskogo instituta*, 140: 1-168. [in Russian]

Sayutina T.A. (1976). On the genus *Sychnoelasma* from Lower Carboniferous of Northern Urals. *Byuletin Moskovskogo obschestva ispytatelej Prirody, Otdel Geologicheskiy,* 51: 111-123. [in Russian]

Sibly T.F. (1906). On the Carboniferous Limestone (Avonian) of the Mendip Area (Somerset) with special reference to the palaeontological sequence. *Quarterly Journal of the Geological Society of London*, 62: 324-380.

Simakova M.A, Degtjarev D.D. & Rakshyn P.P. (1978). Rugose corals. *In* Key sections and fauna from the Visean and Namurian of the Middle and Southern Urals. Leningrad, Nedra: 65-74. [in Russian]

Smith S. & Thomas H.D. (1963). On *Amplexus coralloides* Sowerby and some Ampleximorph corals from the English Devonian. *Annals and Magazine of Natural History,* 13: 161-172.

Somerville I.D. (1994). Early Carboniferous rugose coral assemblages from the Dublin Basin, Ireland: possible bathymetric and palaeoecologic indicators. *Courier Forschungsinstitut Senckenberg,* 172: 223-229.

Somerville I.D. & Jones G.L. (1985). The Courceyan stratigraphy of Pallaskenry borehole, County Limerick, Ireland. *Geological Journal,* 20: 377-400.

Somerville I.D., Mitchell M. & Strank A.R.E. (1986). An Arundian fauna from Dyserth area, North Wales and its correlation within the British Isles. *Proceedings of the Yorkshire Geological Society*, 46: 57-75.

Somerville I.D., Rodríguez S. & Said I. (2016). Carboniferous aulate corals from Azrou-Khenifra Basin (Morocco): Distribution and phylogenetic relationships. *Geobios*, 49: 303-307.

Soshkina E.D. (1960). Turneyskie korally Rugosa i ikh vzaimootnosheniya s devonskimi. *Akademiya Nauk SSSR, Sbornik trudov po geologii i paleontologii, Syktyvkar*: 273-339. [in Russian]

Sowerby J. (1812-1814). The mineral conchyology of Great Britain. 1. 234 pp. B. Meredith [etc.], London.

Spassky N.I. (1974). Dialekticheskoe yedinstvo prostranstvenno-vremennykh zakonomernostey evolyutzii (na primere chetyrekhluchevykh korallov. *Zapiski Leningradskogo Gornogo Instituta*, 67: 127-135. [in Russian]

Stuckenberg A.A. (1895) Corals and bryozoans of the Carboniferous deposits of the Urals and Timan. *Trudy Geologicheskogo komiteta*, 5: 1-44. [in Russian]

Tolmatchev I.P. (1924-1931). Lower Carboniferous fauna of the Kuztetsk coal basin. Geologicheskij Komitet. *Materialy po Obschei i Prikladnoi Geologii*, 25: 1-663. [in Russian]

Vassiljuk N.P. (l959). New Tetracorals from the Lower Carboniferous of the Donets Basin. *Paleontological Journal*, 4: 85-88. [in Russian].

Vassiljuk N.P. (1960). Lower Carboniferous corals of the Donets Basin. *Trudy Instituta Geologicheskikh Nauk. Seria Stratigrafia i Paleontologia, Akademiya Nauk Ukrainskoi SSR*, 13: 1-179. [in Russian]

Vaughan A. (1906). The Carboniferous Limestone series (Avonian) of the Avon Gorge. *Proceedings of the Bristol Naturalists' Society*, 4: 73-166.

Verrill A.E. (1865). Classification of polyps (Extract condensed from a synopsis of the polypi of the North Pacific Exploring Expedition, under captains Ringgold and Rogers, U.S.N.). *Proceedings of the Essex Institute*, 4: 145-149.

Volkova M.S. (1941). Lower Carboniferous corals from Central Kazakhstan. *Materials on the Geology and Useful Minerals of Kazakhstan*, 11: 1-120. [in Russian and English]

Von Schouppé A. (1970). Lower Carboniferous corals from Badakhshan (North-East Afghanistan). *In* Desio A. (ed.), Italian Expedition to the Karakorum and Hindu-Kush. Scientific

Reports - IV Palaeontology, Zoology, Botany: Fossils of the North-East Afghanistan, 2: 1-23.

Vuillemin C. (1990). Les Tétracoralliaires (Rugosa) du Carbonifère Inférieur du Massif Armoricain (France). Cahiers de Paléontologie, 20. 171 pp. Muséum national d'Histoire naturelle, Paris.

Wang H.C. (1950). A revision of Zoantharia Rugosa in the light of their minute skeletal structures. *Philosophical Transactions of the Royal Society of London,* 611: 175-246.

Webb G.E. (1990). Lower Carboniferous coral fauna of the Rockhampton Group, East-Central Queensland. *Memoirs of the Association of Australasian Palaeontologists,* 10: 1-167.

Wedekind R. (1927). Die Zoantharia Rugosa von Gotland (bes. Nordgotland). Nebst Bemerkungen zur Biostratigraphie des Gotlandium. *Sveriges Geologiska Undersökning*, 19: 1-94.

Weyer D. (1993). Korallen aus dem Obertournai und Untervisé des Inseln Hiddensee und Rügen. *Abhandlungen und Berichte für Naturkunde*, 16: 31-69.

Weyer D. (2006). *Cyathoclisia* Dingwall 1926 (Anthozoa, Rugosa) im Unterkarbon des Rheinischen Schiefergebirges. *Abhandlungen und Berichte für Naturkunde*, 29: 23-71.

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New data on the Serpukhovian (Carboniferous) coral assemblages from the northwestern part of the Moscow Basin (Russia)

Ian D. Somerville, Olga L. Kossovaya, Sergio Rodríguez* & Pedro Cózar

I.D. Somerville, UCD School of Earth Sciences, University College Dublin, Belfield, Dublin 4, Ireland; ian.somerville@ucd.ie
O.L. Kossovaya, All-Russian Geological Survey Institute VSEGEI, Srednyy Prospect 74, R-199026 St. Petersburg, Russia; Kremlyovskaya St. 18, Kazan, Republic of Tatarstan, Russia, 420008; Olga_Kossovaya@vsegei.ru
S. Rodríguez, Departamento de Paleontología, Universidad Complutense de Madrid, c/ José Antonio Nováis 12, Ciudad Universitaria, E-28040 Madrid, Spain; Instituto de Geociencias (CSIC-UCM), c/ Severo Ochoa 7, Ciudad Universitaria, E-28040 Madrid, Spain; sergrodr@ucm.es *corresponding author*
P. Cózar, Instituto de Geociencias (CSIC-UCM), c/ Severo Ochoa 7, Ciudad Universitaria, E-28040 Madrid, Spain; p.cozar@igeo.ucm-csic.es

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ABSTRACT - Research in two quarries of the Borovichi area near the Uglovka town (northwestern Moscow Basin) has provided several rugose and tabulate corals that improve the knowledge on the palaeontology of that area. The Zarech'e quarry yielded rare specimens of Syringopora reticulata *and* Dibunophyllum bipartitum*, as well as common specimens of* Actinocyathus floriformis*,* A. borealis *and* A. crassiconus*. The Uglovka quarry provided also* Syringopora reticulata*,* Dibunophyllum bipartitum *but different species of colonial rugosans:* Actinocyathus *sp.,* Lonsdaleia multiseptata *and* Schoenophyllum *sp. The palaeogeographical distribution of the recorded species indicates a good communication of the Eastern European Basin with western and eastern Palaeotethys during the Serpukhovian. The presence of the genus* Schoenophyllum *suggests also connection with North America, probably along the northern coast of Laurussia.*

INTRODUCTION

Mississippian rocks are well exposed in the northwestern part of the Moscow Basin. During the first half of the 20th century, many geologists worked on those rocks and described local sections (Yanishevsky, 1936; Hecker, 1938b; Sokolov, 1944) or undertook regional works (Forsch, 1935; Yanishevsky, 1937; Hecker, 1938a; Sokolov, 1941). The stratigraphy and sedimentology of the Mississippian from that area was simultaneously studied and the facies and cyclicity of the deposits were identified (Bruns, 1939).

The Serpukhovian Stage is widely represented in that region and is documented by three lithostratigraphic units: the Rovnoe Formation (Tarusian Regional Stage), the Poneretka Formation (Steshevian Regional Stage) and the Uglovka Formation (Protvian Regional Stage). Palaeontological studies allowed the identification of the fossil assemblages of that age (Mikhailov, 1939; Sokolov, 1939b; Ganelina, 1951, 1956; Pozner, 1951; Shlykova, 1951; Yanishevsky, 1954, 1960; Vostokova, 1955). Coral assemblages from those units have been largely known since that time (Stuckenberg, 1904; Karaeva, 1935; Sokolov, 1939a; Dobrolyubova, 1958), but their knowledge was improved with the more recent taxonomic works of Hecker (1997, 2001, 2002, 2010), Poty & Hecker (2003) and Savitsky et al. (2007).

New research in two quarries in the Borovichi area, whose coral record has not been previously studied in detail, has provided several rugose and tabulate corals, as well as chaetetids, that improve the knowledge on the regional palaeontology. Chaetetids from Uglovka quarry were figured by Sokolov (1950, pl. XVIII, figs 3-4).

The Zarech'e quarry is located 7.8 km south-west from Uglovka town (Fig. 1) and contains marly limestones belonging to the upper part of the Poneretka Formation. The coral assemblage from that quarry shows a low diversity. It is composed of rare specimens of the tabulate genus *Syringopora* and the solitary rugosan *Dibunophyllum bipartitum* (McCoy, 1849) and common specimens of the colonial rugosan genus *Actinocyathus.* Within the last genus, there are representatives of two different species groups, *A. floriformis* (Martin, 1809) and *A. crassiconus* (McCoy, 1849).

The Uglovka quarry is located 4 km south-east of Uglovka town (Fig. 1) and contains limestones and dolostones belonging to the Uglovka Formation that provided corals from two different beds (Fig. 2, units 2 and 6). Previous sampling in that quarry (Savitsky et al., 2007, 2015) yielded *Corwenia densivesiculosa* Dobrolyubova, 1958 in the lower beds. The Uglovka assemblage recorded herein is composed of common tabulate corals belonging to the genus *Syringopora*, rare solitary rugosans of the genus *Dibunophyllum* and frequent colonial rugosans of the genera *Actinocyathus*, *Lonsdaleia* and *Schoenophyllum* in the lower beds and *Syringopora* in the upper beds. Chaetetids are common in both units.

The Zarech'e quarry contains a rich foraminiferal assemblage, with the remarkable occurrence of *Brenckleina rugosa* (Brazhnikova, 1964) and the narrow form of *Eostaffellina paraprotvae* (Rauser-Chernousova, 1948), both suggesting a Serpukhovian age. Samples of the Uglovka quarry contain more evolved assemblages, with common large and rounded forms of *Eostaffellina*, including *E. actuosa* Reitlinger, 1963 and *E. protvaeensis* Gibshman, 2019 which allow to assign the succession to the late Serpukhovian.

CORAL ASSEMBLAGES

All specimens mentioned below are housed in the All-Russian Geological Survey Institute VSEGEI.

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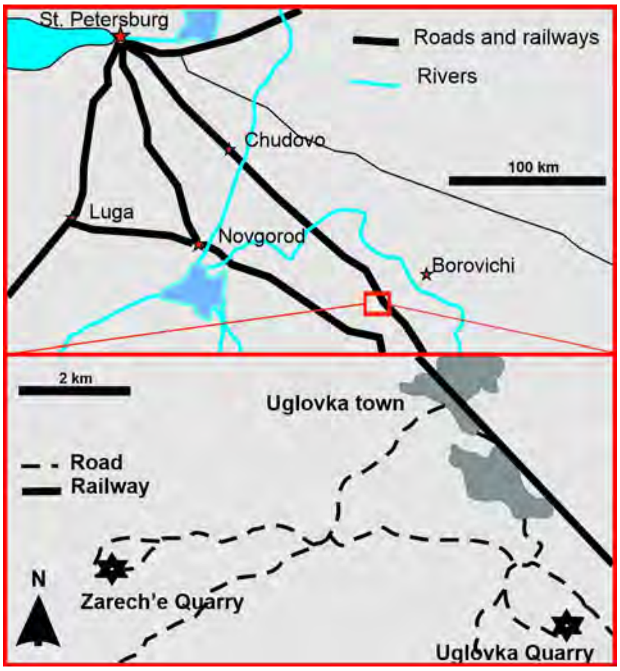

Fig. 1 - (color online) Location map of the studied quarries.

Zarech'e quarry

The assemblage in the Zarech'e quarry is quite impoverished, mainly due to difficult conditions of sampling because of limited accessibility, but also to taphonomic processes. Corals are commonly fragmented and eroded, but large pieces of colonies are preserved.

One single specimen of a solitary coral has been collected (ZAR-14). It is eroded and lacks the apex and part of the calice. Most part of the dissepimentarium is absent by abrasion and the specimen is partly silicified. It belongs to *Dibunophyllum bipartitum* and shows all characteristic features of the species (Fig. 3a).

Three specimens of syringoporoids have been recorded in Zarech'e, from which only one has been sectioned (ZAR-3) because the other two are not well preserved. It is a fragment of a colony and belongs to *Syringopora reticulata* Goldfuss, 1826. The specimen from the Zarech'e quarry, as well as several specimens from that species recorded in the Uglovka quarry (Fig. 3b) have most typical features of the species (axial syrinx, common septal spines, common connecting tubuli and thick lamellar wall, about 0.2-0.25 mm). The diameter of the studied specimens is larger than the typically described (2-2.5 mm against 1.5-2 mm), but no other *Syringopora* species fits with the features of our specimens (Chudinova, 1986; Coronado & Rodríguez, 2014).

Six fragments of colonies belonging to the genus *Actinocyathus* have been recorded in the Zarech'e quarry. Two groups of species of *Actinocyathus* have been distinguished in the Moscow Basin, the *A. crassiconus* group having long minor septa, and the *A. floriformis* group having short or absent minor septa (Hecker, 1997). Both groups are present in Zarech'e. Four specimens have short septa (*A. floriformis* group, ZAR-5, 9, 10, 15). Two of them, ZAR-5 and ZAR-15 bear all diagnostic features of the nominal species (Fig. 3c), but ZAR-9 and ZAR-10 show lower number of septa, smaller tabularium and a smaller and simpler axial structure (Fig. 3d) and belong to *A. borealis* of the same species group (Poty & Hecker, 2003).

Two specimens of massive lonsdaleiinae with long minor septa have been recorded in the Zarech'e quarry. Both can be assigned to *Actinocyathus crassiconus*, based on the long minor septa, 25-27 major septa, tabularium diameter 6-7 mm, 15-20 radial lamellae in the axial structure.

Uglovka quarry

Corals are by far more abundant and slightly more diverse in the Uglovka quarry than in the Zarech'e quarry. Both quarries have some species in common; *Syringopora reticulata* is common, both in units 2 and 6 and *Dibunophyllum bipartitum* which in Uglovka quarry occurs only in unit 2. Seven specimens have been recorded there (UGL2-4, 2-7, 2-12, 2-20, 2-21, 2-22, 2-32B) (Fig. 3a).

In contrast, most colonial lonsdaleiinae are different from the Zarech'e quarry. Four fragments of fasciculate lonsdaleiinae recorded in the Uglovka quarry (UGL2-20, 2-28, 2-31, 2-33) have been identified as *Lonsdaleia multiseptata* Dobrolyubova, 1958 (Fig. 3f). They fit well with all features of the species (about 25-28 septa, well developed minor septa and regular axial structure), but they are slightly smaller than the types described by Dobrolyubova (1958), 9-14 mm against 13-17 mm in tabularium diameter.

Massive lonsdaleiinae are more common, but show poor preservation. Thirteen small fragments of colonies have been recorded (UGL2-8, 2-9, 2-10, 2-13, 2-14, 2-16, 2-18, 2-23, 2-25, UGL9-7, 9-8, 9-10, 9-11) but only four have been sectioned (UGL2-8, 2-10, 2-18, 2-23) (Fig. 3g). Unluckily, all of them show common features that do not fit with any described species. They have short minor septa, which implies that they belong to the species group of *Actinocyathus floriformis*. The axial structure is large and has few radial lamellae (five to ten), and it is similar to *A. lativesiculosus* (of the *A. crassiconus* group), but neither the minor septa nor the dimensions fit with that species. The only species that has comparable dimensions and number of septa is *A. bronni* (Milne-Edwards & Haime, 1851) which has a more complex axial structure, with more radial lamellae and axial tabellae. In addition, none of the cited species fit with the age. The only species registered in the Moscow Basin in the Protvian are *Actinocyathus crassiconus*, *A. gorskyi* (Dobrolyubova, 1958), *A. floriformis*, *A. borealis* (Dobrolyubova, 1958) and *A. ornatus* (Dobrolyubova, 1958) (Hecker, 1997). None of them has similar features to the studied specimens. *A. ornatus* has a similar axial structure, but bears long septa, a smaller size and has fewer septa. Consequently, we leave these specimens in open nomenclature as *Actinocyathus* sp. because the material is not well preserved to erect a new species. But it means that the variety of species in the Serpukhovian from Moscow basin could be higher than known to date.

One single specimen of fasciculate petalaxid coral has been recorded in the Uglovka quarry (Fig. 3h). The sample was collected by E. Poty during a field trip of the X International Symposium on Fossil Cnidaria and Porifera and it was kindly given to one of us (SR). The genus

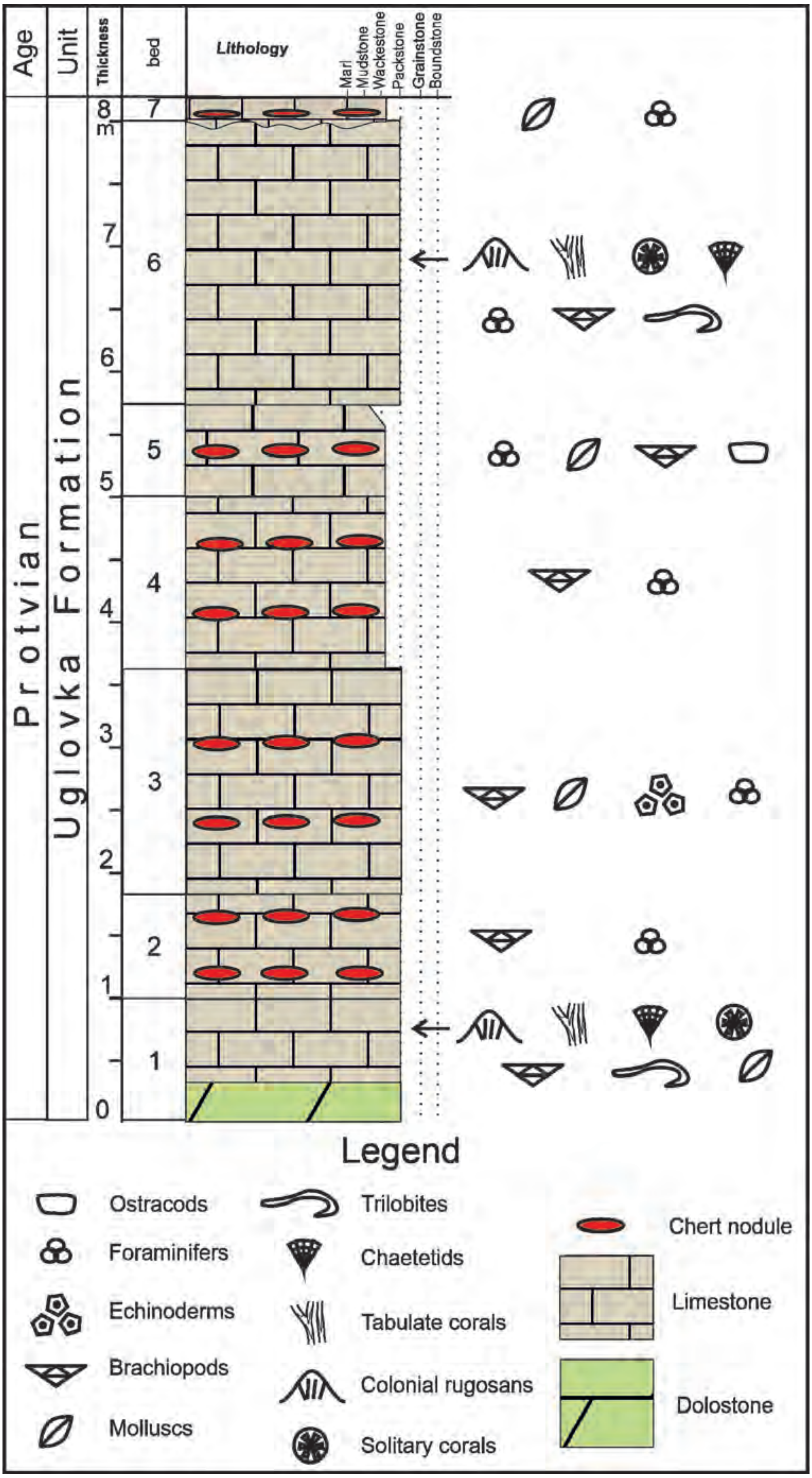

Fig. 2 - (color online) Stratigraphic section at Uglovka quarry (based on Savitsky et al., 2007). The arrows show the location of the samples.

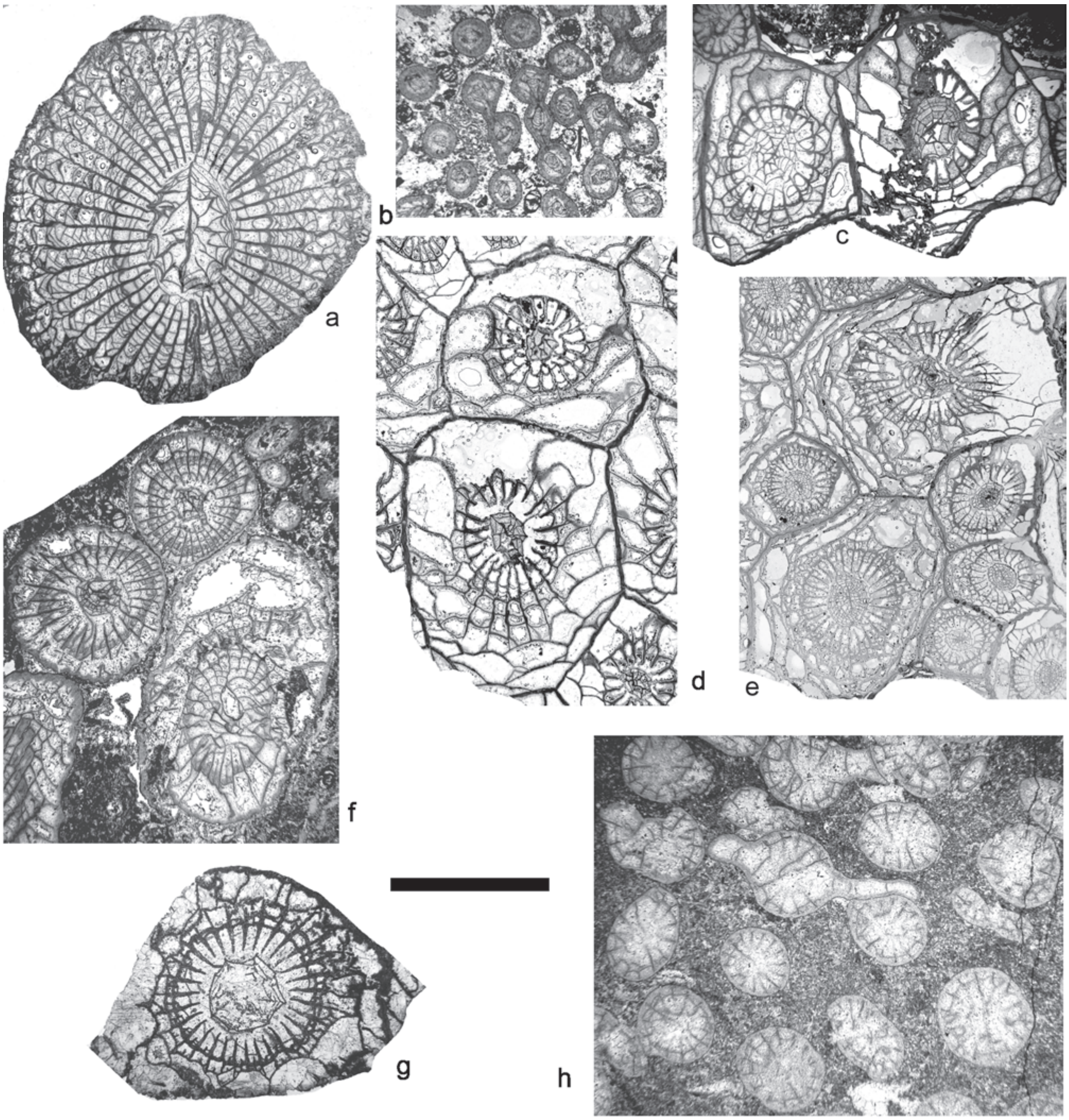

Fig. 3 - Corals recorded in the Zarech'e and Uglovka quarries. a) *Dibunophyllum bipartitum*, specimen UGL2-32B. b) *Syringopora reticulata*, specimen UGL2-29. c) *Actinocyathus floriformis*, specimen ZAR-5. d) *Actinocyathus borealis*, specimen ZAR-10. e) *Actinocyathus crassiconus*, specimen ZAR-7. f) *Lonsdaleia multiseptata*, specimen UGL2-28. g) *Actinocyathus* sp., specimen UGL2-10. h) *Schoenophyllum* sp., specimen UGL2-27. Scale bar is equal to 10 mm.

Schoenophyllum Simpson has been mostly recorded in the uppermost Viséan and Serpukhovian from North America (Bamber et al., 2017). Rodríguez & Bamber (2010) expanded its distribution to the East European Platform when synonymising it with the genus *Paralithostrotion*, which is regarded as a guide fossil for the Serpukhovian in the East European Platform and Urals (Hecker, 2001). Another similar genus, *Tschernowiphyllum* Dobrolyubova was also discussed as being very close to *Schoenophyllum,* but clearly different by the presence of a double elongation of the counter and cardinal septa (Bamber et al., 2017). The specimen from the Uglovka quarry shows several features typical of *Schoenophyllum*, such as fasciculate colonies, thin septa, scarce and irregular dissepiments, complete concave tabulae, irregular axial structure linked to the cardinal septum and lateral increase with unusual offsetting. However, it differs from species of *Paralithostrotion* recorded in the Eastern European Platform (*P. sarmentosa* [Lonsdale, 1845], *P. jermolaevi* Gorsky, 1938 and *P. talkaense* Rakshin, 1965). It shows low development of the axial structure, which is absent in many cases. Some corallites show elongation of the counter septum as well as that of the cardinal septum, showing intermediate features between *Schoenophyllum* and *Tschernowiphyllum*. It could prove the hypothesis of Rakshin that both should be put in synonymy or more simply, that both are closely related and the specimen from Uglovka is a transitional form. As the specimen from Uglovka does not allow to assign it to any known species, and because it is a single fragment of a colony, we leave it in open nomenclature.

DISCUSSION

The assemblage from the Zarech'e quarry is dominated by colonial corals and chaetetids. All the identified species have been previously recorded in the Serpukovian. The depositional environment was a littoral or sublittoral carbonate platform, which coincides with the main environmental requirements of *Actinocyathus crassiconus* (Hecker, 1997).

Dibunophyllum bipartitum is one of the most broadly distributed rugose coral in the upper Viséan and Serpukhovian. It has been widely recorded in the whole Palaeotethys from Japan in the east (Minato & Kato, 1974) to the British Isles and North Africa in the west (Semenoff-Tian-Chansky, 1985; Jones & Somerville, 1996). It has been regarded as a marker of the upper Asbian to Arnsbergian and equivalent regional substages in China (Wang, 1989), in the Urals (Sayutina, 1973), in the Moscow Basin (Altmark, 1978), in Poland (Fedorowski, 1968; Khoa, 1977), in Belgium (Poty, 1994), in Britain (Mitchell, 1989), in France (Perret & Semenoff-Tian-Chansky, 1971), in Spain (Rodríguez et al., 2016) and in North Africa (Aretz, 2011; Said et al., 2013). It has not been recorded outside the Palaeotethys so far in North America or Australia (Fig. 4). However, this species has been also reported in Bashkirian rocks from Arctic Canada (Fedorowski et al., 2012) and Tindouf Basin in North Africa (Rodríguez et al., 2013), where it survived the coral extinctions that occurred during the Serpukhovian. Its maximum geographical expansion took place at the top of the Viséan. So, its occurrence in the Serpukhovian coincides with the declining of the species.

Syringopora reticulata is very common in the Tournaisian-lower Viséan from central and western Palaeotethys (Carruthers, 1910; Gorsky, 1935; Dobrolyubova et al., 1966; Chudinova, 1986; Ogar, 2003), but it has been also cited in the upper Viséan-Serpukhovian from Russia (Sokolov, 1950) and Japan (Minato, 1975) (Fig. 4).

Actinocyathus floriformis is widely distributed in the western and central Palaeotethys. It has been described in the British Isles (McCoy, 1849; Smith, 1916; Hill, 1940; Mitchell, 1989), in Belgium (Poty, 1981), in France (Poty & Hecker, 2003), in Morocco (Rodríguez et al., 2013), in Poland (Khoa, 1977), in the Moscow Basin (Dobrolyubova, 1958; Hecker, 1997), in the Urals and Novya Zemlya (Gorsky, 1938, 1948). It has been also doubtfully mentioned in China (Yü et al., 1983). It appeared in Western Europe in the late Viséan, migrated to eastern basins also in the late Viséan and evolved to several species in the East European Platform during the latest Viséan and Serpukhovian (Hecker, 1997; Poty & Hecker, 2003). It reached its maximum expansion during the Serpukhovian, when it migrated north-east (Urals, Novya Zemlya) and south-west (North Africa) (Fig. 4). It has been recorded previously in the surroundings of the Uglovka town (Dobrolyubova, 1958).

Actinocyathus borealis is a result of the evolution of *A. floriformis* during the Serpukhovian and it is located only

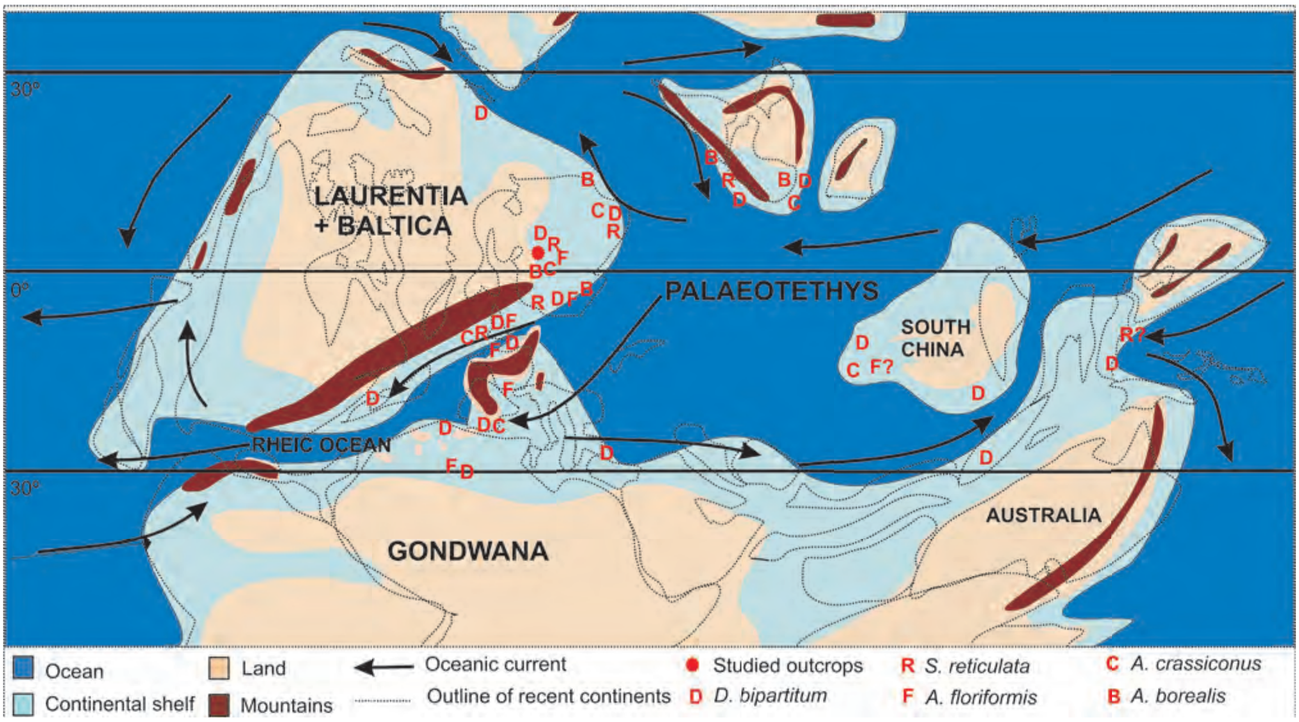

Fig. 4 - (color online) Palaeogeographical distribution of corals recorded in the Zarech'e quarry.

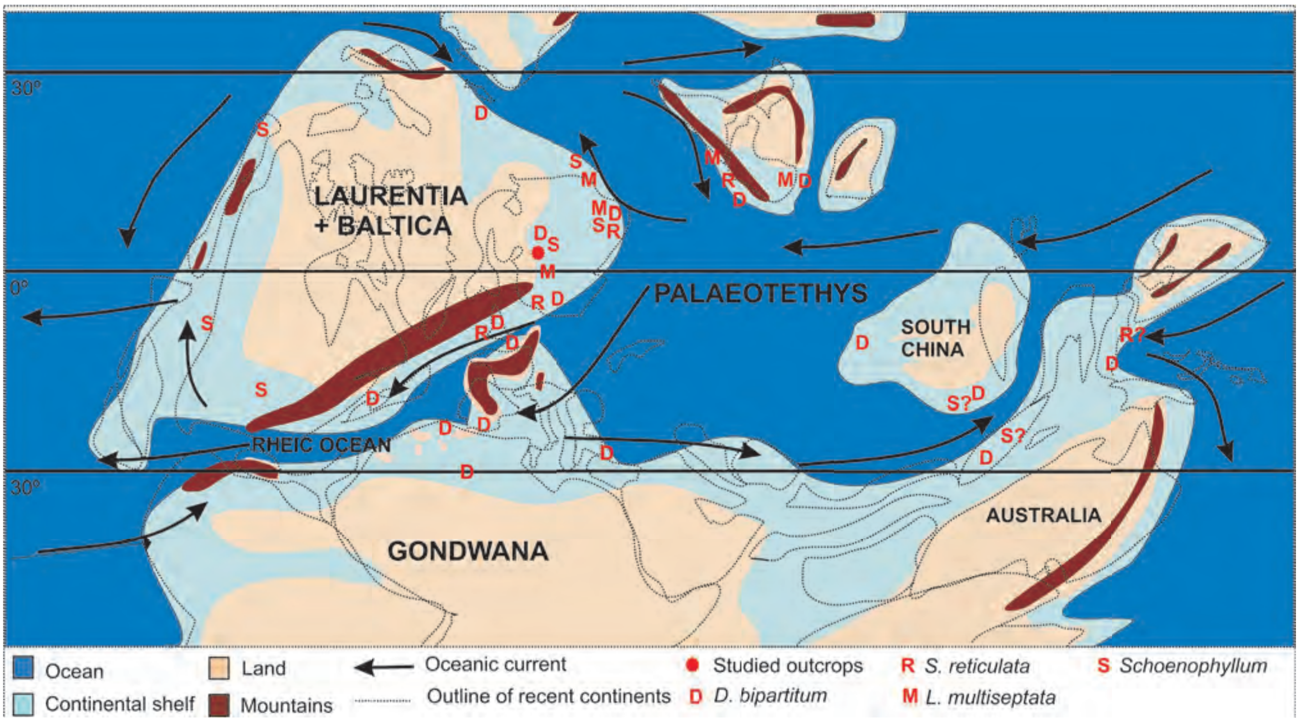

Fig. 5 - (color online) Palaeogeographical distribution of corals recorded in the Uglovka quarry.

in the north-central Palaeotethys, being common in the region of the Msta River (Dobrolyubova, 1958; Savitsky et al., 2007). It reached its maximum abundance during the Steshevian substage.

Actinocyathus crassiconus appeared in the western Palaeotethys during the late Viséan (British Isles; Smith, 1916; Poty & Hecker, 2003) and migrated to the east into the Eastern European Platform, where it evolved to form several closely related species (Hecker, 1997, 2010; Poty & Hecker, 2003) and persisted up to the Protvian substage. It has been also cited in south Spain (Herbig, 1986), Belgium (Conil et al., 1991), Tataria (Altmark, 1975) and China (Fan, 1978).

The palaeogeographical distribution of the species recorded in Zarech'e indicates that the assemblage is typical from the western and central Palaeotethys, and some of the species could also reach the eastern and southern Palaeotethys migrating along the margins of that ocean (Fig. 4).

The assemblage in the Uglovka quarry is dominated by chaetetids and colonial lonsdaleiinae, but solitary corals and tabulates are also common. As the distribution of *Dibunophyllum bipartitum* and *Syringopora reticulata* has been discussed in the Zarech'e assemblage, it is not developed here.

Lonsdaleia multiseptata has been recorded only in the East European Basin (Dobrolyubova, 1958). It has been previously cited in the vicinity of the Uglovka town (Dobrolyubova, 1958).

Several specimens belong to a species previously not described. It is not formally introduced here because of the incompleteness of the recorded specimens.

The genus *Schoenophyllum* has been documented in the Viséan and Serpukhovian from North America (Bamber et al., 2017) and in the Serpukhovian from central Palaeotethys (Gorsky, 1938; Rakshin, 1965). Several species have been described in the Pennsylvanian from China (*Paralithostrotion huanglongense* Yu, 1991; *P. huanjiangense* Xu in Jia et al., 1977; *P. jiangsuense* Yu, 1980; *P. minor* Fan, 1978). All those species show most typical features of the genus, but none of the checked figures show its typical offsetting. It leaves in doubt if the Chinese species belong to another closely related petalaxid. *P. ceriodium* Xu, in Jia et al., 1977 is cerioid and it is not a true *Paralithostrotion*.

The assemblage from Uglovka quarry reveals that at least two species have not been previously described, indicating a certain degree of endemism in the Protvian of the Eastern European Basin. In addition, it confirms that in spite of many years of studies on corals from that region, the variety of species in the Serpukhovian from the Eastern European Basin could be higher than known to date, as pointed out by Hecker (2010), who described two new species of *Actinocyathus* from the southern Moscow Basin.

The palaeogeographical distribution of the species recorded in Uglovka indicates a higher degree of endemism than in the Zarech'e quarry. However, the presence of a petalaxid close to the genus *Schoenophyllum* indicates a palaeogeographic connection with North America. *Schoenophyllum* is recorded in the upper Viséan and Serpukhovian from Mid-Continent, Western Interior and the Rockies (Bamber et al., 2017) and also in the Eastern European Basin (Fig. 5). The migration route should be along the north of Laurentia, because that genus is not recorded in the western and southern Palaeotethys. But the presence of *Schoenophyllum* in lower beds in other areas of the Eastern European Basin (Gorsky, 1938; Rakshin, 1965) indicates that such a migration occurred earlier during the Serpukhovian. The occurrences in eastern Palaeotethys are doubtful (see above), but the communication along the northern and southern coast of the Palaeotethys is proved by the presence of other species (*Syringopora reticulata*, *Dibunophyllum bipartitum*, etc.).

CONCLUSIONS

The study of the coral assemblages from two quarries in the surroundings of the Uglovka village (northwestern Moscow Basin) yielded two different assemblages. The assemblage in the Zarech'e quarry is composed of *Syringopora reticulata*, *Dibunophyllum bipartitum*, *Actinocyathus floriformis*, *A. borealis* and *A. crassiconus.* The assemblage in the Zarech'e quarry is composed of *Syringopora reticulata*, *Dibunophyllum bipartitum, Actinocyathus* sp.*, Lonsdaleia multiseptata* and *Schoenophyllum* sp.

The age of the rocks at the Zarech'e and the Uglovka quarry is Serpukhovian.

The assemblages from both quarries indicate that the degree of endemism increased during the Serpukhovian in the Eastern European Basin. During the sedimentation of the rocks recorded in the Zarech'e quarry there was clear communication with western, southern and eastern Palaeotethys. Later, the increase in endemism indicates that communication was reduced, but still active.

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REFERENCES

Altmark M.S. (1975). Ecological features and living conditions of corals in the early Carboniferous basin of Tataria. *Transactions of the Institute of Geology and Geophysics, Academy of Sciences USSR (Siberian Branch)*, 2: 37-47, 124-129, 180-194. [in Russian]

Altmark M.S. (1978). The significance of corals in the correlation of sections from the Lower Carboniferous. *The Stratigraphy and Paleontology of the Eastern Part of the Russian Platform.* Kazan University Publishers, Kazan: 113-118. [in Russian]

Aretz M. (2011). Corals from the Carboniferous of the central Sahara (Algeria): the collection "Marie Legrand-Blain". *Geodiversitas*, 33: 581-624.

Bamber E.W., Rodríguez S., Richards B.C. & Mamet B.L. (2017). Uppermost Viséan and Serpukhovian (Mississippian) rugose corals and biostratigraphy, Canadian Cordillera. *Palaeontographica Canadiana*, 36: 1-169.

Brazhnikova N.E. (1964). On the study of *Eosigmoilina* from the Lower Carboniferous of the Greater Donets Basin. *In* Material on the Upper Palaeozoic Fauna of the Donets Basin. A*kademiya Nauk Ukrainskoi SSR, Trudy Instituta Geologicheskikh Nauk, Seriya Stratigrafii i Paleontologii*, 48: 3-15. [in Russian]

Bruns E.P. (1935). The lithology of the sandy-clay unit of C_1^{hn} of Borovichi district. *Izvestia Leningrad geologo-gidrogeodezich tresta*, 2-3: 52-64. [in Russian]

Carruthers R.G. (1910). On the evolution of *Zaphrentis delanouei* in Lower Carboniferous times. *Quarterly Journal of the Geological Society of London*, 66: 523-538.

Chudinova I.I. (1986). The composition, system and phylogeny of fossil corals. Order Syringoporida. *Trudy Paleontologicheski Institut*, 216: 1-204. [in Russian]

Conil R., Groessens E., Laloux M., Poty E. & Tourneur F. (1991). Carboniferous guide foraminifera, corals and conodonts in the Franco-Belgian and Campine basins. Their potential for widespread correlation. *Courier Forschungsinstitut Senckenberg*, 130: 15-30.

Coronado I. & Rodríguez S. (2014). Carboniferous auloporids from the Iberian Peninsula: palaeocology, diversity, and spatio-temporal distribution. *Journal of Iberian Geology*, 40: 61-85.

Dobrolyubova T.A. (1958). Lower Carboniferous colonial tetracorals of the Russian platform. *Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR*, 70: 1-224. [in Russian]

Dobrolyubova T.A., Kabakovich N.V. & Sayutina T.A. (1966). Lower Carboniferous corals from the Kuznetsk Basin. *Trudy Paleontologicheski Instituta,* 3: 1-276. [in Russian]

Fan Y.N. (1978). Subclass Rugosa. *In* Atlas of fossils of Southwest China, Chengdu Institute of Geology and Mineral Resources, Sichuan Volume, Part II, Carboniferous to Mesozoic: 149-210, 620-631. [in Chinese]

Fedorowski J. (1968). Upper Viséan Tetracoralla from some borings in the Lublin Coal measures (Poland). *Acta Palaeontologica Polonica*, 13: 203-217.

Fedorowski J. (1981). Carboniferous corals: distribution and sequence. *Acta Palaeontologica Polonica*, 26: 87-160.

Fedorowski J., Bamber E.W. & Baranova D.V. (2012). An unusual occurrence of Bashkirian (Pennsylvanian) rugose corals from the Sverdrup Basin, arctic Canada. *Journal of Paleontology*, 86: 979-995.

Forsh N.N. (1935). New data on the structure of the Okian deposits of the Borovichi and Tikhivinian districts and significance of this issue for problem for C1. *Izvestia of Leningrad Geologo-gidrogeodezich. tresta,* 2-3: 18-33. [in Russian]

Ganelina R.A. (1951). Eostaffells and Millerells of the Viséan and Namurian of the western part of the Moscow basin. *Sbornik statei*: 179-210. [in Russian]

Ganelina R.A. (1956). Foraminifers of the Viséan deposits of the northwestern regions of the Moscow Basin. *Trudy VNIGRI, Nova Seriya*, 98: 61-183.

Gibshman N.B. (2019). Morphological evolution and detailed biostratigraphy of *Eostaffellina* Reitlinger, 1963 (Foraminifera) in the Serpukhovian stage of the Moscow Basin. *In* Bogdanova T.N., Brugrova E.M., Vuks V.Ya., Gabrilova V.A., Evdokimova I.O., Ivanov A.O., Kossovaya O.L., Modzalevskaya T.L., Oshurkova M.V., Popov E.V., Raevskaya E.G., Sapelko T.V., Suyarkova A.A., Tesakov A.A., Titov V.V., Tomacheva T.Yu. & Yanina T.A. (eds), Morphologic evolution and stratigraphical problems; Season LXV Palaeontological Society, St. Petersburg 2019. All-Russian Geological Survey Institute, St. Petersburg: 39-41. [in Russian]

Goldfuss A. (1826). Petrefacta Germaniae, Arnz & Co. Düsseldorf, 1: 1-76.

Gorsky I.I. (1935). Some Coelenterata from the Carboniferous beds of Novaya Zemlya. *Trudy Arktiki Instituta,* 28: 1-128. [in Russian]

Gorsky I.I. (1938). Carboniferous corals of Novaya Zemlya. *In* Nalivkin D.V. (ed.), Paleontology of the Soviet Arctic. *Vsesoyuznyi Arkticheskii Institut, Souz Sovetskykh Socialisticheskikh Respublik*, 93: 7-221. [in Russian]

Gorsky I.I. (1948). Stratigraphic significance of rugose corals on the example from the upper Paleozoic coral fauna from Urals. *Vsesoiuznyi nauchno-issled geologicheskii institute. Materialy paleontologiia i stratigrafia,* 5: 104-119. [in Russian]

Hecker M. (2001). Lower Carboniferous (Dinantian and Serpukhovian) rugose coral zonation of the East European Platform and Urals, and correlation with Western Europe. *Bulletin Tohoku University Museum*, 1: 298-310.

Hecker R.F. (1938a). The organization of the palaecological study of the lower Carboniferous deposits of the Leningrad district.

Materialy po regional'noi i prikladnoi geologii Lenoblasti i Karelskoi Avtonomnaya Sovetskaya Socialisticheskaya Respublica, 2: 3-15. [in Russian]

Hecker R.F. (1938b). Section of the "unit of alternation (a)" Oka Formation of the Lower Carboniferous along the Msta River. *Materialy po regional'noi i prikladnoi geologii Lenoblasti i Karelskoi Avtonomnaya Sovetskaya Socialisticheskaya Respublica*, 2: 15-22. [in Russian]

Herbig H-G. (1986). Rugosa und Heterocorallia aus Obervisé-Geröllen der Marbella-Formation (Betische Kordillere, Südspanien). *Paläontologische Zeitschrift*, 60: 189-225.

Hill D. (1938-41). A monograph on the Carboniferous rugose corals of Scotland. 213 pp. Palaeontographical Society, London.

Jia H., Xu S., Kuang G., Zhang B., Zuo Z. & Wu J. (1977). Class Anthozoa. *In* Paleontological atlas of the central South China Region (2). Hubei Provincial Geological Science Research Institute: 109-270, 675-742, 763-789. [in Chinese]

Jones G.L. & Somerville I.D. (1996). Irish Dinantian biostratigraphy: practical application. *In* Strogen P., Somerville I.D. & Jones G.L. (eds), Recent Advances in Lower Carboniferous Geology. *Geological Society of London, Special Publication,* 107: 371-385.

Karaeva M.V. (1935). Significance of the coral fauna for the stratigraphy of the Lower Carboniferous of the Leningrad District. *Leningradskyi geologo-gidrogeodezicheskyi Trest*, 2-3: 36-38. [in Russian]

Khoa N.D. (1977). Carboniferous Rugosa and Heterocorallia from boreholes in the Lublin region (Poland). *Acta Palaeontologica Polonica*, 22: 301-404.

Lonsdale W. (1845). Description of some Palaeozoic Corals of Russia, *In* Murchison R.I., de Verneuil E. & von Keyserling A., The Geology of Russia in Europe and the Ural Mountains: 591-634.

Martin W. (1809). Petrificata derbiensia, or Figures and Descriptions of Petrifactions collected in Derbyshire. D. Lyon (Wigan): 1-102.

McCoy F. (1849). On some new genera and species of Palaeozoic corals and Foraminifera. *Annals and Magazine of Natural History, Series 2*, 3: 1-20, 119-136.

Mikhailov A.V. (1939). About Palaeozoic Ammodiscidae. Lower Carboniferous deposits of the northwestern part of the Moscow Basin. *Sbornik Leningradskogo Geologicheskogo Upravlenia*, 3: 47-62. [in Russian]

Milne-Edwards H. & Haime J. (1851). Monograph de Polypiers fossiles des terrains palaeozoiques, précédée d'un tableau général de la classification des polypes. *Archives Muséem Histoire Naturelles Paris*, V: 1-502.

Minato M. (1975). Japanese Palaeozoic corals. *Journal of the Geological Society of Japan,* 81: 103-126.

Minato M. & Kato M. (1974). Upper Carboniferous corals from the Nagaiwa series, Southern Kitakami Mountains, NE Japan. *Journal of the Faculty of Science Hokkaido University. Series IV. Geology and Mineralogy*, 16: 43-119. [in Japanese]

Mitchell M. (1989). Biostratigraphy of Viséan (Dinantian) rugose coral faunas from Britain. *Proceedings of the Yorkshire Geological Society*, 47: 233-247.

Ogar V. (2003). Corals (rugosa and tabulata) at the Tournaisian-Visean boundary of median Tien Shan. *Berichte der Institut von Geologie und Paläontologie der Universität Graz*, 7: 76.

Perret M.-F. & Semenoff-Tian-Chansky P. (1971). Coralliaires des calcaires carbonifères d'Ardengost (Hautes-Pyrénées). *Bulletin de la Société d'Histoire naturelle de Toulouse*, 107: 567-594.

Poty E. (1981). Recherches sur les Tétracoralliaires et les Hétérocoralliaires du Viséan de la Belgique. *Mededelingen Rijks Geologische Dienst*, 35: 1-161.

Poty E. & Hecker M.R. (2003). Parallel evolution in European rugose corals of the genus *Lonsdaleia* McCoy, 1849 (Lower Carboniferous). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique. Sciences de la Terre*, 73: 109-135.

Poty P. (1994). Nouvelles précisions sur les corrélations stratigraphiques du Dinantien du Boulonnais et de la Belgique: application de la biozonation corallienne. *Comptes Rendus de l'Académie des Sciences,* 319: 467-473.

Pozner V.M. (1951). Ostracodes of the Lower Carboniferous of the western part of the Moscow basin. *Sbornik statei*: 5-108. [in Russian]

Rakshin P.P. (1965). New Visean rugose corals from west slopes of Urals. *Paleontologicheskii Zhurnal*, 1: 54-59. [in Russian]

Rauser-Chernousova D.M. (1948). Some new species of foraminifers from Lower Carboniferous deposits of the Moscow Basin. *Akademiya Nauk Souza Sovetskikh Socialisticheskikh Respublik, Trudy Instituta Geologicheskikh Nauk*, *Geologicheskaya Seriya (No. 19)*, 62: 227-238. [in Russian]

Reitlinger E.A. (1963). Paleontological criteria for establishing the boundaries of the Lower Carboniferous Division (based on foraminiferal fauna). *Akademiya Nauk SSSR, Voprosy Mikropaleontologii*, 7: 22-56. [in Russian]

Rodríguez S. & Bamber E.W. (2010). Unusual offsetting in Serpukhovian (Lower Carboniferous) representatives of the rugose coral genus *Schoenophyllum* Simpson, 1900. *Palaeoworld*, 19: 401-409.

Rodríguez S., Somerville I., Cózar P., Coronado I. & Said I. (2016). Inventory and analysis of the distribution of Viséan corals from the Guadiato Area (Córdoba, SW Spain). *Spanish Journal of Paleontology*, 31: 181-220.

Rodríguez S., Somerville I., Said I. & Cózar P. (2013). An Upper Viséan (Asbian-Brigantian) and Serpukhovian coral succession at Djebel Ouarkziz (northern Tindouf Basin, southern Morocco). *Rivista Italiana di Paleontologia e Stratigrafia*, 119: 3-18.

Said I., Somerville I.D., Rodríguez S. & Cózar P. (2013). Mississippian coral assemblages from the Khenifra area, Central Morocco: Biostratigraphy, biofacies, palaeoecology and palaeobiogeography. *Gondwana Research*, 13: 367-379.

Savitsky Y.V., Kossovaya O.L. & Vevel Y.A. (2007). Lower Carboniferous of the northwestern part of the Moscow Syncline. Guidebook of pre-conference field trip, X International Congress on Fossil Cnidaria and Porifera*.* 96 pp. All-Russian Geological Survey Institute, Publishing House, St. Petersburg.

Savitsky Y.V., Kossovaya O.L., Vevel Y.A. & Evdokimova I.O. (eds) (2015). Lower Carboniferous of the St. Petersburg region (northwest Russia). A field Guidebook of XVIII International Congress on the Carboniferous and Permian. 77 pp. All-Russian Geological Survey Institute, Publishing House, St. Petersburg.

Sayutina T.A. (1973). Lower Carboniferous corals of the northern Urals; Suborder Acrophyllina. *Akademiya Nauk SSSR, Trudy Paleontologicheskogo Institut*, 140: 1-168. [in Russian]

Semenoff-Tian-Chansky P. (1985). Corals. *In* Wagner R.H., Winkler-Prins C.F. & Granados L.F. (eds), The Carboniferous of the World, II, Australia, Indian subcontinent, South Africa, South America and North Africa. International Union of Geological Sciences Publication, 20: 374-381, 431-435.

Shlykova T.I. (1951). Foraminifers of the Viséan and Namurian stages of the Lower Carboniferous of the western part of the Moscow basin. *Sbornik statei*: 109-178. [in Russian]

Simpson G.B. (1900). Preliminary descriptions of new genera of Paleozoic rugose corals. *Bulletin of the New York State Museum*, 39: 199-222.

Smith S. (1916). *Aulina rotiformis*, gen. et sp. nov., *Phillipsastraea hennahi* (Lonsdale) and *Orionastraea* gen. nov. *Quarterly Journal of the Geological Society of London*, 72: 280-307.

Sokolov B.S. (1939a). Significance of Rugosa and tabulate corals in the stratigraphy of the C1 of the Moscow basin. *Doklady Academii Nauk Souza Sovetskikh Socialisticheskikh Respublik*: 2. [In Russian]

Sokolov B.S. (1939b). Stratigraphical significance and types of Chaetetidae of the Carboniferous in the USSR. *Doklady Academii Nauk Souza Sovetskikh Socialisticheskikh Respublik*: 4. [in Russian]

Sokolov B.S. (1940). Sandy-clay deposits of the Lower Carboniferous of the Moscow basin. *Sovetskaya Geologia*, 5-6: 145-152. [in Russian]

Sokolov B.S. (1941). Stratigraphical scheme of the northern part of the Moscow basin. *Izvestia Academii Nauk Souza Sovetskikh Socialisticheskikh Respublik, Seriya Geologicheskaya*: 13-22. [in Russian]

Sokolov B.S. (1944). New data on stratigraphy and palaeogeography of the north of the Moscow basin (Ljubytino district). *Uchenye Zapisky Leningradskogo Universita, Seriya Geologicheskaya*, 70: 112-136. [in Russian]

Sokolov B.S. (1950). Carboniferous Chaetetidae of southeastern Ukraine and contiguous regions. *Trudy VNIGRI*, 27: 3-144. [in Russian]

Stuckenberg A. (1904). Anthozoan and bryozoan of the lower Carboniferous from Central Russia. *Trudy Geologicheskogo Komiteta*, 14: 1-128. [in Russian]

Vostokova B.A. (1955). Lower Carboniferous gastropods “Rovnoe Limestone”. *Voprosy palaeontologii*, 2: 70-81. [in Russian]

Wang Z.G. (1989). On lithostrotionelloid corals. *Acta Paleontologica Sinica*, 28: 522-545. [in Chinese]

Yanishevsky M.E. (1936). The brief report about the work of 1935 year. *Uchenye Zapisky Leningradskogo Universiteta, seriya geologo- pochvovedennykh u- geograficheskikh nauk*, 3: 80-95. [in Russian]

Yanishevsky M.E. (1937). Carboniferous deposits. *Articles to the geological map of the south part of the Leningrad District*: 64-83.

Yanishevsky M.E. (1954). Brachiopod fauna of the Lower Carboniferous of the Leningrad District. *Isdatelstvo Leningradskogo Gosudarstvennogo Universiteta*: 1-46. [in Russian]

Yu C.C., Lin Y.D., Shi Y., Huang Z.X. & Yu X.G. (1983). Carboniferous and Permian corals. 391 pp. Jilin People’s Publishing House, Jilin, China. [in Chinese]

Yu X. (1980). Upper Carboniferous Chuanshanian tetracorals of Southern Jiangsu. *Professional Papers of the Chinese Academy of Geological Sciences. Stratigraphy and Paleontology*, 9: 48-88. [in Chinese]

Yu X. (1991). New genus and species of Carboniferous tetracorals from Jiangsu and Anhui. *Acta Palaeontologica Sinica*, 30: 420-444. [in Chinese]

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A soft-bodied endosymbiont in Serpukhovian (late Mississippian, Carboniferous) rugose corals from South China

Wei LIN & Hans-Georg HERBIG*

W. Lin, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, East Beijing Road 39, 210008 Nanjing, China; wlin@nigpas.ac.cn
H.-G. Herbig, Institut für Geologie und Mineralogie, Universität zu Köln, Zülpicher Str. 49a, D-50674 Köln, Germany; herbig.paleont@uni-koeln.de
**corresponding author*

KEY WORDS - Late Palaeozoic, Lower Yangtze Platform, endosymbiosis in corals, skeletal distortion, bioclaustration.

*ABSTRACT - An endosymbiotic relation between the solitary rugose corals ?*Yuanophyllum *and ?*Dibunophyllum *and a large soft-bodied worm-like organism is described from the Hezhou Formation (Serpukhovian), Lower Yangtze Platform, South China. The endosymbiont lived in a U-shaped tube, probably with a horizontally sideways bent base connecting the vertical shafts. A membranous epidermis and relicts of a probable cuticulo-muscular tube are preserved. The corals reacted with skeletal encasement of the infesting organism and irregular, in part dense growth of additional skeletal elements adjacent to it. This is the first description of such an endosymbiotic, parasitic or commensal relation of solitary rugose corals after the Frasnian-Famennian Boundary Event. Similarities between the Devonian association of pleurodictyoform tabulates and the ichnotaxon* Hicetes *are remarkable. Moreover, the association proves the extraordinarily rare persistence of bioclaustrations in corals after the Hangenberg Event at the Devonian-Carboniferous boundary during the Permo-Carboniferous period of arrested endosymbiont development.*

INTRODUCTION

Symbiosis, in its wide sense, is defined as the intimate association of two organisms "living together." According to Darrell & Taylor (1993), it ranges from parasitism through commensalism and amensalism to mutualism, but the kind of relationship between the two organisms is already difficult to evaluate in modern, and even more in fossil examples (Smith & Douglas, 1987; Fagerstrom, 1996; Taylor, 2015). If there are great size differences between both symbionts, the larger one is called host, the smaller one symbiont (Smith & Douglas, 1987).

In spite of the limitations, evidence of symbiotic interactions of organisms through time helps us to better understand the evolutionary history of the ecosystem, exploitation of ecospace (Bambach et al., 2007), and formation of specific niches. Palaeozoic corals, as a major group of marine calcareous skeleton producers, dwell in a wide range of habitats from reefs to bottom-level communities (Aretz, 2010). Together with other skeletal colonial organisms like stromatoporoids and bryozoans, they were the most favoured hosts for symbiotic organisms. Endosymbiotic interactions between corals (Tabulata and Rugosa) and other macro-organisms in the Palaeozoic have been frequently reported (e.g., Sokolov, 1948; Plusquellec, 1968; Oekentorp, 1969; Oliver, 1983; Zapalski et al., 2008; Zapalski, 2009; Stewart et al., 2010; Vinn & Wilson, 2015; Vinn et al., 2017; also see the reviews by Darrell & Taylor, 1993; Tapanila, 2005; Vinn, 2017a, b). They are most easily recognised when organisms caused changes in the growth of the coral skeleton. In many cases, the organisms settling within a living coral were embedded in the skeleton of the host during growth, with apertures connected to the outside, or were totally overgrown, resulting in internal tubes or cavities. Such process is termed "bioclaustration" (Palmer & Wilson, 1988), and provides direct evidence of symbiotic activities. Bioclaustrations have been often studied and described in the manner of ichnology and can be used as proxies for the health of reef ecosystems of the past (Tapanila, 2005; Vinn et al., 2018).

The oldest records of endosymbiosis between macro-organisms and corals are from the Late Ordovician, with corals either as hosts (Elias, 1986) or as endosymbionts (Vinn et al., 2016). Abundance and diversity of endosymbiosis in corals during the Palaeozoic peaked in the Middle Devonian. Both dropped dramatically in the Late Devonian (Darrell & Taylor, 1993; Tapanila, 2005; Zapalski, 2009). In fact, the extreme drop of the coral diversity caused by the Kellwasser Event at the Frasnian-Famennian boundary also almost wiped out the symbiotic dependant ecosystem (Tapanila, 2005; Vinn, 2017b) and, as a consequence, the Famennian was almost devoid of endosymbiosis in corals. Hitherto, the youngest record of bioclaustration was from the late Famennian ("Strunian") tabulate coral *Yavorskia* (Zapalski et al., 2008).

Despite the fact that diversity and abundance of corals recovered in the Mississippian, bioclaustrations caused by endosymbiotic worms and tentaculitoid tubeworms were missing and the ecospace apparently was vacant. An exception outside of corals is the tentaculitoid genus *Streptindytes*, which infested Pennsylvanian chaetetid sponges (Tapanila, 2005; Vinn, 2010, 2016). The few records for macro-symbiosis of corals in the Carboniferous refer to intergrowth or encrustation (Darrell & Taylor, 1993; Tapanila, 2005; see review in Vinn, 2017b). The roles that different taxonomic groups of corals played in the symbiotic associations also differed. Tabulate corals had been more preferable hosts than rugose corals. In the latter group, records as hosts are rare, even more for solitary taxa (Darrell & Taylor, 1993; Tapanila, 2005).

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Two specimens of solitary rugose corals retrieved from the upper Mississippian (lower Carboniferous) from South China bear structures of endosymbiotic origin, shortly described by Lin & Herbig (2019). The aim of this contribution is to detail these structures that are extremely scarce in the Carboniferous, and to compare them with older endosymbiotic ichnofossil types.

GEOLOGICAL SETTING AND LOCALITY

During the Carboniferous, the South China block was located in the northeastern Palaeotethys near the palaeoequator. Its northeastern part was constituted by the Lower Yangtze Platform, which was bound by the northern margin of the Yangtze Land to the south and modern day Tanlu Fault Zone and Qingling-Dabie Orogen to the north. The Mississippian strata of this region are largely composed of carbonate rocks (mudstones, wackestones, packstones, dolostones), sandstones, and siltstones intercalated with coal-bearing strata (Wang et al., 2013).

The Wangjiacun section (Fig. 1, GPS coordinates: N 31°31’00”, E 117°48’18”) is located close to the eastern banks of Chaohu Lake, Yingping County, Anhui Province. Geologically, the section is located near the northern margin of the Lower Yangtze Platform. Two lithostratigraphic units can be recognised: the lower part represents the upper part of the Gaolishan Formation, which mainly consists of calcareous mudstone with a thin layer of sandstone (about 20 cm thick) near the top; the upper part represents the Hezhou Formation, which mainly consists of argillaceous limestone intercalated with calcareous mudstone, topped by a seven meters thick dolomite, sometimes being referred as a separate lithostratigraphic unit named Laohudong Formation. The Gaolishan and Hezhou formations yielded relatively abundant rugose corals (Wang et al., 2010; Lin, 2013). The specimens bearing the endosymbiotic structures were retrieved from the Hezhou Formation.

In the Gaolishan Formation, the rugose coral fauna is dominated by solitary corals, including *Arachnolasma*, *Dibunophyllum* and *Koninckophyllum*, associated with a few colony fragments of *Siphonodendron pauciradiale* (McCoy, 1844). The coral fauna in the lower and middle part of the Hezhou Formation is more diverse than in the formation below. It comprises *Koninckophyllum*, *Yuanophyllum*, *Bothrophyllum*, *Arachnolasma*, *Dibunophyllum*, *Axophyllum*, *Siphonophyllia* and cf. *Empachyphyllum*, with more numerous occurrences of the colonial coral *Lithostrotion*. In the upper part of the Hezhou Formation, just below the dolomite, only two fragments of *Aulina rotiformis* Smith, 1917 were recovered.

Further corals from the Hezhou Formation were described by Xia & Xu (1980) some 20 km north of Wangjiacun from the Fenghuangshan section, which is a parastratotype of the Hezhou Formation (Li & Jiang, 1997).

The coral assemblage of the Wangjiacun section in general is typical of the *Yuanophyllum* Zone of South China (Yu, 1931; Wu, 1964; Tan, 1987), which has a range from middle Visean to Serpukhovian. *Aulina rotiformis*, which occurs in the top of the section, is a characteristic latest Visean to early Serpukhovian marker

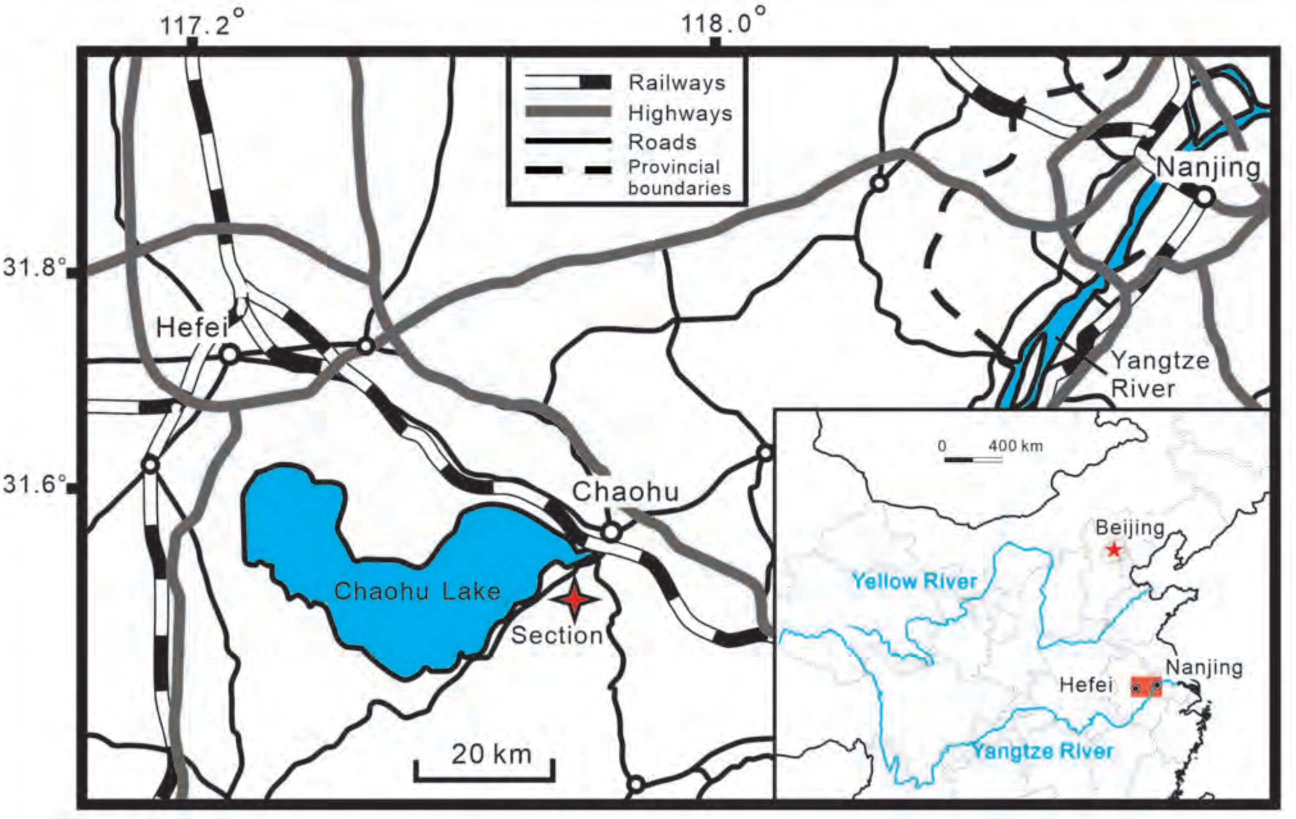

Fig. 1 - (color online) Location of the Wangjiacun section east of Chaohu Lake, Anhui Province.

in South China (e.g., Poty et al., 2011; Lin et al., 2012), opposed to western Europe, where it enters at the base of the Serpukhovian (Rugose coral Zone RC9; Poty et al., 2006, 2011). However, based on foraminifers, and refining the earlier stratigraphic assignment of Xia & Xu (1980) and Cai & Xi (1985), Sheng et al. (2018) defined the Tarussian *Plectomillerella tortula* Interval Zone and placed the complete Hezhou Formation into the Serpukhovian. This relies on the occurrence of the foraminifers *Plectomillerella tortula* (Zeller, 1953) (= *Millerella tortula* auct.), *Asteroarchaediscus* cf. *postrugosus* (Reitlinger, 1949) (= *Neoarchaediscus postrugosus* auct.) from the base of the Hezhou Formation, and the entry of *Janischewskina delicata* (Malakhova, 1956) slightly above.

MATERIAL AND METHODS

Totally 126 specimens were collected from the Wangjiacun section for taxonomic and biostratigraphic studies (Lin, 2013). Among them, only two solitary coral specimens, tentatively assigned to ?*Yuanophyllum* and ?*Dibunophyllum*, carry the endosymbiotic structures. Both specimens are incomplete, missing the apex, the calice and part of the dissepimentarium. For the purpose of taxonomy, they were originally sectioned, including: four transverse sections for ?*Yuanophyllum*; four transverse sections and one longitudinal section for ?*Dibunophyllum*. Herein, the description of each specimen includes two parts: host and endosymbiont. The description of the endosymbiont remains informal, as it is not assigned to an existing or new taxon.

Thin sections were studied with a Wild M420 optical microscope and photographed using the 500 megapixel Leica MC170 HD microscope camera. Specimens described herein are deposited in Nanjing Institute of Geology and Palaeontology (repository number of thin sections for ?*Yuanophyllum:* 171989-171992; for ?*Dibunophyllum*:191993-191997).

INFESTATION OF ?*YUANOPHYLLUM* SP.

The host

Two transverse sections are from the neanic stage (Fig. 2a-b). They are 7.3 mm and 15.6 mm in diameter and have 28 and 36 major septa, respectively. The major septa in cardinal quadrant are strongly dilated and almost contiguous to each other in the tabularium. In the first (smallest) transverse section (Fig. 2a), the cardinal septum

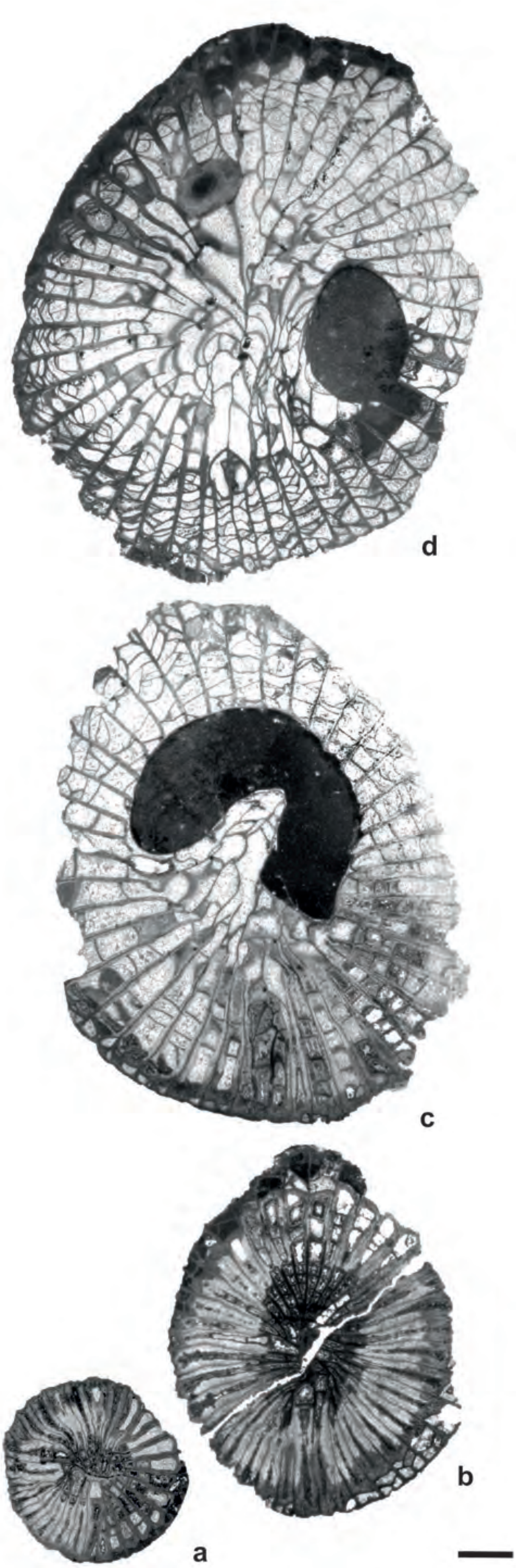

Fig. 2 - Transversal sections of ?*Yuanophyllum*. a) Neanic stage with 28 major septa. Repository no. 171989. b) Neanic stage with 36 major septa, both not affected by the endosymbiont. Repository no. 171990. c) Ephebic stage with U-shaped tube of soft-bodied endosymbiont in the counter quadrants. Repository no. 171991. d) Ephebic stage showing two cavities interpreted to be vertical shafts of the endosymbiont which rise from the U-shaped tube of the underlying transversal section figured in (c). Larger cavity presumably associated with tentacle-bearing mouth of the organism, smaller one with the anus. Repository no. 171992. Scale bar is equal to 2 mm.

is continuous with the counter septum. In the centre of this continuation, the plate is thickened and shows the early development of a columella. In both neanic sections, a few major septa reach the centre and connect to the columella, whereas others are contratingent to their neighbouring septa.

The other two transverse sections are from the ephebic stage (Fig. 2c-d). They are 18.9 mm and 22.5 mm in diameter and have 44 and 47 major septa respectively. In the third transverse section (Fig. 2c), most of the major septa do not reach the centre. The cardinal septum significantly retreats from the axis and an open fossula can be seen. No columella is present in this section, probably due to the interference of the endosymbiont. In the fourth transverse section (Fig. 2d), the adaxial end of the counter septum extends to the centre and connects to the cardinal septum with a thin lamella. In both sections, the major septa in the cardinal quadrants are more dilated than those in the counter quadrants. A few series of herringbone dissepiments can be seen in the partly preserved dissepimentarium.

This specimen is assigned to *Yuanophyllum* with doubt due to the lack of a longitudinal section and the unstable development of the columella.

The endosymbiont

Both transverse sections of the early growth stages do not show any trace of the endosymbiont (Fig. 2a-b). In the third transverse section (Figs 2c and 3a) a U-shaped, sediment-filled tube with a maximum diameter of 3.6 mm and occupying more than one quarter of the area of the section occurs in the tabularium of both counter quadrants.

In the uppermost, fourth thin-section (Fig. 2d), two slightly elliptical cavities are seen. They occur in comparable position as the tube in the transverse section below, which is proved by the position of the cardinal septum of the coral. According to their distance, they fit to the outermost parts of the U-shaped tube below. Therefore, they are interpreted to be its vertical shafts. The larger cavity, measuring 4.8 x 3.65 mm, is completely filled with sediment. An "inflow" of sediment between two septa seems to be related to a hole within the wall of the tube-dweller after death. The smaller cavity measures 2.8 x 1.7 mm. Its outer part is closed by dense yellowish calcite; only the central part, about half the diameter of the hole remained sediment filled (Fig. 3b).

Sediment filling of tube and cavities consists of blackish carbonate mud including abundant tiny idiomorphic dolomite rhombs. The inner margin of the endosymbiotic structure is partly lined by a very thin black line which is interpreted to be a membranous epidermis and overlying cuticula. This is supported by small parts that peeled off after death of the endosymbiont (Fig. 3c). Inside, an about 0.32 mm thick, fragmentarily preserved layer is observed (Fig. 3a, d-f). Darker than the sediment infill, it is interpreted to be the organic remain of the typical muscular tube forming the hydrostatic skeleton of a worm-like organism.

The U-shaped tube from the third section is mostly encased by the coral skeleton (Fig. 3a). The encasement appears to be an integrative part of the stereoplasmatic thickening of dissepiments. In some cases, the axial ends of the septa protruded faintly into the tube causing a festoon-like dilated external margin (Fig. 3e); in others they stopped at the encasement with a sharp boundary, which is related to their frontal growth zone. Finally, in a third case the distal ends of the septa are bent laterally aside at the boundary of the tube (Fig. 3d). Rarely, the boundary of the tube is only formed by thin dissepiment-like structures and even small cement-filled spaces might remain between the skeleton of the coral and the tube-forming organism (Fig. 3f). The axial structure of the coral is completely distorted. It is formed by the extensions of irregularly connected axial ends of the major septa (Figs 2c and 3a).

In the overlying fourth transverse section, the encasement of the larger cavity is similar to the section below; some irregular vesicles that formed in the tabularium part of the major septa are close to this cavity (Fig. 2d). The type of dense yellowish calcite filling the outer part of the smaller cavity is also seen along a very short segment of the bigger cavity, forming a thin, callus-like rim (Fig. 3c). The septa connected to the calcite filling of the smaller hole and septa near-by are thickened (Fig. 3b).

INFESTATION OF ?*DIBUNOPHYLLUM* SP.

The host

All four transverse sections are from ephebic stage. The axial structure mainly consists of loosely spaced axial tabellae and a few septal lamellae which relate to the major septa. No distinct columella is seen (Fig. 4a). There are 52 long major septa, all dilated in tabularium (more in the cardinal quadrant). Their adaxial ends connect to the axial structure with thin lamellae which all bend to one side. Although only partly preserved, the dissepimentarium is obviously wide and consists of herringbone dissepiments. In longitudinal section (Fig. 4b), the axial tabellae are more densely spaced than the abaxial tabellae, though the boundary between both is not very distinct. Dissepiments are large, elongated on the inner side and globular on the outer side.

This specimen is assigned to *Dibunophyllum* with doubt due to a missing columella (compare Hill, 1981, fig. 237, 1g) and the asymmetrical shape of the axial structure, which, however, might be caused by the endosymbiont.

The endosymbiont

In the available longitudinal section (Fig. 4b) a tear-shaped, sediment-filled cavity is observed, 6.7 mm long and 3.3 mm wide. At its right side a smaller, somewhat irregular roundish, sediment-filled pouch is seen, 1.2-1.6 mm wide. It is connected to the larger cavity along a neck slightly outside the plane of the thin-section (Fig. 4c-d). Sediment infill of the complete structure is identical to that of the endosymbiont in ?*Yuanophyllum.* Existence of its black external lining is doubtful. Instead, a dark greyish line is seen resembling the median lines present in all skeletal elements of the coral skeleton (Fig. 4c).

The external margin of the tear-shaped cavity connects to the axial end of a septum, which is identified by its dense calcitic fibres (Fig. 4b, d). Below and above the cavity, and along its internal side, dense, irregular tabulae are developed, which considerably differ from the smooth,

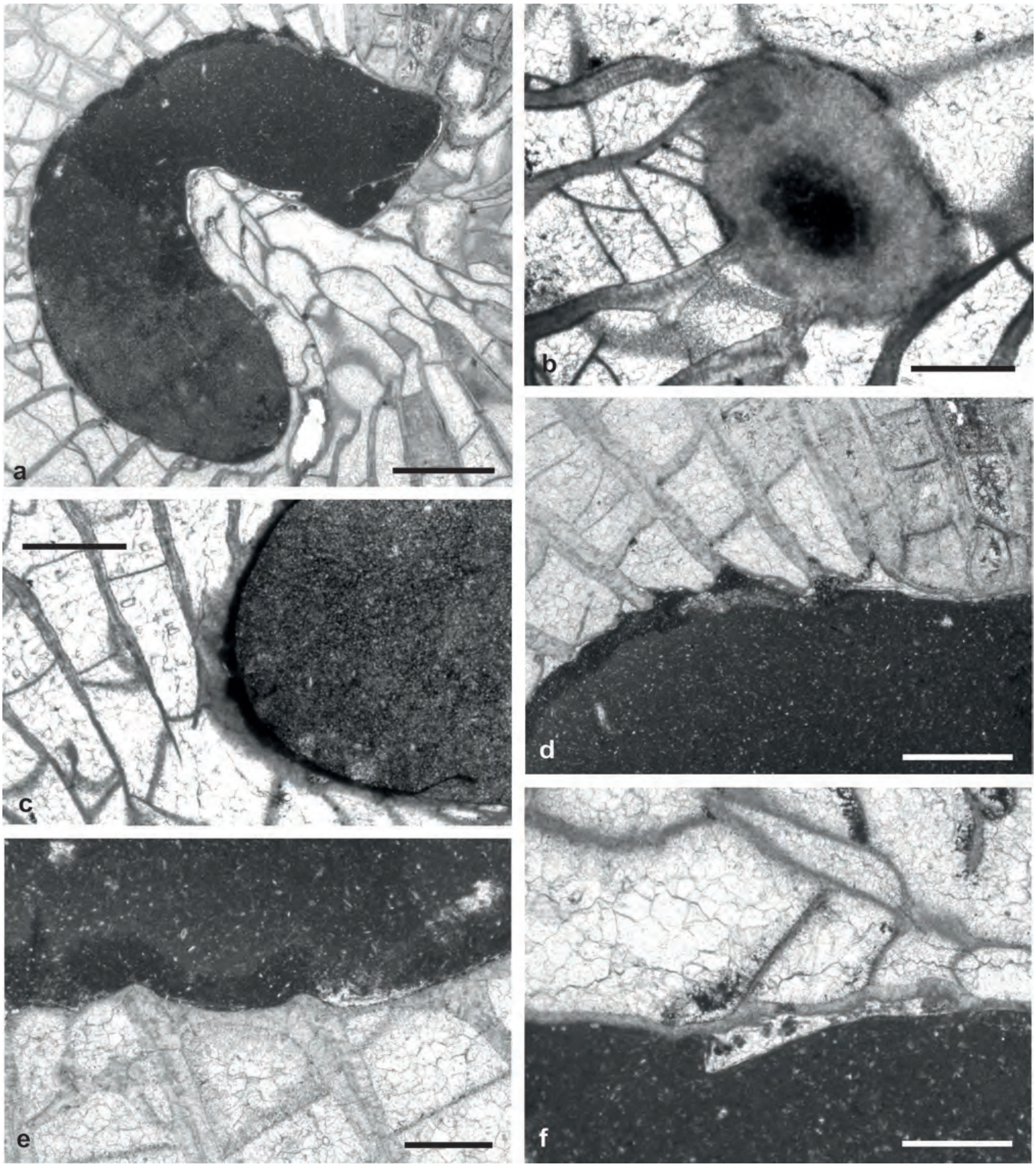

Fig. 3 - Details of the endosymbiont in ?*Yuanophyllum*. a) U-shaped tube almost completely encased by the coral skeleton with a completely distorted axial structure. Blackish external lining of the tube interpreted as remnants of the cuticulo-muscular tube; lower ephebic stage (Fig. 2c) (scale bar = 2 mm). b) The smaller cavity from the upper ephebic stage (Fig. 2d), mostly closed by callus-like skeletal material secreted by the coral; cavity additionally encapsulated by thickened septa and added small skeletal elements (scale bar = 1 mm). c) Detail of the larger cavity from the upper ephebic stage (Fig. 2d) (scale bar = 1 mm). Cavity separated from the coral by skeletal encasement, in part callus-like thickened. Thin black structure peeled off from the rim of the cavity at lower right interpreted as membranous epidermis and cuticula of the tube dweller. d) Laterally bent aside septa in reaction to the growth of the endosymbiont. Blackish lining of cavity interpreted as remnants of cuticulo-muscular tube, lower ephebic stage (Fig. 2c) (scale bar = 1 mm). e) Continued growth of septa causing festoon-like dilatation of the supposed cuticulo-muscular tube of the soft-bodied tube dweller, lower ephebic stage (Fig. 2c) (scale bar = 0.5 mm). f) Supposed epidermal-cuticular layer and underlying cuticulo-muscular tube peeled-off from the encasing coral skeleton, lower ephebic stage (Fig. 2c) (scale bar = 0.5 mm).

wide spaced tabulae on the other side of the wide axial structure. Also the development of a discontinuous columella, bent away from the cavity is apparently related to the formation of the cavity (Fig. 4b). Externally of the dark greyish line that rims the cavity, a thick, multi-layered stereoplasmatic calcareous layer completely encases the

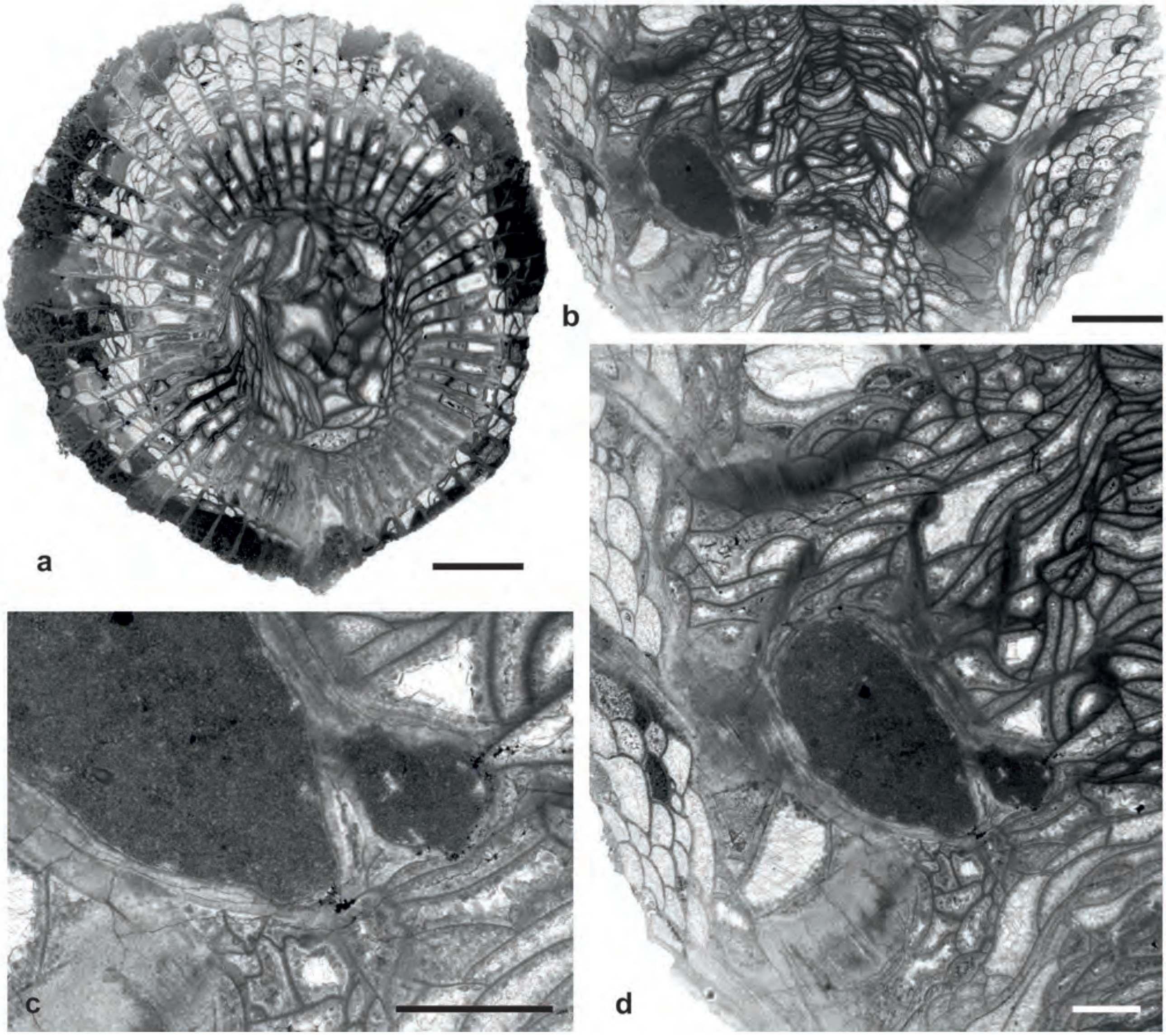

Fig. 4 - Endosymbiotic infestation of ?*Dibunophyllum*. a) Transversal section; endosymbiotic infestation not seen, but most probably documented by the asymmetrical shape of the axial structure and missing columella. Repository no. 171993 (scale bar = 5 mm). b) Longitudinal section with sediment-filled endobiotic cavity (left) surrounded by dense, irregular tabulae and dilated axial structure with discontinuous columella bent away from the cavity. Size and shape of normally developed tabulae on right side of the axial structure clearly differ from those adjacent to the cavity. Repository no. 171995 (scale bar = 5 mm). c) Detail of the tear-shaped cavity and small, secondary pouch connected by a neck to the main cavity. The external lining of the cavities resembles the median lines of the skeletal elements of the coral. Its origin is doubtful. Cavities completely encased by thick, multi-layered stereoplasmatic skeletal material secreted by the coral (scale bar = 2 mm). d) Position of the large, tear-sized cavity adjacent to septum (left), encasement by multi-layered stereoplasmatic skeletal material and surrounding by irregular, densely growing skeletal elements (scale bar = 2 mm).

structure (Fig. 4c-d). At least the latter is thought to be secreted by the coral.

DISCUSSION

The Chinese material

The evident reaction of the coral hosts that encased the endosymbiont with skeletal material as well as the irregular structure of the surrounding skeleton proves the interaction of both organisms and, therefore, the syn-vivo relation. According to the comparable size of the endosymbiontic structures in both corals, the same type of organism might be assumed. Some doubts remain, as in ?*Yuanophyllum* only transverse sections were available, while in ?*Dibunophyllum* only the longitudinal section bears such a structure. Moreover, the organic lining of the cavity as well as the assumed muscular tube below that occur in ?*Yuanophyllum* are not seen in ?*Dibunophyllum*. The somewhat different shapes of the cavities (elliptical versus tear-shaped) might be related to the different plane of sectioning (transversal versus longitudinal), to the reaction of the host, or to growth restrictions of the endosymbiont due to its position close to a septum in ?*Dibunophyllum*.

The syn-vivo relationship means that the endosymbiont settled at the base of the calice above the coral skeleton. At least in ?*Yuanophyllum*, settlement took place during the adult stage of the coral, as neanic growth phases are not affected. The reason is unknown. It solely might be late infesting, but also related to the size of the neanic host versus the infesting organism. Interestingly, also Zapalski (2009) noted the absence of endosymbionts in the early astogenetic stages of Emsian-Eifelian *Favosites*. It is not clear whether the infestation occurred from the lateral side, between the tissue of the polyp and the skeleton, or if the organism could settle from above, vanquishing the obstacle of the coral tentacles. During further growth of the coral, the organism was gradually encased in the host skeleton. In the case of ?*Yuanophyllum*, this resulted in an initially more or less horizontal U-shaped tube, later growing upward into two parallel vertical shafts (Fig. 5). As a working hypothesis, the smaller tube, which is partially sealed by secreted coral skeleton, is interpreted to be the posterior of the endosymbiont, whereas the larger tube appears to be connected with its anterior end. The larger size at the mouth might have been related to feeding tentacles, whereas the anal opening might be situated at the end of a thin cauda, as known for example in modern tube-building sabellariids (sandcastle worms, Polychaeta) (Dales, 1963; Rouse et al., 2000; Rouse & Pleijel, 2001; Capa et al., 2012, fig. 5; Sanfilippo et al., 2019, fig. 5). The related terebellids (bristle worms, Polychaeta) that are mostly encased in particle-encrusted mucous tubes also have a wide, tentacle-bearing anterior end and a long tapering posterior end (Dales, 1963; Rouse et al., 2000; Rouse & Pleijel, 2001).

In the longitudinal section of ?*Dibunophyllum* no hint of a three-dimensional shape of the tube is recorded. The reason remains unclear, but might be related to rapid lethal overgrow of the endosymbiont by the coral.

Both endosymbiontic structures are interpreted to represent soft-bodied worm-like organisms that differ from the tube-forming sabellariids and terebellids mentioned above. This is indicated by a missing external shell. Instead, the outer, thin black organic lining is interpreted as a membranous epidermal tissue and external cuticula (e.g., Hausen, 2005, for polychaetes). The partially preserved blackish layer of regular thickness below is regarded as the muscular tube of the hydrostatic skeleton of the organism. Both structures form the cuticulo-muscular tube of worm-like phyla. Strength and thickness of the cuticula varies widely and therefore might be preserved. It has to be noted that an extremely flexible and resilient cuticle in nematodes is of special relevance in parasitic life-forms (Wright, 1987; Bird & Bird, 1991), though we are not aware of nematodes parasitising in corals.

The soft-bodied anatomy of the organism is also indicated by some minor indentations of its outer margin, produced by the continued growth of septa. In spite of the almost complete encasing by the coral skeleton, few small cement-filled spaces between the epidermis/cuticula of the endosymbiont and elements of the coral skeleton might indicate the earlier direct contact between the coral tissue and the endosymbiont.

Various abnormal structures in the coral skeletons indicate that the hosts tried to fend off the endosymbiont and to strengthen their skeletal structure. Based on the large size of the endosymbionts that might occupy more than a quarter of the transverse section in one specimen,

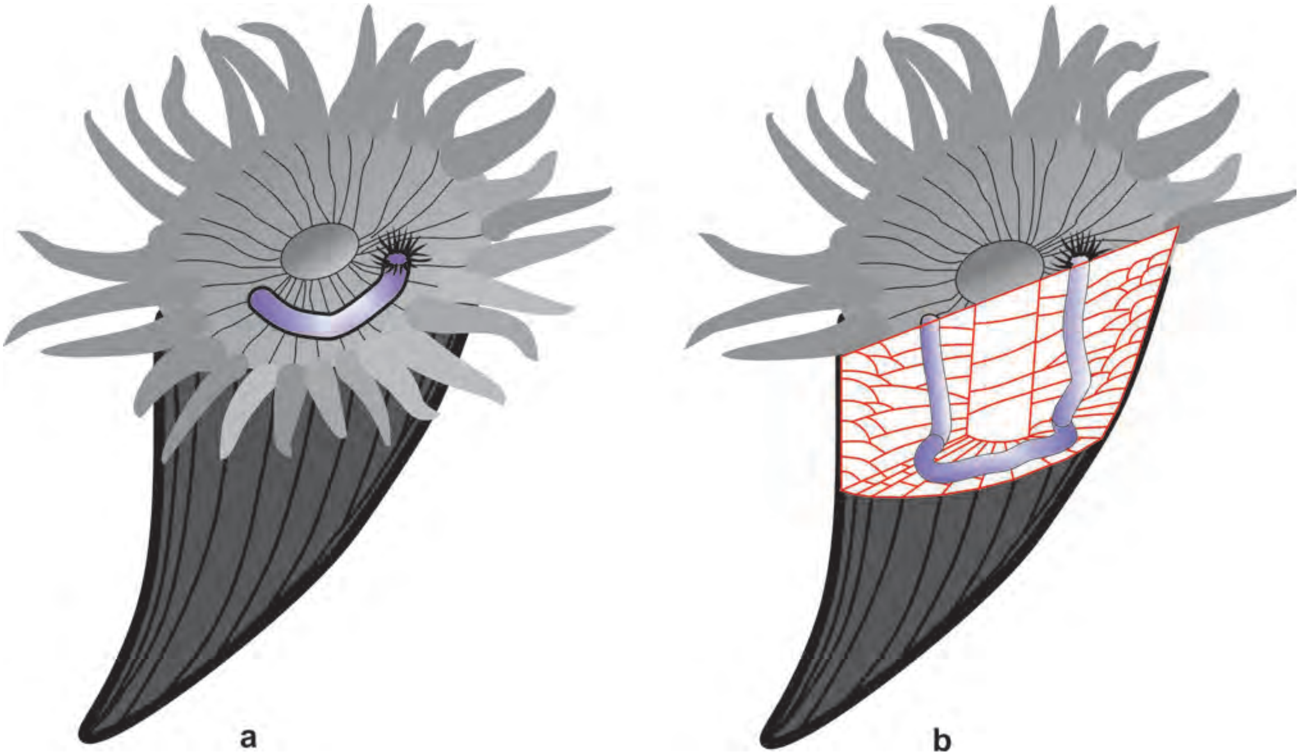

Fig. 5 - (color online) Reconstruction of the endosymbiontic relation between ?*Yuanophyllum* and a soft-bodied endosymbiont, Hezhou Formation (Serpukhovian, Wangjiacun section, Lower Yangtze Platform, South China). a) First stage of settlement consisting of a horizontal U-shaped tube nested inside the soft tissue of the coral calice. b) Late stage of settlement showing development of two vertical shafts and pace keeping of the endosymbiont with further growth of the coral. In ?*Dibunophyllum* from the same section the vertical tubes were not observed, probably due to completed overgrowth by the coral and death of the endosymbiont. Coral drawing strongly schematic.

it is reasonable to assume that the fitness of the hosts must have been reduced by the symbiotic relationship. However, the level of deduction seems to have been low. In spite of almost complete encasement of the endosymbiont and secretion of additional irregular skeletal elements, all septa in the two available transverse sections of ?*Yuanophyllum* remained intact and there is no indication of further major defects, like reduction of the coral diameter. Thus, the feeding function of the coral polyp apparently remained normal. Concerning the soft-bodied worm-like endosymbiont, it must have benefitted from the protection of the coral polyp and gained advantages in feeding, which might have been taken place by a tentacle apparatus intermingling with the tentacles of the coral polyp (Fig. 5). Additionally, intermingling of the tentacles might result in a protecting camouflage effect for the endosymbiont. As a result, the relationship of both specimens probably was parasitic, at best commensal.

Comparisons

A certain modern comparison concerning the assumed tentacle apparatus is provided by Christmas tree worm *Spirobranchus* that can aggregate within many coral taxa. However, opposed to our material this serpulid secretes a calcareous tube. Also the infestation differs. *Spirobranchus* larvae settle on hard substrate and are overgrown and embedded by the coral host except for the tentacle crown (Hoeksema et al., 2019, cum lit.).

Similar overgrowth is observed between the solitary corals *Heterocyathus* (Caryophylliidae) and *Heteropsammia* (Dendrophylliidae). They settle on and overgrow dead gastropod shells, rarely other shells like scaphopods, inhabited by the sipunculan worm *Aspidosiphon muelleri* Diesing, 1851. Even if the shell is completely overgrown, the worm will maintain a more or less horizontally spiralled housing with a main pore and several small pores in the lower part of the corallum. The extensively documented association (e.g., Hoeksema & Best, 1991, cum lit.) is known since the Early Cretaceous (Albian; Stolarski et al., 2001, cum lit.). This is an example of an endosymbiontic relation between corals and a soft-bodied worm, but without distinct mouth tentacles, and proboscis narrower than trunk. In spite of the similar size of the endobiont, the scleractinian-sipunculid association differs from our material by the type of infestation, the shape of the worm tube and positioning of its orifices.

In size, shape, and type of infestation, the endosymbiont is strongly similar to the common association between pleurodictyform tabulate corals and the worm-like incertae sedis *Hicetes innexus* Clarke, 1908, which is known from the Lower and Middle Devonian (Nicholson, 1879; Clarke, 1908, 1921; Gerth, 1952; Schindewolf, 1959; Fuchs & Plusquellec, 1982; Plusquellec, 2007). *Hicetes* is almost constantly associated with certain genera (*Pleurodictyum*, *Kerfoneidictyum*), and occasionally seen or completely unknown in other pleurodictyforms (Plusquellec, 2007). Secretion of an own tube-forming skeleton is missing. The tube is cylindrical; diameter depends on the size of the host and might grow from 0.6-0.8 mm up to 3.0-3.5 mm (Schindewolf, 1959; Fuchs & Plusquellec, 1982). The endosymbiont settles on the protocorallite with a simple arc-shaped outline and during further defined mode of budding and adding of corallites rapidly develops its S-shaped base (Fuchs & Plusquellec, 1982; Plusquellec, 2007). Further growth results in vertical, U-shaped tubes (Nicholson, 1979; Clarke, 1921; Gerth, 1952; nicely depicted also by Tapanila & Ekdale, 2007, fig. 19.7). Settling of the endosymbiont on the protocorallite clearly differs from the scleractinian-sipunculid association described above, as suggested by Gerth (1952) for the pleurodictyform-*Hicetes* association (for rejection see Schindewolf, 1959; Fuchs & Plusquellec, 1982; Plusquellec, 2007). Destruction of certain corallites by *Hicetes* points to a parasitic relationship (Schindewolf, 1959; Fuchs & Plusquellec, 1982; Plusquellec, 2007).

Also comparable in size is the Late Ordovician to middle Silurian bioclaustration ichnogenus *Cornulites*. It is probably obligatorily associated with tabulate corals and stromatoporoids (Dixon, 2010). The maximum diameter of cornulitid tubes in general ranges from 1.0 mm to 11.8 mm (Dixon, 2010; Vinn & Wilson, 2010; Vinn & Mötus, 2012). Major difference from our specimen concerns its low-divergent conoidal shape, secretion of a calcareous tube, and the presumably obligatory occurrence in colonial hosts. Cornulitids surviving into the Carboniferous did not form endosymbiotic associations (Vinn, 2016, 2017b).

As elucidated above, bioclaustrations in tabulate and rugose corals caused by endosymbiotic worms and tentaculitoid tubeworms hitherto were not recorded from the Carboniferous and the association was thought to became extinct in the latest Famennian (Tapanila, 2005; Zapalski et al., 2008). In fact, besides our record, only a single specimen of *Kiyasarophyllum fluegeli* Ogar, Falahatgar & Mosaddegh, 2013 infested by a large-sized endosymbiont is known to us (Ogar et al., 2013, fig. 12A$_1$-A$_2$). Like in our material, two roundish, but smaller cavities, maximum 1.5 mm × 1.6 mm wide, were figured that are completely encased by the coral skeleton; one cavity is also surrounded by dense irregular skeletal elements.

Endosymbionts infesting solitary or fasciculate corals were much less frequently recorded than those associated with massive colonial Rugosa or with tabulate corals. Oliver (1983) reported vermiform tubes in phaceloid and solitary rugose corals from the Devonian. Elias (1986) recorded *Trypanites* borings and a tubular chamber in Late Ordovician solitary Rugosa. In both cases, the tubes of the infesters were parallel to the axes of the corals and surrounded by skeletal material secreted by the coral hosts.

Despite the considerable size differences, the Late Ordovician and Devonian endosymbionts in general are similar to our specimens in the assumed behaviour. They entered the hosts through the calice openings and stayed there for a long term symbiotic relationship with direct contact to the polyps of the hosts.

The late Palaeozoic arrested development of endosymbionts

The diversity and abundance of endosymbionts declined after the Givetian and collapsed during the Kellwasser biotic crisis (Tapanila, 2005; Vinn, 2017a, b). They apparently were missing in the Carboniferous except for the record of the tentaculitoid *Streptindytes* in chaetetid sponges (Tapanila, 2005; Vinn, 2010, 2016). This was related to the decline, respectively extinction of the favoured, in part genus-specific host taxa among stromatoporoids, tabulate and cerioid rugose corals. In spite of the recovery of the coral diversity in the Visean (Scrutton, 1997; Aretz, 2010), colonial rugose corals were of relatively low diversity (Flügel, 1974; Yao et al., 2020). Tabulate corals remained a subordinate faunal element, mostly composed of fasciculate and small coralla (Herbig et al., 2011). Coral-dominated reefs also remained mostly small, in spite of some notable exceptions, and occurred relatively scarcely in space and episodically in time (e.g., Copper, 1994; Webb, 1994; Aretz, 2002, 2010; Shen & Webb, 2005; Aretz & Chevalier, 2007; Aretz et al., 2010; Rodríguez et al., 2012; Yao & Wang, 2016). The relatively low number of suitable colonial organisms and the unstable conditions concerning especially the growth of coral reefs (Copper, 1988; Webb, 1994, 2002; Aretz, 2002; Aretz & Chevalier, 2007) were major obstacles for the recovery of endosymbionts, which apparently were almost completely missing during the late Palaeozoic. Missing recovery appears to be related to the intricate process to acquire a long-term symbiotic relationship, as both the host and the endosymbiont must reach a balanced status living together without killing each other quickly, e.g., by overgrowth or encrustation (e.g., Zann, 1987). This problem was also addressed by Cowen (1988) concerning the presumed protracted reestablishment of photosymbiosis in ancient reefs. Thus, the arrested development of endosymbionts after the Frasnian-Famennian boundary event mostly mirrors the arrested reef development lasting throughout the Carboniferous, as described by Copper (1988, 1989) and Webb (2002, p. 239: "depressed reef building").

CONCLUSIONS

After the extinction events at the Frasnian-Famennian boundary, symbiotic associations between corals and macro-organisms had collapsed due to extinction of the hosts. Hitherto, endosymbiotic relations by bioclaustration were thought to became finally extinct during the Hangenberg Event at the Devonian-Carboniferous boundary. Succeeding symbiotic associations differed, consisting of intergrowth or encrustation, but documented examples remained rare throughout the Late Palaeozoic (e.g., Tapanila, 2005; Vinn, 2016, 2017b) during a period of arrested endosymbiont development. In general, solitary rugose corals are less affected than massive colonial Rugosa and Tabulata. Herein, the first symbiotic occurrence of a soft-bodied, worm-like organism and solitary rugose corals is documented from the Serpukhovian (late Mississippian) Hezhou Formation, Lower Yangtze Platform, South China. Moreover, it is the first bioclaustration, i.e., endosymbiotic relation in Carboniferous corals proving that in extraordinary rare, inadvertent cases this ecospace could be settled after the Hangenberg Event. The organism strongly resembles in size, shape and type of infestation the Devonian ichnotaxon *Hicetes*. It consists of a horizontal, U-shaped tube during first settling in the calice of the coral. During further skeletal secretion of the hosting coral, frontal and anal ends are bent upwards into vertical raising shafts. The organism, respectively the resulting endosymbiotic ichnofossil remains unnamed due to the scarce material. According to the large size of the endosymbiont and the reaction of the coral, a parasitic or commensal mode of life of the infesting organism is assumed.

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REFERENCES

Aretz M. (2002). Habitatanalyse und Riffbildungspotential kolonialer rugoser Korallen im Unterkarbon (Mississippium) von Westeuropa. *Kölner Forum für Geologie und Paläontologie*, 10: 1-155.

Aretz M. (2010). Habitats of colonial rugose corals: the Mississippian of western Europe as example for a general classification. *Lethaia*, 43: 558-572.

Aretz M. & Chevalier E. (2007). After the collapse of stromatoporid-coral reef-the Famennian and Dinantian reefs of Belgium: much more than Waulsortian mounds. *In* Álvaro J.J., Aretz M., Boulvain F., Munnecke A., Vachard D. & Vennin E. (eds), Palaeozoic reefs and bioaccumulations: climatic and evolutionary controls. *Geological Society London, Special Publications*, 275: 163-188.

Aretz M., Herbig H.-G., Somerville I.D. & Cózar P. (2010). Rugose coral biostromes in the late Viséan (Mississippian) of NW Ireland: Bioevents on an extensive carbonate platform. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 292: 488-506.

Bambach R.K., Bush A.M. & Erwin D.H. (2007). Autecology and the filling of ecospace: key metazoan radiations. *Palaeontology*, 50: 1-22.

Bird A. & Bird J. (1991). The structure of Nematodes, 2nd edition. 317 pp. Elsevier Science, Amsterdam.

Cai R.H. & Xi Y.H. (1985). Zones of fusulinids in the Carboniferous in Fenghuangshan of Chaoxian, Anhui. *Journal of Anhui University of Science and Technology*, 3: 1-11. [in Chinese with English abstract]

Capa M., Hutchings P. & Peart R. (2012). Systematic revision of Sabellariidae (Polychaeta) and their relationships with other polychaetes using morphological and DNA sequence data. *Zoological Journal of the Linnean Society*, 164: 245-284.

Clarke J.M. (1908). The beginning of dependant life. *New York State Museum Bulletin*, 121: 146-169.

Clarke J.M. (1921). Organic dependence and disease. Their origin and significance. *New York State Museum Bulletin*, 221-222: 1-113.

Copper P. (1988). Ecological succession in Phanerozoic reef ecosystems: is it real? *Palaios*, 3: 136-151.

Copper P. (1989). Enigmas in Phanerozoic reef development. *Memoirs of the Association of Australasian Palaeontologists*, 8: 371-385.

Copper P. (1994). Reefs under stress: the fossil record. *Courier Forschungsinstitut Senckenberg*, 172: 87-94.

Cowen R. (1988). The role of algal symbiosis in reefs through time. *Palaios*, 3: 221-227.

Dales R.P. (1963). Annelids. 200 pp. Hutchinson University Library, London.

Darrell J.G. & Taylor P.D. (1993). Macrosymbiosis in corals: a review of fossil and potentially fossilizable examples. *Courier Forschungsinstitut Senckenberg*, 164: 185-198.

Diesing K.M. (1851). Systema helminthum. Vol. 2. 558 pp. Wilhelm Braumüller, Vindobonae, Vienna.

Dixon O.A. (2010). Endobiotic cornulitids in Upper Ordovician tabulate corals and stromatoporoids from Anticosti island, Quebec. *Journal of Paleontology*, 84: 518-528.

Elias R.J. (1986). Symbiotic relationships between worms and solitary rugose corals in the Late Ordovician. *Paleobiology*, 12: 32-45.

Fagerstrom J.A. (1996). Palaeozoic brachiopod symbioses: testing the limits of modern analogues in paleoecology. *Geological Society of America Bulletin*, 108: 1393-1403.

Flügel H.W. (1974). Die Entwicklung der rugosen Korallen im Bereich der Devon/Karbon-Grenze. Compte Rendu du 7ème Congrès International de Stratigraphie et de Gèologie du Carbonifère, Krefeld 1971, 3: 81-87.

Fuchs G. & Plusquellec Y. (1982). *Pleurodictyum problematicum* Goldfuss 1829 (Tabulata, Dévonien). Statut, morphologie, ontogénie. *Geologica et Palaeontologica*, 15: 1-26.

Gerth H. (1952). Die von Sipunculiden bewohnten lebenden und jungtertiären Korallen und der wurmförmige Körper von *Pleurodictyum*. *Paläontologische Zeitschrift*, 25: 119-126.

Hausen H. (2005). Comparative structure of the epidermis in polychaetes (Annelida). *Hydrobiologia*, 535/536: 25-35.

Herbig H.-G., Nardin E. & Müller A. (2011). Palaeodiversity and faunal dynamics of post-Frasnian Tabulates, Western Palaeotethys. *In* Aretz M., Delculée S., Denayer J. & Poty E. (eds), 11th Symposium on Fossil Cnidaria and Porifera, Liège, August 19-29, 2011. Abstracts. *Kölner Forum für Geologie und Paläontologie*, 19: 51-52.

Hill D. (1981). Coelenterata: Anthozoa. Subclasses Rugosa, Tabulata. *In* Teichert C. (ed.), Treatise on Invertebrate Paleontology. Part F. Coelenterata, suppl. 1, Rugosa and Tabulata. 762 pp. Geological Society of America and University of Kansas Press, Boulder, Lawrence.

Hoeksema B.W. & Best M.B. (1991). New observations on scleractinian corals from Indonesia: 2. Sipunculan-associated species belonging to the genera *Heterocyathus* and *Heteropsammia*. *Zoologische Mededelingen Leiden*, 65: 221-245.

Hoeksema B.W., Wels D., van der Schoot R.J. & ten Hove H.A. (2019). Coral injuries caused by *Spirobranchus* opercula with and without epibiotic turf algae at Curaçao. *Marine Biology*, 166: 60.

Li Y.F. & Jiang L.F. (1997). The lithostratigraphy of the Anhui Province. 271 pp. China University of Geosciences Press, Wuhan. [in Chinese]

Lin W. (2013). Late Viséan-Serpukhovian rugose corals from South China. 200 pp. Unpublished Ph.D. thesis, Chinese Academy of Science, Nanjing Institute of Geology and Palaeontology.

Lin W. & Herbig H.-G. (2019). Endosymbionts in late Mississippian (Carboniferous) rugose corals from South China. *In* Bosellini F., Aretz M., Papazzoni C.A. & Vescogni A. (eds),13th International Symposium on Fossil Cnidaria and Porifera, Modena, 3-6 September 2019, Abstract Book: 41.

Lin W., Wang X., Poty E. & Aretz M. (2012). Late Viséan to early Serpukhovian rugose corals from the Yashui section, Guizhou, South China. *Geologica Belgica*, 15: 329-339.

Malakhova N.P. (1956). Foraminifera of the limestones of the Shartymka River in the southern Urals. *Akademiya Nauk SSSR, Ural'skii Filial, Trudy Gorno-Geologicheskovo Institut, vypusk* 24*, Sbornik po Voprosam Stratigrafii*, 3: 72-124. [in Russian]

McCoy F. (1844). A synopsis of the characters of the Carboniferous limestone fossils of Ireland. 207 pp. Dublin University Press, Dublin.

Nicholson H.A. (1879). On the structure and affinities of the "Tabulate Corals" of the Palaeozoic Period: With critical descriptions of illustrative species. XIII + 342 pp. Blackwell & Sons, Edinburgh - London.

Oekentorp K. (1969). Kommensalismus bei Favositiden. *Münstersche Forschungen zur Geologie und Paläontologie*, 12: 165-217.

Ogar V., Falahatgar M. & Mosaddegh H. (2013). Visean corals of the Kiyasar area, south of Sari, Northern Iran. *Revista Brasileira de Paleontologia*, 16: 375-396.

Oliver W.A. (1983). Symbioses of Devonian rugose corals. *Memoirs of the Association of Australasian Palaeontologists*, 1: 261-274.

Palmer T.J. & Wilson M.A. (1988). Parasitism of Ordovician bryozoans and the origin of pseudoborings. *Palaeontology*, 31: 939-949.

Plusquellec Y. (1968). Commensaux des Tabulés et Stromatoporoides du Dévonien armoricain. *Annales de la Société Géologique du Nord*, 88: 47-56.

Plusquellec Y. (2007). Histoire naturelle des Pleurodictyformes (Cnidaria, Tabulata, Devonien) du Massif Amoricain et des regions Maghrebo-Europeennes principalement. *Mémoires de la Société Géologique et Minéralogique de Bretagne*, 23: 1-138.

Poty E., Aretz M. & Xu S. (2011). A comparison of Mississippian colonial rugose corals from Western Europe and South China. *In* Aretz M., Delculée S., Denayer J. & Poty E. (eds), 11th Symposium on Fossil Cnidaria and Porifera, Liège, August 19-29, 2011. Abstracts. *Kölner Forum für Geologie und Paläontologie*, 19: 135-136.

Poty E., Devuyst F.-X. & Hance L. (2006). Upper Devonian and Mississippian foraminiferal and rugose coral zonations of Belgium and northern France: a tool for Eurasian correlations. *Geological Magazine*, 143: 829-857.

Reitlinger E.A. (1949). Smaller foraminifers in the lower part of the middle Carboniferous of the Middle Urals and Kama River area. *Izvestiya Akademii Nauk SSSR, Seriya Geologicheskaya*, 6: 149-164. [in Russian]

Rodríguez S., Somerville I.D., Said I. & Cózar P. (2012). Late Viséan coral fringing reef at Tiouinine (Morocco): implications for the role of rugose corals as building organisms in the Mississippian. *Geological Journal*, 47: 462-476.

Rouse G.W., Hutchings P.A., Wilson R.S., Glasby C.J., Paxton H. & Watson Russell C. (2000). Canalipalpata Polychaeta. *In* Fauna of Australia. Volume 4A. Polychaetes & Allies: 230-320.

Rouse G. & Pleijel F. (2001). Polychaetes. 384 pp. Oxford University Press, Oxford.

Sanfilippo R., Rosso A., Mastandrea A., Viola A., Deias C. & Guido A. (2019). *Sabellaria alveolata* sandcastle worm from the Mediterranean Sea: new insights on tube architecture and biocement. *Journal of Morphology*, 280: 1839-1849.

Schindewolf O. (1959). Würmer und Korallen als Synöken. Zur Kenntnis der Systeme *Apsidosiphon*/*Heteropsammia* und *Hicetes*/*Pleurodictyum*. *Akademie der Wissenschaften und der Literatur Mainz, Abhandlungen der mathematisch-naturwissenschaftlichen Klasse*, 1958: 263-328.

Scrutton C.T. (1997). The Palaeozoic corals. I: origins and relationships. *Proceedings of the Yorkshire Geological Society*, 51: 177-208.

Shen J.-W. & Webb G.E. (2005). Metazoan-microbial framework fabrics in a Mississippian (Carboniferous) coral-sponge-microbial reef, Monto, Queensland, Australia. *Sedimentary Geology*, 178: 113-133.

Sheng Q.-Y., Wang X.-D., Brenckle P. & Huber B.T (2018). Serpukhovian (Mississippian) foraminiferal zones from the Fenghuangshan section, Anhui Province, South China: implications for biostratigraphic correlations. *Geological Journal*, 53: 45-57.

Smith D.C. & Douglas A.E. (1987). The biology of symbiosis. 302 pp. Edward Arnold, London.

Smith S. (1917). *Aulina rotiformis*, gen. et. sp. nov., *Phillipsastraea hennahi* (Lonsdale), and *Orionastraea*, gen. nov. *The Quarterly Journal of the Geological Society of London*, 72: 280-307.

Sokolov B.S. (1948). Kommensalizm u Favositid. *Izvestija Akademii Nauk SSSR, Seriya Biologicheskaya*, 1: 101-110.

Stewart L.A., Elias R.J. & Young G. (2010). Stromatoporoids and colonial corals hosting borers and linguloid brachiopods, Ordovician of Manitoba, Canada. *Palaeoworld*, 19: 249-255.

Stolarski J., Zibrowius H. & Löser H. (2001). Antiquity of the scleractinian-sipunculan symbiosis. *Acta Palaeontologica Polonica*, 46: 309-330.

Tan Z., Dong Z., Jin Y., Li S., Yang Y. & Jiang S. (1987). The Late Devonian and Early Carboniferous strata and palaeobiocenosis of Hunan. 200 pp. Geological Publishing House, Beijing.

Tapanila L. (2005). Palaeoecology and diversity of endosymbionts in Palaeozoic marine invertebrates: Trace fossil evidence. *Lethaia*, 38: 89-99.

Tapanila L. & Ekdale A.A. (2007). Early history of symbiosis in living substrates: trace-fossil evidence from the marine record. *In* William Miller III (ed.), Trace fossils: concepts, problems, prospects: 345-355.

Taylor P.D. (2015). Differentiation parasitism and other interactions in fossilized colonial organisms. *In* De Baets K. & Littlewood T.J. (eds), Fossil parasites. *Advances in Parasitology*, 90: 329-347.

Vinn O. (2010). Adaptive strategies in the evolution of encrusting tentaculitoid tubeworms. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 292: 211-221.

Vinn O. (2016). Tentaculitoid tubeworms as endobiotic symbionts of Paleozoic corals and sponges. *Palaios*, 31: 440-446.

Vinn O. (2017a). Symbiosis between Devonian corals and other invertebrates. *Palaios*, 32: 382-387.

Vinn O. (2017b). Symbiosis in Late Devonian-Mississippian corals: a review. *Palaeobiodiversity and Palaeoenvironments*, 97: 723-729.

Vinn O., Ernst A. & Toom U. (2016). Earliest symbiotic rugosans in cystoporate bryozoan *Ceramopora intercellata* Bassler, 1911 from Late Ordovician of Estonia (Baltica). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 461: 140-144.

Vinn O., Ernst A. & Toom U. (2018). Bioclaustrations in Upper Ordovician bryozoans from northern Estonia. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 289: 113-121.

Vinn O., Liang Kun & Toom U. (2017). Endobiotic rugose coral symbionts in Silurian tabulate corals from Estonia (Baltica). *Palaios*, 32: 158-165.

Vinn O. & Mõtus M.-A. (2012). Diverse early endobiotic coral symbiont assemblage from the Katian (Late Ordovician) of Baltica. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 321-322: 137-141.

Vinn O. & Wilson M.A. (2010). Endosymbiotic *Cornulites* in the Sheinwoodian (Early Silurian) stromatoporoids of Saaremma, Estonia. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 257: 13-22.

Vinn O. & Wilson M.A. (2015). Symbiotic interactions in the Ordovician of Baltica. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 436: 58-63.

Wang X.-D., Qie W., Sheng Q., Qi Y., Wang Y., Liao Z., Shen S.-Z. & Ueno K. (2013). Carboniferous and Lower Permian sedimentological cycles and biotic events of South China. *In* Gąsiewicz A. & Słowakiewicz M. (eds), Palaeozoic climate cycles: their evolutionary and sedimentological impact. *The Geological Society, London, Special Publications*, 376: 33-46.

Wang X.-D., Zhang Y.-Q. & Lin W. (2010). Carboniferous-Permian rugose coral *Cyathaxonia* faunas in China. *Science China. Earth Sciences*, 53: 1864-1872.

Webb G.E. (1994). Non-Waulsortian Mississippian bioherms: a comparative analysis. *In* Embry A.F., Beauchamp B. & Glass D.J. (eds), Pangea. Global environments and resources. *Canadian Society of Petroleum Geologists, Memoir*, 17: 701-712.

Webb G.E. (2002). Latest Devonian and Early Carboniferous reefs: depressed reef building after the middle Palaeozoic collapse. *In* Kiessling W., Flügel E. & Golonka J. (eds), Phanerozoic reef patterns. *SEPM Special Publication*, 72: 239-269.

Wright K.A. (1987). The nematode cuticle - its surface and epidermis: function, homology, analogy - a current census. *Journal of Parasitology*, 73: 1077-1083.

Wu W.S. (1964). Lower Carboniferous corals from central Hunan. *Memoirs of Nanjing Institute of Geology and Paleontology, Academia Sinica*, 3: 1-100.

Xia G.S. & Xu J.C. (1980). Lower Carboniferous strata in Chaohu area, Anhui Province. *Journal of Stratigraphy*, 4: 87-95. [in Chinese]

Yao L., Aretz M., Wignall P.B., Chen J., Vachard D., Qi Y., Shen S. & Wang X. (2020). The longest delay: re-emergence of coral reef ecosystems after the Late Devonian extinctions. *Earth-Science Reviews*, 203: 103060.

Yao L. & Wang X. (2016). Distribution and evolution of Carboniferous reefs in South China. *Palaeoworld*, 25: 362-372.

Yu C.C. (1931). The correlation of the Fengningian System, the Chinese Lower Carboniferous, as based on coral zones. *Bulletin of the Geological Society of China*, 10: 1-30.

Zann L.P. (1987). A review of macrosymbiosis in the coral reef ecosystem. *International Journal for Parasitology*, 17: 399-405.

Zapalski M.K. (2009). Parasites in Emsian-Eifelian *Favosites* (Anthozoa, Tabulata) from the Holy Cross Mountains (Poland): changes of distribution within colony. *In* Königshof P. (ed.), Devonian Change: Case studies in palaeogeography and palaeoecology. *The Geological Society, London, Special Publications*, 314: 125-129.

Zapalski M.K., Pinte E. & Mistiaen B. (2008). Late Famennian ?*Chaetosalpinx* in *Yavorskia* (Tabulata): the youngest record of tabulate endobionts. *Acta Geologica Polonica*, 58: 321-324.

Zeller D.E.N. (1953). Endothyroid foraminifera and ancestral fusulinids from the type Chesterian (Upper Mississippian). *Journal of Paleontology*, 27: 183-199.

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Donezella-chaetetid mounds in the Valdeteja Formation (Bashkirian, Pennsylvanian) at Truébano, Cantabrian Mountains, northern Spain

Isabel Rodríguez-Castro*, Sergio Rodríguez & Marián Fregenal-Martínez

I. Rodríguez-Castro, Departamento de Geodinámica, Estratigrafía y Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, c/ José Antonio Novais 2, E-28040 Madrid, Spain; isrodr01@ucm.es **corresponding author*

S. Rodríguez, Departamento de Geodinámica, Estratigrafía y Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, c/ José Antonio Novais 2, E-28040 Madrid, Spain; Departamento de Geología Sedimentaria y Cambio Medioambiental, Instituto de Geociencias, CSIC, UCM, c/ José Antonio Novais 2, E-28040 Madrid, Spain; sergrodr@ucm.es

M. Fregenal-Martínez, Departamento de Geodinámica, Estratigrafía y Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, c/ José Antonio Novais 2, E-28040 Madrid, Spain; mariana@ucm.es

KEY WORDS - Carboniferous, algospongia, León, limestone, palaeontology.

ABSTRACT - The Bashkirian-lower Moscovian Valdeteja Formation crops out in the Cantabrian Zone (NW Spain). It is composed of pale grey limestone with a diverse fossil content, calcareous breccias and massive limestone composed of algal and microbial mounds accumulated in a high relief carbonate platform. Outstanding outcrops of that formation appear near the village of Truébano (León Province, North Spain) at the old coal mine "Mina Rosario." The mine is a peculiarity in the formation as it shows interbedded siltstones and coal beds containing coal balls. The studied succession above the coal seam is lower Bashkirian and 20.2 m thick. Dark grey, massive to well-bedded limestones interbedded with thin marly beds are dominant in that interval. The main component of the limestones is the algospongia Donezella *that is found in two different facies: packstone of resedimented* Donezella*, which appears in the lower beds of the section, and boundstone of* Donezella*,* Girvanella *and chaetetids, in the upper beds. Additional components are highly diverse including foraminifera, other calcified microbes, rhodophyta, sponges, echinoderms, arthropods, brachiopods, bryozoans and scarce corals and molluscs. Organic matter is abundant in the marly beds, but palynomorphs are poorly preserved. An interbedded layer of quartz sandstones lacking fossil content occurs in the upper part of the sequence.*

The depositional environment of the facies is part of a carbonate platform top near the fair-weather wave base, within subtidal zone, with development of "algal" mounds and sedimentation of debris from the same buildups. The composition and components distribution of both microfacies fit well with the mounds previously described in other outcrops of the Valdeteja Formation, with the exception of the participation of chaetetids as a main building component in some beds.

INTRODUCTION

Algal mounds are common in the Pennsylvanian and have been described in locations such as the American Midcontinent China, the Carnic Alps and the Cantabrian Mountains, in Spain (Samankassou, 2001, 2003; Gong et al., 2007). The main builders of these mounds are phylloid algae, but there are reports of mounds built by other organisms. For instance, Dasycladales (Samankassou, 2001) and algospongia such as donezellids, formerly considered algae (Vachard & Cozar, 2010). "Algospongia" is a Class proposed by Vachard & Cózar (2010). It includes problematic organisms, traditionally assigned to Porifera, Chlorophyta and Rhodophyta, and regroups them in two orders: Moravamiinida and Aoujgaliida. Algal mounds are common in the Carboniferous limestones from the Cantabrian Mountains (northern Spain), mainly in the Valdeteja, Picos de Europa and San Emiliano formations. The algospongia *Donezella* is the main builder of many of these mounds, which have been reported and studied in different locations by authors such as Bowman (1979), Riding (1979), Eichmuller (1985), Samankassou (2001), Della Porta et al. (2002a) and Chesnel et al. (2016, 2017). All the *Donezella* mounds reported by those researchers are upper Bashkirian and Moscovian, except for the lower Bashkirian mounds studied by Eichmüller (1985) near the Valdeteja village.

This study focuses on the "Mina Rosario", an abandoned coal mine that provides an excellent outcrop of the Valdeteja Formation. The mine is in the place known as "Cuesta del Sol" next to Truébano, a village in the San Emiliano municipality in the León Province, northern Spain (Fig. 1).

Here we report the first description and analysis of the *Donezella*-bearing limestones strata overlying the carbonaceous marls of the coal mine. The aim of the palaeontological and sedimentological analyses herein presented is to establish the sedimentary environment and the age of the *Donezella* mounds. This analysis is part of a larger study about the palaeontology and microfacies in the "Mina Rosario" outcrop, part of which is published by Rodríguez-Castro et al. (2019).

GEOLOGICAL SETTING

The Valdeteja Formation (Bashkirian) crops out in Northwest Spain in the Cantabrian Zone of the Iberian Massif. The Cantabrian Zone consists in a thick succession of Palaeozoic deposits that was deformed into a set of imbricated thrusts during the Variscan Orogeny (Bahamonde et al., 2000; Alonso et al., 2009). It is characterised by a low-degree or null metamorphism, low deformation and thin-skinned tectonic structure (Julivert, 1971; Bastida, 2004). The thrust sheets divide the zone

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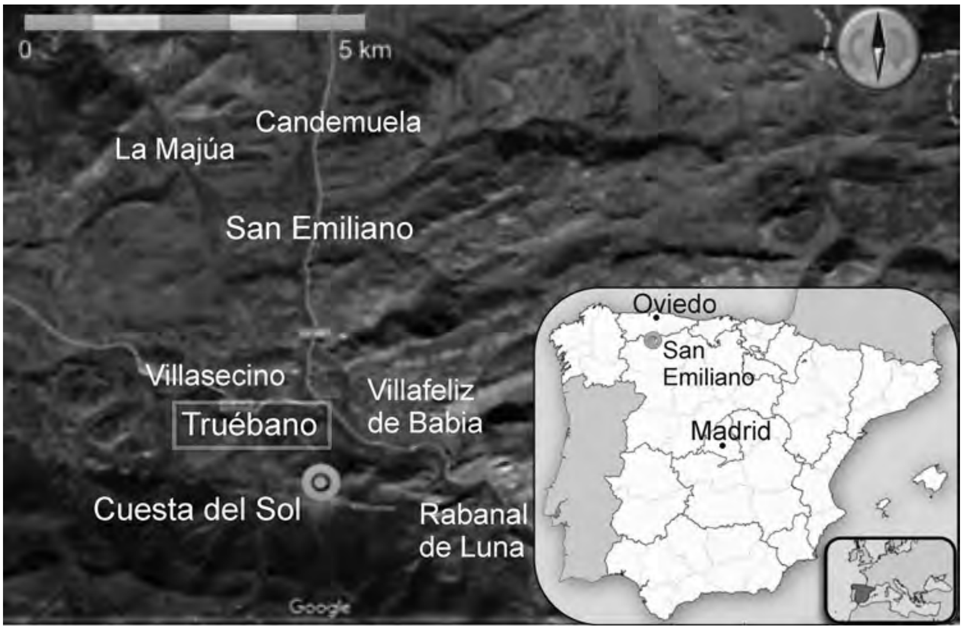


Fig. 1 - Location of the Mina Rosario outcrops. Modified from google maps (image property of TerraMetrics) and WikimediaCommons (author HansenBCN).

in multiple tectonic units (Bastida, 2004), such as the Sobia-Bodón Unit, where the study area is located.

The sedimentary record of the Cantabrian Zone can be divided in two thick sedimentary sequences: the pre-orogenic sequence (Precambrian-Devonian) and the syn-orogenic sequence (Carboniferous) (Julivert, 1978; Marcos & Pulgar, 1982), which records the sedimentation in carbonate platforms developed in the foreland basin of the Variscan orogen currently located in the north of the Iberian Massif. The studied succession belongs to this sequence.

Winkler Prins (1968) originally defined as "Valdeteja" the Valdeteja Member of the Caliza de Montaña Formation. This member is now a formation of its own, and "Caliza de Montaña" has turned into an informal term for both the Barcaliente Formation (Serpukhovian-Bashkirian) and the Valdeteja Formation (Bashkirian). The former appears in all the tectonic units of the Cantabrian Zone, while the latter is limited to the Sobia-Bodon, Áramo and Picos de Europa units, and to the Central Carboniferous Basin (Bastida, 2004).

Bastida (2004) described the Valdeteja Formation as an ensemble of light-coloured limestones with diverse fossil content, calcareous breccias and massive microbial and algal boundstones. Although it is a well-known formation, detailed sedimentological and microfacies studies of the Valdeteja Formation are scarce in the León Province. The facies of the Carboniferous carbonate platform have been studied in higher detail in several outcrops in Asturias, especially in the Sierra de Cuera, where it is hard to distinguish the Valdeteja Formation from the overlying Picos de Europa Formation (Moscovian) (Bahamonde et al., 1997). Moreover, most of those studies focus on the later formation and substage (Bahamonde et al., 2004, 2008), and when they also address the Bashkirian they usually just include a few samples or a small section of the stratigraphic logs from the upper Bashkirian (Della Porta et al., 2002a, b, 2003, 2004; Verwer et al., 2004). The main exceptions are Bahamonde et al. (1997, 2007), which analyse more in detail the facies of Valdeteja.

Most studies in the León Province focus on its palaeontological content and biostratigraphy based on foraminifera and macroflora (Wagner et al., 1971; Villa, 1982; Ginkel & Villa, 1991; Villa et al., 2001). The main sedimentological study of the Valdeteja Formation in the province is that of Eichmüller (1985), who established the depositional environment of the formation as a high relief carbonate platform surrounded by a deep siliciclastic basin. This interpretation is confirmed by Bahamonde et al. (2000), Della Porta et al. (2002b), Kenter et al. (2002) and Chesnel et al. (2016, 2017). These authors described accurately the geometry and stratigraphic architecture of the carbonate platform in the Picos de Europa unit based on exceptional outcrop conditions at Las Llacerias, Sierra de Cuera and Valdorria.

The "Mina Rosario" outcrop is a peculiarity inside the Valdeteja Formation, because of the presence of carbonaceous marls with coal balls. It was first studied while the mine was still active (Gómez-de-Llarena & Rodríguez-Arango, 1946). Those authors described the coal balls, called "Tacañas" by the miners, and their fossil content (*Calamites*, other vegetal remains, corals, crinoids, brachiopods and small gastropods). They also established the age of the carbonaceous marls as early Westfalian (Moscovian).

Other authors that studied the mine have also focused on the coal balls, analysing their depositional environment, formation processes and their fossil content, specifically the foraminifera and algae (Vachard & Beckary, 1988, 1991). Despite the interest that the carbonaceous bed has awakened among the researchers, the rest of the outcrop and its unique features have been ignored until now.

METHODS

Field work includes measurement of stratigraphical log (Fig. 2), observation and description of rock structures and textures and sedimentological and palaeontological sampling of each bed. The carbonaceous marls serve as the base of the log, while the top is the first bed that could not be measured due to the difficult access. The palaeontological samples include palynomorphs, microfossil and macrofossil samples, which are stored in the Facultad de Ciencias Geológicas (Universidad Complutense de Madrid). The palynological samples have been treated with acids for extraction of palynomorphs in the laboratory of the Huelva University by F. González, who also analysed them. Horizontal and vertical thin sections have been prepared from each sedimentological and palaeontological sample. They have been studied with optical microscope. The thin sections from bed 9 have been stained for checking the presence of carbonate cements (Lindholm & Finkelman, 1972). The carbonate rocks have been described using the Dunham (1962) and Embry & Klovan (1971) classifications, while for sandstones we apply Pettijohn (1954). For the environmental reconstruction we employed the method described by Said et al. (2010). It consists in the identification of environmental factors (such as hydrodynamic energy, salinity, depth and oxygenation), which then are used to deduce the sedimentary environment.

DESCRIPTION OF THE "MINA ROSARIO" OUTCROP

The studied succession crops out in two open pit mines at the Mina Rosario (Fig. 3). In the biggest open pit, the bedding planes strike roughly east-west and dip almost vertical due to its location next to the overthrust of the Sobia-Bodón Unit by the Somiedo Unit, which in this area is E-W directed. In the western open pit, of smaller size, the bedding planes' strike and dip are conditioned by a local fault (Fig. 3). The carbonaceous marls are lenticular and present lateral thickness changes.

The measured and studied succession is 20.2 metres thick. It is mainly composed of decimetric to metric grey limestones and marl beds. The limestones are laterally continuous in thickness along the mine, while the marl beds are thinner, and some of them disappear laterally. Stratification is irregular because of the amalgamation of the mounds, already reported in other areas of the Cantabrian mountains (Bahamonde et al., 2000; Corrochano et al., 2011). Bioturbation is common in all the carbonate beds.

The packstones that occur in the 13.5 m thick lower part of the succession (beds 1-6 in Fig. 2) are fine-grained, bioclastic, and do not contain any fossil identifiable at field scale. Beds 2 and 6 are well bedded in decimetric layers, and bed 6 even contains interbedded thin marl layers, but most of the limestone levels are massive. Petrographic

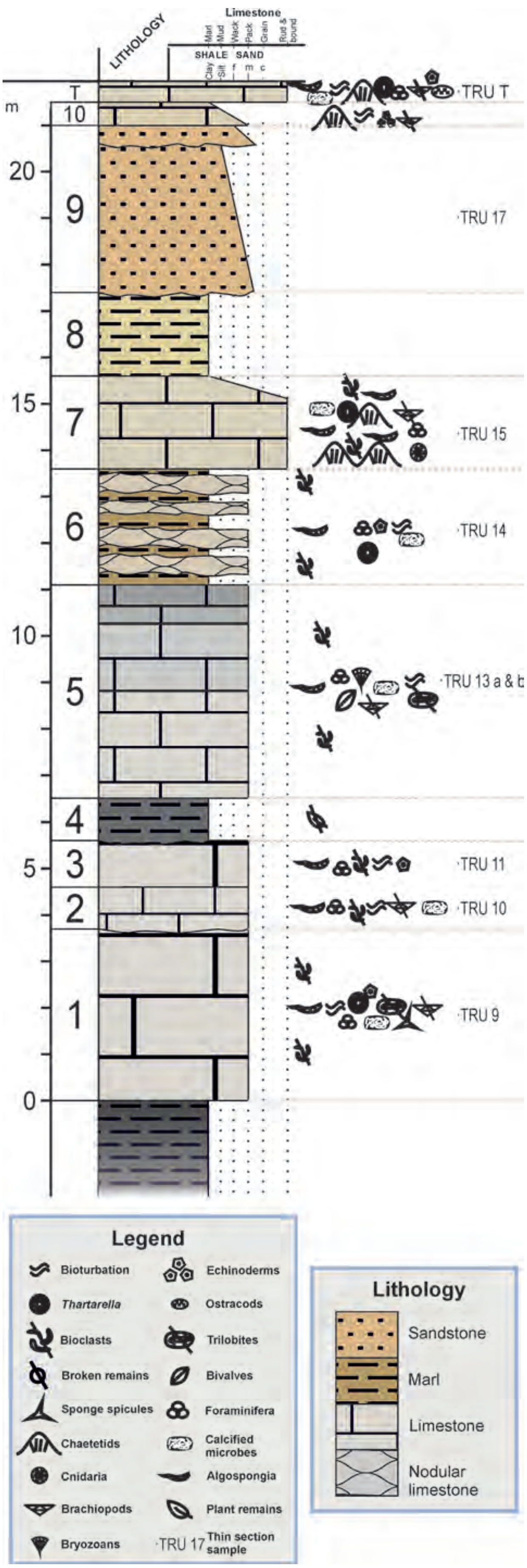


Fig. 2 - (color online) Stratigraphic log of the studied succession. The carbonaceous marls serve as a base for the log, while the top (T) marks the start of beds that could not be reached. Intervals 1 to 10 based on lithological features. Colors in the log represent the actual colors of the rocks on the field.

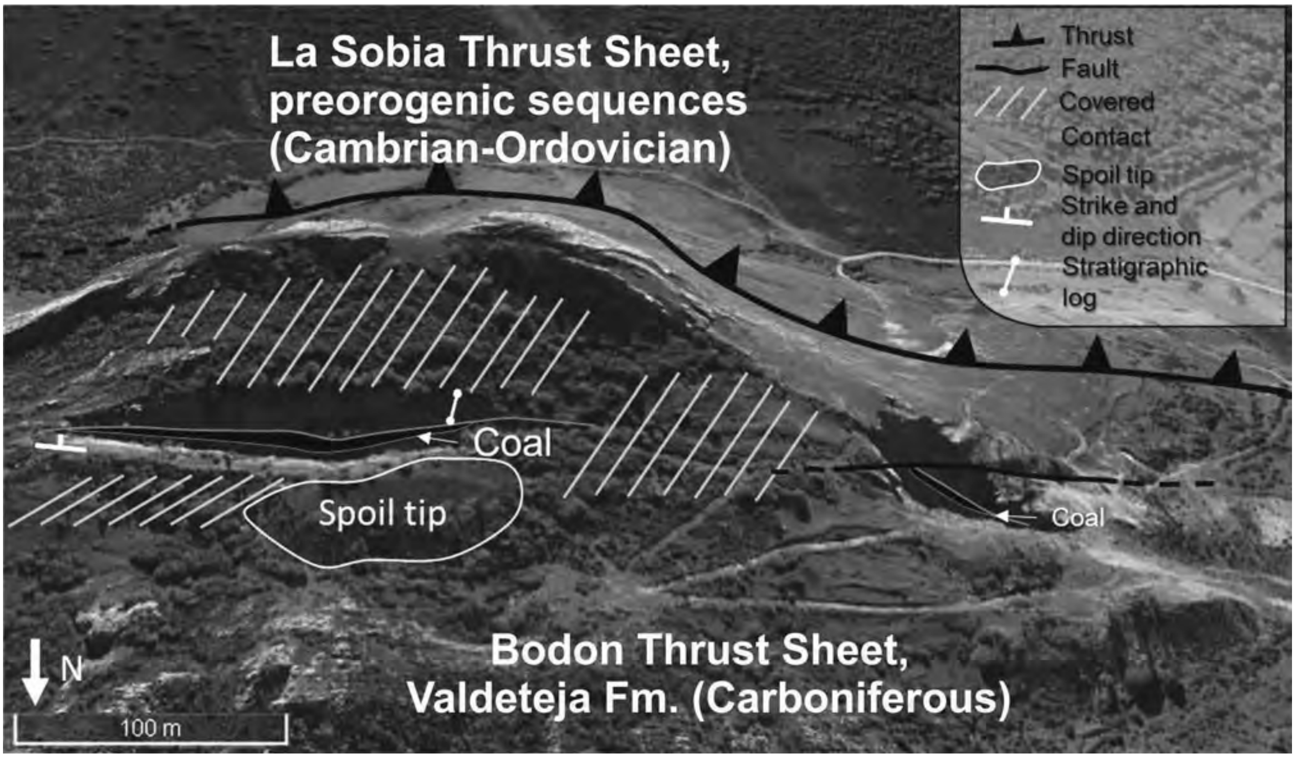


Fig. 3 - Sketch diagram of the outcrop over aerial photograph. Satellite image from google maps (image property of TerraMetrics).

analysis shows a diverse fossil assemblage, composed mainly of broken *Donezella* thalli and other algospongia genera such as *Ungdarella*, *Petschoria*, *Faciella*, *Beresella* and *Uraloporella*. Other components are crinoids and undetermined echinoderm plates, foraminifera (mainly fusulinids and endothyrids), broken brachiopod shells, ostracods, bryozoans and *Girvanella*. Scarce trilobites, mollusc fragments, rugose corals and sponge spicules are found in some samples.

The limestones of the upper part of the succession (beds 7 to top in Fig. 2) are boundstones, and their main components are chaetetids, algospongia (mainly

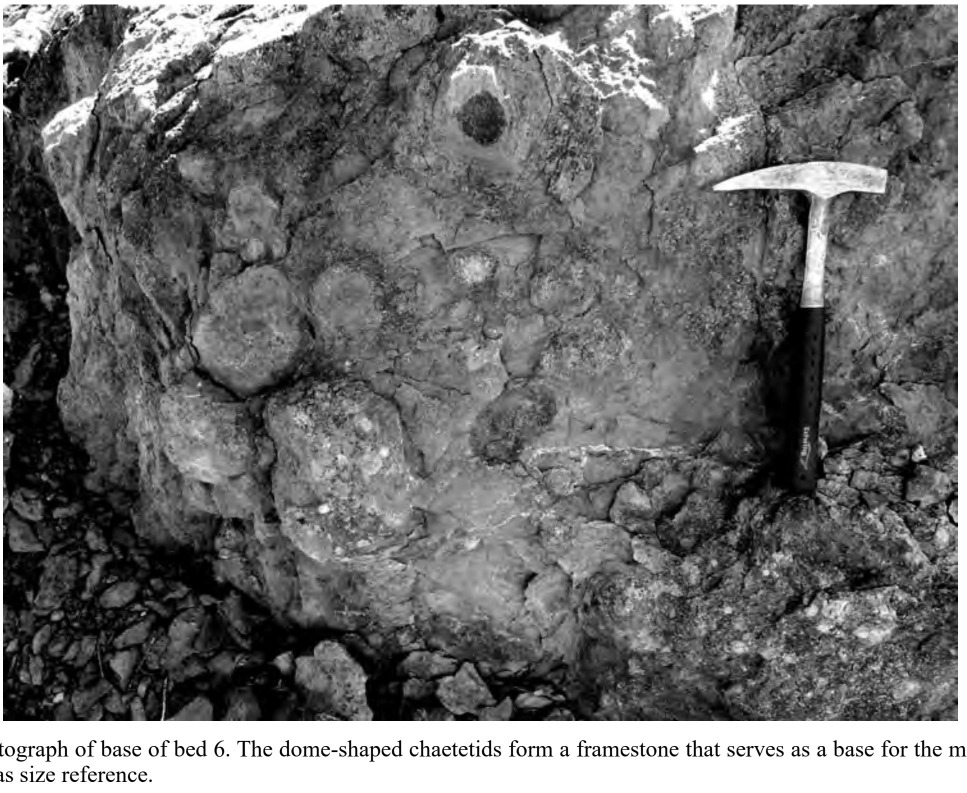


Fig. 4 - Field photograph of base of bed 6. The dome-shaped chaetetids form a framestone that serves as a base for the mound. Geological hammer (30 cm) as size reference.

Donezella) and *Girvanella*. The mounds range from 40 centimetres to two metres in thickness. The base of some of the buildups is a continuous framestone of chaetetids (Fig. 4), which become less common towards the upper part of the stratum. The spaces between the chaetetids are filled with a bafflestone composed of *Donezella* and *Girvanella*, and with bioclasts. The grain size decreases upwards, and bed 7 passes gradually upwards to a marl layer. The beds overlying the studied succession appear to be similar buildups, with different thickness of the individual beds.

The marl beds are laminated and do not contain macrofossils. They vary from black and dark brown marls in bed 4 to brown in bed 6 and to light brown in bed 8. The darker levels contain abundant organic matter and degraded phytoclasts.

An ochre quartz sandstone appears near the top of the succession (bed 9). It is composed of two fining-upwards sequences with irregular bases. The sandstone completely lacks fossil content or carbonate components, as it is only composed of well sorted quartz grains. Until now, this is the only sandstone bed described for the Valdeteja Formation in the León Province.

FOSSIL CONTENT

The thin sections show a high-diversity assemblage, where at least seven animal Phyla are represented: Porifera, Cnidaria, Arthropoda, Echinodermata, Mollusca, Brachiopoda, Bryozoa (Fig. 5). There are also members of the Phyla Foraminifera, Cyanobacteria, Rhodophyta and the Class Algospongia (undetermined Phylum and Kingdom) (Fig. 6). The palinomorph samples just yielded scarce and unidentifiable spores and continental amorphous organic matter (degraded phytoclasts).

Most fossil remains are broken and/or disarticulated. It was possible to identify foraminifera, algospongia, cyanobacteria, rhodophyta, rugose corals and sponges on the genus level. The abundance and diversity of foraminifera and algospongia made possible to identify even some species.

Porifera - Chaetetids are one of the main components of the boundstones in beds 7 and 10. They range from 10 to 20 centimeters and are dome-shaped (Fig. 4). Moreover, scarce sponge spicules appear in bed 1.

Cnidaria - Scarce tabulated and rugose corals appeared in scree from the section. The only identifiable specimen was the rugose coral *Semenophyllum* sp., which was found in scree probably from bed 7.

Arthropoda - Ostracods occur as a secondary component in all units, and scarce broken trilobite fragments appear in beds 1 and 5.

Echinodermata - Echinoderm plates are frequent in every bed. Most of them are crinoid and undetermined plates, but Echinoidea spines appear in some thin sections too.

Brachiopoda - They occur in the whole outcrop as a secondary component of the fossil assemblage. All of them are broken shells that cannot be assigned to any Class.

Mollusca - Molluscs are scarce and mainly found in the first bed. Most of them are broken unidentifiable shells, but a few gastropods are present in thin sections.

Bryozoa - They occur in every bed of the outcrop, but they are not abundant. Most of them are broken and cannot be identified, but a few of them belong to the Order Fenestrata.

Algospongia, algae and cyanobacteria - Those are some of the most diverse groups in the studied section. The most abundant fossils in the studied outcrop belong to Algospongia, such as *Donezella*, the main mound-builder (along with chaetetids and some cyanobacteria). *Ungdarella* is also abundant, along with the red algae *Archaeolithophyllum* and the cyanobacteria *Girvanella*.

Foraminifera - Foraminifera are the most diverse Phylum in the outcrop. At least twenty species and genera have been identified. They are frequent in every bed, and most of them belong to Fusulinida and Endothyrida, while Archeodiscida are scarcer. There is just one genera (*Tuberitina*) of Afusulinina, but it is abundant in all the samples.

The list of all the identified taxa and their distribution is shown in Fig. 7.

MICROFACIES

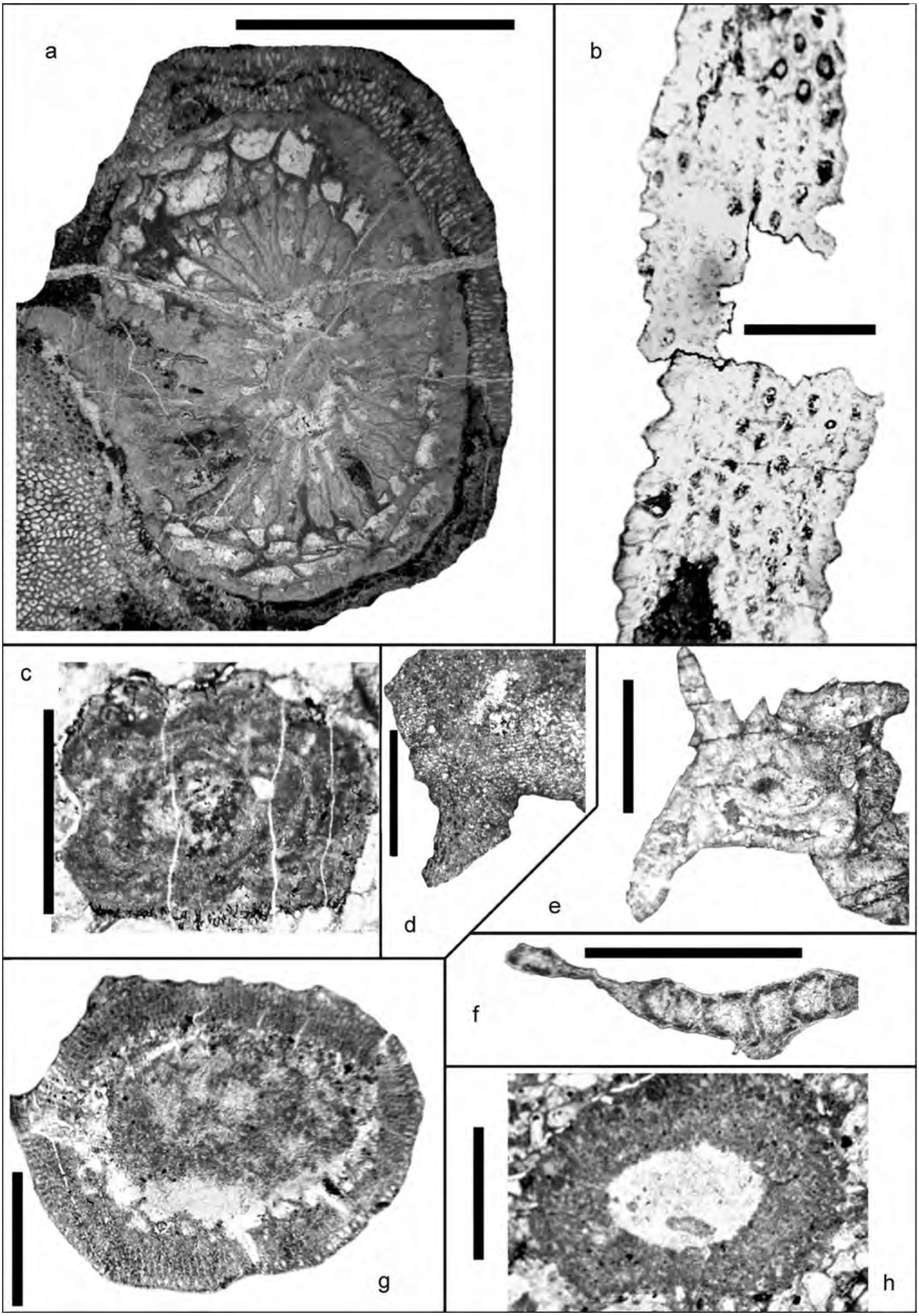
Two carbonate microfacies, characterised by distinct depositional textures, fossil assemblages and taphonomic preservation states, can be differentiated in the studied section.

Microfacies 1: resedimented algospongia packstone

It is the most frequent microfacies in the studied levels and appears in samples in all limestone beds (Fig. 2). This packstone is defined by the presence of broken and resedimented *Donezella* as the main component (Fig. 8). Grain size varies between samples and even between different areas of the same sample, but most samples are fine-grained.

The secondary components are other algospongia such as *Beresella*, *Petschoria* and *Fasciella*, broken brachiopod shells, crinoid plates, sea urchin spines and foraminifera. There are abundant fusulinids, endothyrids and *Tuberitina*, and scarce or even absent archaeodiscids. There are also ostracods, abundant red algae (*Archaeolithophyllum*), mollusc remains, some bryozoans, trilobite fragments, cyanobacteria (*Girvanella* and *Renalcis*) and isolated rugose corals.

This assemblage is relatively diverse, with seven animal Phyla and more than twenty-five genera of Foraminifera, Algospongia, Cyanobacteria and Rhodophyta (Fig. 7). The equitability is low, as *Donezella* absolutely dominates the assemblage.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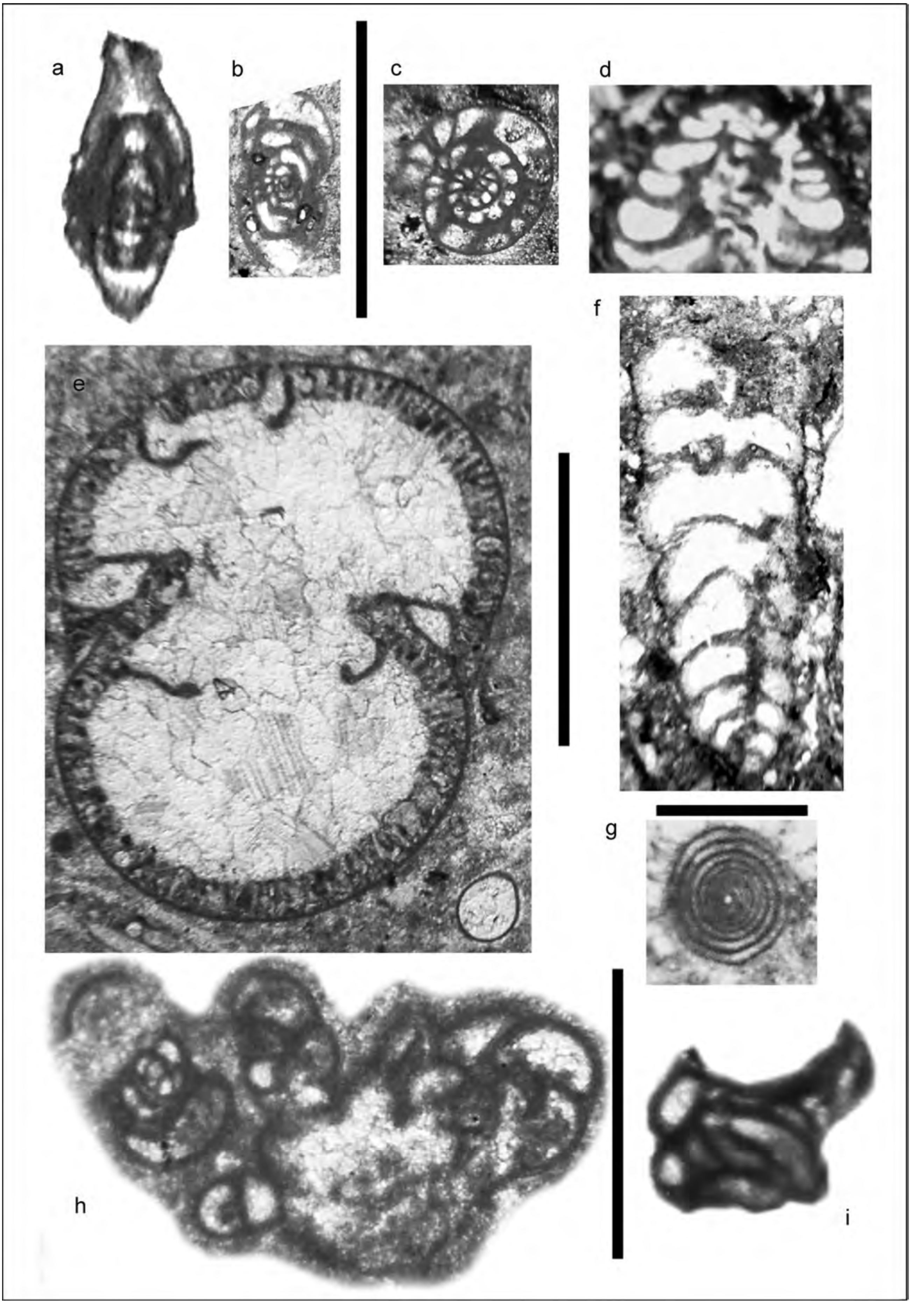
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Fig. 5 - (pag. vi) Mound builders and dwellers. a) Rugose corals, *Semenophyllum* sp. incrusted by a chaetetid, scree, DPM 12066 TRU 0. b) Bryozoans, fenestrate bryozoan, DPM 12066 TRU 13. c) Calcified microbes, *Girvanella* sp., DPM 12066 TRU 14. d-g) Algospongia, *Ungdarella* sp. (d), DPM 12066 TRU 9; *Fasciella* sp. (Aoujgaliida) (e), DPM 12066 TRU 13b, *Donezella lutugini* Maslov, 1929 (Moravamminida) (f), DPM 12066 TRU 10; *Uraloporella* sp. (Moravamminida) (g), DPM 12066 TRU 10. h) Ichnofossil, *Thartarella* sp. (worm tubes), DPM 12066 TRU 14. Scale bars: a, 1 cm; b-h, 1 mm.

Fig. 6 - (pag. vii) Foraminifera. a) *Ozawainella umbonata*, DPM 12066 TRU 15. b) *Eostaffella postmosquensis*, DPM 12066 TRU 15. c) *Pseudostaffella* sp., DPM 12066 TRU 15. d) *Tetrataxis* sp., DPM 12066 TRU 13b. e) *Bradyina nautiliformis* Möller, 1878, DPM 12066 TRU 10. f) *Climacammina* sp., DPM 12066 TRU 18. g) *Monotaxinoides* sp., DPM 12066 TRU 11. h) *Insolethiteca* sp., DPM 12066 TRU 9. i) *Hemiegordierina* sp., DPM 12066 TRU 10. Scale bars: 1 mm for all specimens, except g = 0.25 mm.

Fossil remains are disorganised, with some areas composed almost exclusively of *Donezella* remains, while others are more diverse. Most fossils appear to be oriented roughly horizontally, and most remains are broken and disarticulated, specially the bigger ones. These features suggest the fossils are resedimented (sensu Fernández-López, 1991), but there are no signs of prolonged transport.

Microfacies 2: Donezella*,* Girvanella *and chaetetids boundstone*

It occurs in the limestone beds in the upper part of the succession, specifically in some areas of samples TRU 15 and TRU T (Fig. 2). It is defined by the presence of chaetetids and *Donezella* in growth position, creating an organic framewortk with gaps inhabited by cyanobacteria like *Girvanella* and burrowers, like the *Thartarella* producers (Fig. 9).

Besides *Donezella* and *Girvanella*, which are the absolute main components of the assemblage, there are fusulinids, Endothyrida (specially paleotextularids), archaeodiscids, *Tuberitina*, red algae, some disperse echinoderm plates and broken brachiopods shells.

This boundstone presents a fossil assemblage very similar to the "algal" mounds described in other outcrops of the Valdeteja Formation, which have been thoroughly studied by Eichmüller (1985), Samankassou (2001), Della Porta et al. (2002a), and Chesnel et al. (2016, 2017). The main difference between the boundstone from the Mina Rosario and those described by these researchers is the higher abundance of *Girvanella* and chaetetids occurring in the mine.

This fossil assemblage is less diverse than the assemblage of the microfacies 1, but the equitability is higher, since chaetetids and cyanobacteria are also main components of the limestone, along with *Donezella*. Some remains are broken and may have undergone resedimentation, but most of them are in growth position.

ENVIRONMENTAL RECONSTRUCTION

The previous observations allow the identification of some environmental factors for the limestone sedimentary environment.

The presence of *Donezella* and chaetetids in growth position suggests a low to moderate hydrodynamic energy, while the abundance of broken and disarticulated remains appears to indicate the opposite. Moreover, the presence of abundant micrite implies periods of low energy. These features suggest an environment with moderated and discontinuous sea swell influence. The cyanobacteria and chaetetids in the mounds provide a stronger framework that allows the *Donezella* to resist the waves, but some specimens are still broken and deposited around the mounds. The limestones in the lower half of the section represent the sedimentation of the debris and broken fossils from the mounds, while the buildups form beds 7 and 10.

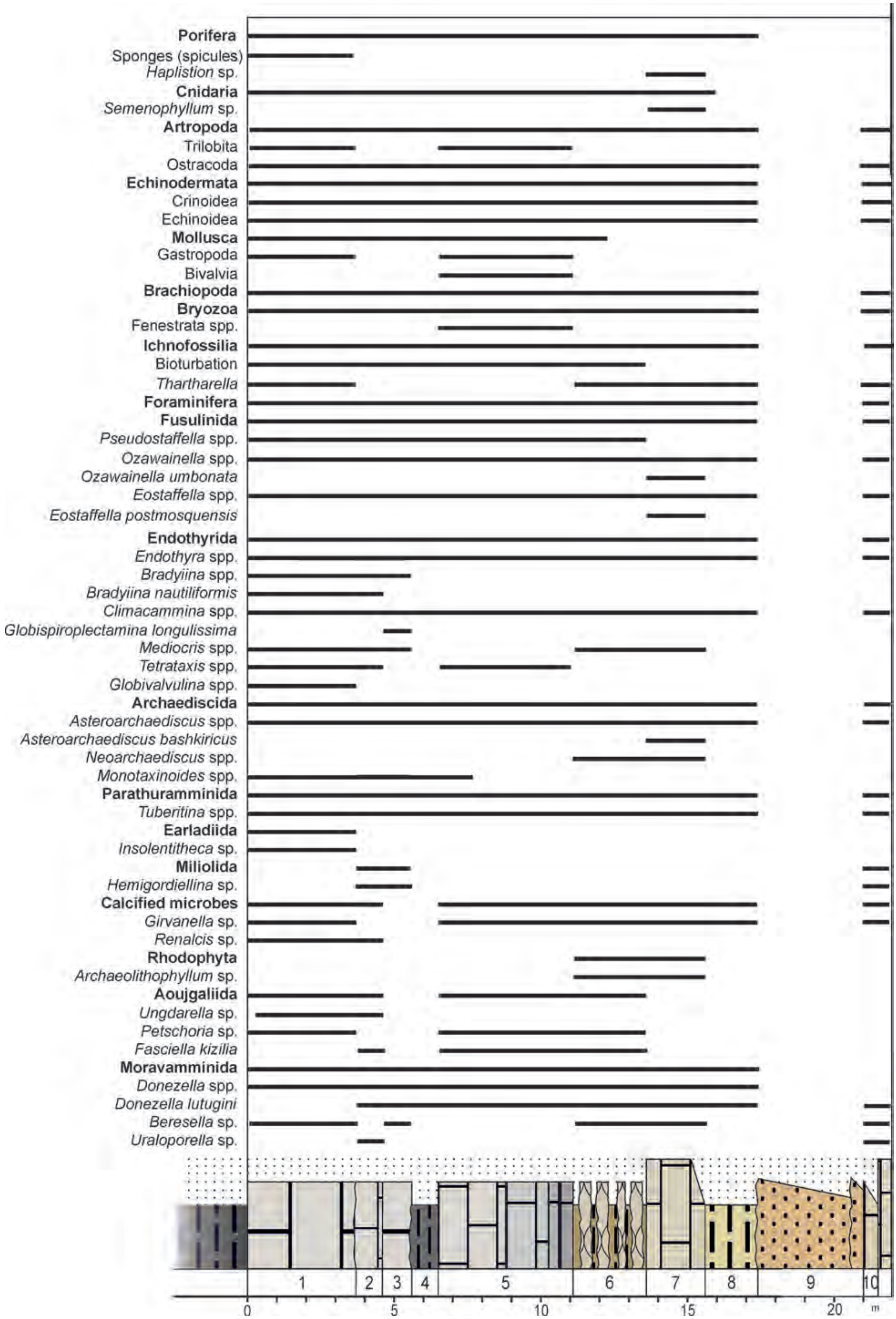
The diversity of the fossil assemblages and the presence of stenohaline organisms, such as brachiopods, echinoderms and chaetetids, indicate a normal marine salinity, about 36-40 ppm (Fürsich, 1993). Moreover, the abundant bioturbation and the biodiversity both suggest a well-oxygenated environment. All these features are characteristic of an open sea and imply that the mounds did not form a barrier that isolated the inner platform, but they represent patches widely developed in a shallow platform, in a situation similar to that of the *Donezella* buildups described in Della Porta (2002a).

The presence of autochthonous inferred photosynthetic organisms, such as cyanobacteria (*Girvanella*) and algae, indicates that the mounds were in the photic zone. The influence of the sea swell also rules out a high depth. This implies that the mound organisms inhabited a relatively shallow environment, but with no evidences of subaerial exposure. Presence of beds in the lower part of the succession with abundant *Donezella* shingle indicates periodical erosion by waves and resedimentation of the mounds.

The marl beds are the result of the sedimentation in periods with less hydrodynamic energy and higher influx of sediment from the continent, which includes fine clastic sediment and organic matter.

Therefore, the sedimentary environment would have been a carbonate platform close to the fair-weather wave base, in the subtidal zone. The rocks that crop out in the Mina Rosario are the result of the development of "algal" mounds in that platform (microfacies 2), and the detrital sedimentation of thalli between and around them (microfacies 1).

Fig. 7 - Stratigraphical distribution of the identified fossils. Patterns according to the legend in Fig. 2.


Porifera
Sponges (spicules)
Haplistion sp.
Cnidaria
Semenophyllum sp.
Artropoda
Trilobita
Ostracoda
Echinodermata
Crinoidea
Echinoidea
Mollusca
Gastropoda
Bivalvia
Brachiopoda
Bryozoa
Fenestrata spp.
Ichnofossilia
Bioturbation
Thartharella
Foraminifera
Fusulinida
Pseudostaffella spp.
Ozawainella spp.
Ozawainella umbonata
Eostaffella spp.
Eostaffella postmosquensis
Endothyrida
Endothyra spp.
Bradyiina spp.
Bradyiina nautiliformis
Climacammina spp.
Globispiroplectamina longulissima
Mediocris spp.
Tetrataxis spp.
Globivalvulina spp.
Archaediscida
Asteroarchaediscus spp.
Asteroarchaediscus bashkiricus
Neoarchaediscus spp.
Monotaxinoides spp.
Parathuramminida
Tuberitina spp.
Earlandiida
Insolentitheca sp.
Miliolida
Hemigordiellina sp.
Calcified microbes
Girvanella sp.
Renalcis sp.
Rhodophyta
Archaeolithophyllum sp.
Aoujgaliida
Ungdarella sp.
Petschoria sp.
Fasciella kizilia
Moravamminida
Donezella spp.
Donezella lutugini
Beresella sp.
Uraloporella sp.
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Further data are required to understand the spatial distribution, extension and morphology of the mounds, since this analysis comprises just one stratigraphic succession, which is not enough to completely characterise the carbonate platform.

AGE

There are few previous biostratigraphic studies conducted in the Mina Rosario. Vachard & Béckary (1991) studied the foraminifera from the coal bed and determined a Prikamian (Askinbasian) age, which is the highest horizon of the lower Bashkirian, according to the chronostratigraphic scale defined in the Russian platform. Vachard & Béckary (1991) also studied the macroflora they found in the coal balls, which belongs to the Namurian C regional substage (Yealdonian). However, they state that it is hard to distinguish between Namurian C and Westphalian A (Langsetian) regional substages with the findings from the mine. Other authors that have studied the macroflora from the Mina Rosario in the past (Gómez de Llarena & Rodríguez Arango, 1946, 1948) also maintain this ambivalent situation between upper Namurian and lower Westphalian.

The new results are consistent with previous studies. Since there were more identifiable species in the lower beds, the Fusulinoidea recorded in the whole outcrop were used, instead of relying on the specimens from the beds over the coal level. *Eostaffella postmosquensis* Kireeva in Rauzer-Chernousova,1951, *Millerella concinna* Potievskaya, 1964, *Ozawainella umbonata* Brazhnikova & Potievskaya, 1948 and *Pseudostaffella variabilis* Reitlinger, 1961 were also found by Vachard & Béckary (1991). These species only overlap in Severokeltmenian (Akavasian) and Prikamian horizons (lower Bashkirian). Vachard & Béckary (1991) were able to narrow the age down to the Prikamian horizon because of the presence of *Pseudostaffella praegorskyi* Rauzer-Chernousova, 1949, which has not been found in our thin sections. However, we have no reason to argue their findings, so it is most likely that the outcrop belongs to the Prikamian and not the Severokeltmenian with no doubt that it is lower Bashkirian. Moreover, the overall assemblage matches the one described by Vachard & Béckary (1991) as the usual assemblage in both Spain and the Donetz basin: the firsts *Ozawainella* and abundant *Monotaxinoides transitorius* Brazhnikova & Yartseva, 1956, Archaediscida and Ozawainelloidea, like *Eostaffella*, *Millerella* and *Plectostafella*.

The Rugosa genus *Semenophyllum* is reported exclusively in the Bashkirian (Rodríguez-García, 1984; Coronado & Rodríguez, 2009), which further supports the age based on the foraminifera.

Most *Donezella* mounds in the Valdeteja Formation are upper Bashkirian and/or Moscovian (Bahamonde et al., 2004; Chesnel et al., 2016). This means that these results imply that these are some of the oldest mounds described in the Valdeteja Formation, along with the mounds from the type section, described by Eichmüller (1985).

CONCLUSIONS

The Mina Rosario outcrop is unique in the Valdeteja Formation because of the carbonaceous marls with coal

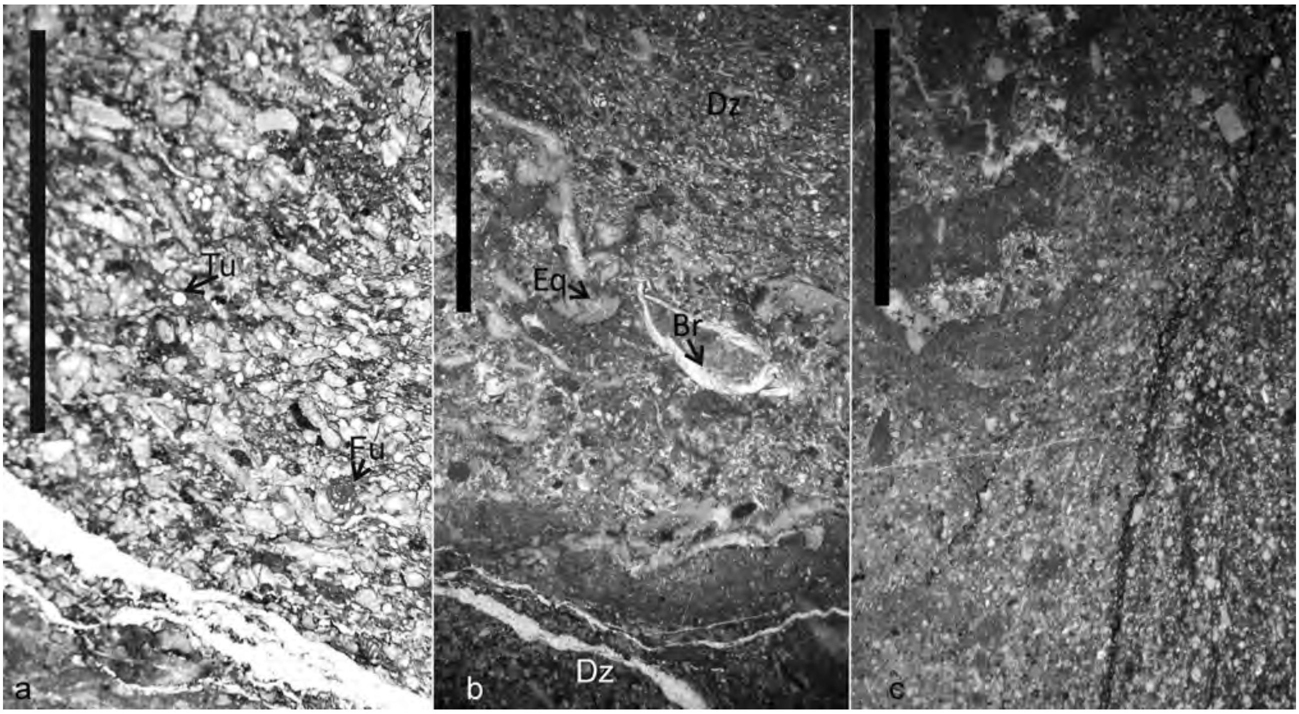

Fig. 8 - Microfacies 1. a) Resedimented algospongia packstone, vertical thin section (bed 2). Very small bioclasts, mostly algospongia fragments with homogeneous distribution. Fu: Fusulinina, Tu: *Tuberitina* sp. Scale bar: 5 mm. b) Horizontal thin section (bed 1) showing some larger bioclasts. Eq: echinoderm plates, Br: brachiopod shell, Dz: *Donezella* fragments of branches. Scale bar: 1 cm. c) Horizontal thin section (bed 3) showing intense bioturbation (upper left). Scale bar: 1 cm.

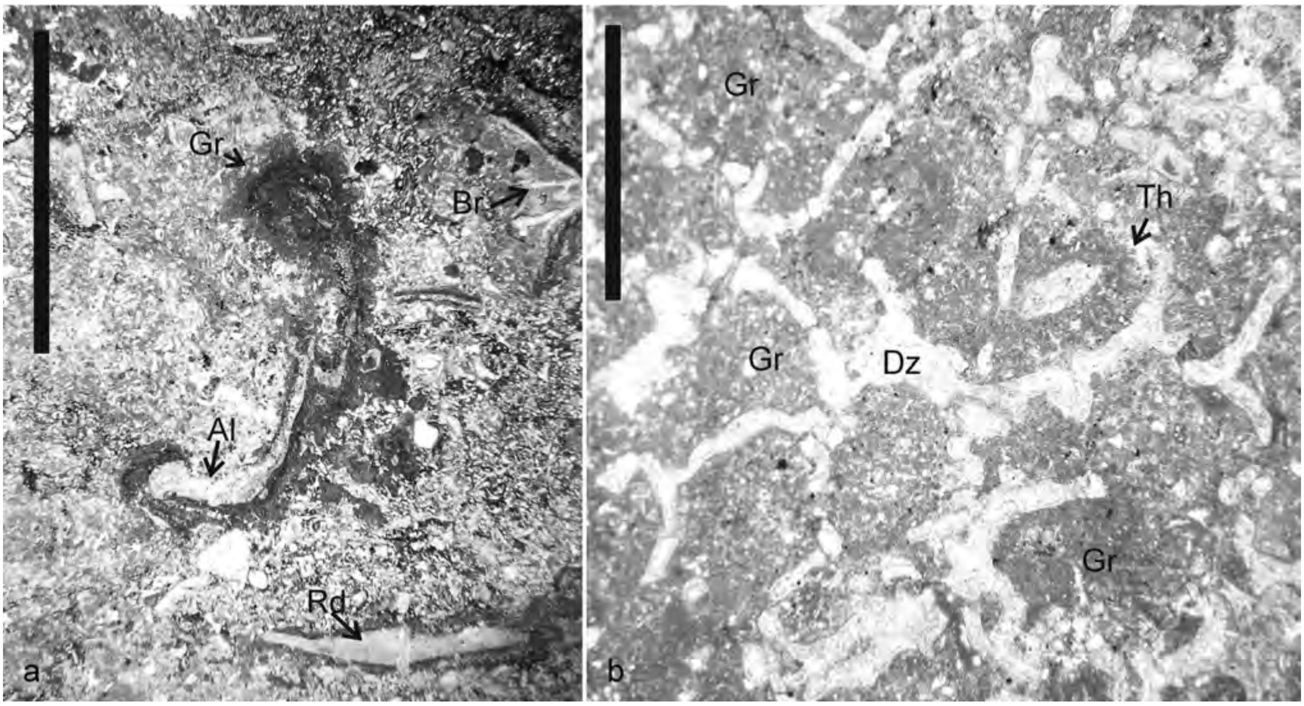

Fig. 9 - Microfacies 2. a) Horizontal thin section (bed 7). *Girvanella* masses coating different clasts. Gr: *Girvanella*, Al: algospongia, Br: brachiopod, Rd: Rhodophyta. Scale bar: 1 cm. b) Horizontal thin section (bed T). *Donezella* in growth position (Dz), masses of *Girvanella* (Gr) and *Thartarella* (Th) worm tubes. Scale bar: 2 mm.

balls that were mined in the 1940s. The strata above the coal bed are composed of marl and limestone beds, formed mainly by resedimented *Donezella* or by chaetetids, *Donezella* and *Girvanella* in growth position, building mounds. These beds have a relatively high diversity and contain abundant Foraminifera, crinoids and undetermined echinoderm plates, brachiopods, ostracods, bryozoans and corals. We have differentiated two carbonate microfacies: resedimented algospongia packstone limestones (microfacies 1) and chaetetids, *Donezella* and *Girvanella* boundstone (microfacies 2). The latter is very similar to the typical “algal” mounds in the Valdeteja Formation. The sedimentary environment is part of an open carbonate platform. The limestones were deposited near the fair-weather wave base. The fossils identified in this study support the previous dating by other authors. The fusulinid assemblage confirms the early Bashkirian age and places the outcrop between the Severokeltmenian and Prikamian Russian horizons. The west-European equivalent would be the Namurian C and Westphalian A substages.

ACKNOWLEDGEMENTS

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REFERENCES

Alonso J.L., Marcos A. & Suárez A. (2009). Paleogeographic inversión resulting from large out of sequence breaching thrusts: The Leon Fault (Cantabrian Zone, NW Iberia). A new picture of the external Variscan Thrust Belt in the Ibero-Armorican Arc. *Geologica Acta*, 7: 451-473.

Bahamonde J.R., Colmenero J.R. & Vera C. (1997). Growth and demise of Late Carboniferous carbonate platforms in the eastern Cantabrian Zone, Asturias, northwestern Spain. *Sedimentary Geology*, 110: 99-122.

Bahamonde J.R., Kenter J.A.M., Della Porta G. & Hoeflaken F. (2008). Facies belt of a Carboniferous carbonate platform (San Antolin-La Huelga section, NE Cantabrian Zone). *Trabajos de Geologia*, Universidad de Oviedo, 28: 69-86.

Bahamonde J.R., Kenter J.A.M., Della Porta G., Keim L., Immenhauser A. & Reijmer J.J.G. (2004). Lithofacies and depositional processes on a high, steep-margined Carboniferous (Bashkirian–Moscovian) carbonate platform slope, Sierra del Cuera, NW Spain. *Sedimentary Geology*, 166: 145-156.

Bahamonde J.R., Merino-Tomé O.A. & Heredia N. (2007). A Pennsylvanian microbial boundstone-dominated carbonate shelf in a distal foreland margin (Picos de Europa Province, NW Spain). *Sedimentary Geology*, 198: 167-193.

Bahamonde J.R., Vera C. & Colmenero J.R. (2000). A steep-fronted Carboniferous carbonate platform: clinoformal geometry and lithofacies (Picos de Europa Region, NW Spain). *Sedimentology*, 47: 645-664.

Bastida F. (2004). Zona Cantábrica (Capítulo 2, Macizo Ibérico). *In* Vera J.A. (ed.), *Geología de España*, SCE-IGME: 25-49.

Bowman M.B.J. (1979). The depositional environment of a limestone unit from the San Emiliano Formation (Namurian/Westphalian), Cantabrian Mountains, NW-Spain. *Sedimentary Geology*, 24: 25-43.

Brazhnikova N.E. & Potievskaya P.D. (1948). Results of the foraminiferal study of materials from wells of the western outskirts of Donbass. *Collection of works about paleontology and stratigraphy*, 1: 76-101.

Brazhnikova N.E. & Yartseva M.V. (1956). To the question of evolution of the genus *Monotaxis*. *Academy of Sciences Union of Soviet Socialist Republics Questions of Micropaleontology*, 1: 62-68.

Chesnel V., Merino-Tomé O.A., Fernández L.P., Villa E. & Samakassou E. (2017). Spatial and temporal distribution of microbial carbonates, skeletal and non-skeletal grains in a Pennsylvanian carbonate platform (Valdorria, Northern Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology,* 476: 106-139.

Chesnel V., Samankassou E., Merino-Tomé Ó., Fernández L.P. & Villa E. (2016). Facies, geometry and growth phases of the Valdorria carbonate platform (Pennsylvanian, northern Spain). *Sedimentology*, 63: 60-104.

Coronado I. & Rodríguez S. (2009). Análisis de microfacies de los montículos de la Formación Cosgaya. Sección de Las Ilces, Pensilvánico, Cantabria. *Coloquios de Paleontología*, 59: 61-91.

Corrochano D., Barba P. & Colmenero J.R. (2011). Transgressive-regressive sequence stratigraphy of Pennsylvanian *Donezella* bioherms in a foreland basin (Lena Group, Cantabrian Zone, NW Spain). *Facies*, 28: 457-476.

Della Porta G., Kenter J.A.M. & Bahamonde J.R. (2002a). Microfacies and Paleoenvironment of *Donezella* Accumulations across an Upper Carboniferous High-rising Carbonate Platform (Asturias, NW Spain). *Facies*, 46: 149-168.

Della Porta G., Kenter J.A.M. & Bahamonde J.R. (2004). Depositional facies and stratal geometry of an Upper Carboniferous prograding and aggrading high-relief carbonate platform (Cantabrian Mountains, NW Spain). *Sedimentology*, 51: 267-295.

Della Porta G., Kenter J.A.M., Bahamonde J.R., Immenhauser A. & Villa E. (2003). Microbial boundstone dominated carbonate slope (Upper Carboniferous, N Spain): microfacies, lithofacies distribution and stratal geometry. *Facies*, 49: 175-208.

Della Porta G., Kenter J.A.M., Immenhauser A. & Bahamonde J.R. (2002b). Lithofacies character and architecture across a Pennsylvanian inner-platform transect (Sierra de Cuera, Asturias, Spain). *Journal of Sedimentary Research*, 72: 898-916.

Della Porta G., Villa E. & Kenter J.A.M. (2005). Facies distribution of Fusulinina in a Bashkirian-Moscovian carbonate-platform top (Cantabrian Mts, NW Spain). *Journal of Foraminiferal Research*, 35: 1-24.

Dunham R.J. (1962). Classification of Carbonate Rocks According to Depositional Textures. *In* Ham W.E. (ed.), *Memoires of the American Association of Petroleum Geologists*, 1: 108-121.

Eichmüller K. (1985). Die Valdeteja Formation: Aufbau und Geschichte einer oberkarbonischen Karbonatplattform (Kantabrisches Gebirge, Nordspanien). *Facies*, 13: 45-155.

Embry A.F. & Klovan J.E. (1971). A late Devonian reef tract on northeastern Banks Island, N.W.T. *Bulletin of Canadian Petroleum Geology*, 19: 705-724.

Fernández-López S. (1991). Taphonomic concepts for a theoretical biochronology. *Revista Española de Paleontología*, 6: 37-49.

Fürsich F.T. (1993) Palaeoecology and evolution of Mesozoic salinity-controlled benthic macroinvertebrate associations. *Lethaia*, 26: 327-348.

Ginkel A.C. van & Villa E. (1991). Some fusulinids from the Moscovian-Kasimovian transition in the Carboniferous of the Cantabrian Mountains (NW Spain). *Proceedings of the Koninklijke Nederlandse Akaddemie van Wetenschappen*, 94: 299-359.

Gómez de Llarena J. & Rodríguez Arango C. (1946). Las «tacañas» (Coal balls) de la Mina «Rosario», de Truébano (Leon). *Notas y Comunicaciones del Instituto Geológico y Minero de España*, 16: 215-236.

Gomez de Llarena J. & Rodríguez Arango C. (1948). Datos para el estudio geológico de la Babia Baja (León). *Boletín del Instituto Geológico y Minero de España*, 61: 79-206.

Gong E., Zhang Y., Guan C., Samankassou E. & Sun B. (2007). Paleoecology of Late Carboniferous Phylloid Algae in Southern Guizhou, SW China. *Acta Geologica Sinica*, 81: 566-572.

Julivert M. (1971). Décollement tectonics in the Hercynian cordillera of Northwest Spain. *American Journal of Science*, 270: 1-29.

Julivert M. (1978). Hercynian orogeny and Carboniferous paleogeography in Northwestern Spain: A model of deformation-sedimentation relationships. *Zeitschrift der Deutschen Geologischen Gesellschaft*, 129: 565-592.

Kenter S.A.M., Van Hoeflaken F., Bahamonde J.R., Bracco Gartner G.L., Kleim L. & Besems R.E. (2002). Anatomy and lithofacies of an intact and seismic-scale Carboniferous carbonate platform (Asturias, NW Spain): analogues of hydrocarbon reservoirs in the Pricaspian basin (Kazakhstan). *In* Zemplolich W. & Cook H.E. (eds), Paleozoic Carbonates of the Commonwealth of Independent States (CIS): Subsurface Reservoirs and Outcrops Analogues. *Society of Economic Paleontologists and Mineralogists, Special Publication*, 74: 181-203.

Lindholm R.C. & Finkelman R.B. (1972). Calcite Staining: Semiquantitative Determination of Ferrous Iron: NOTES. *Journal of Sedimentary Petrology*, 42: 239-242.

Marcos A. & Pulgar F.J. (1982). An approach to the tectonostratigraphic evolution of Cantabrian thrust and fold belt, Variscan Cordillera of NW Spain. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 163: 256-260.

Maslov V.P. (1929). Microscopic algae of the Carboniferous limestones from the Donetz Basin. *Bulletin du Comité géologique*, 48: 115-139.

Möller V. von (1878). Die Spiral-gewundenen Foraminiferen des russischen Kohlenkalks. *Mémoires de l'Académie impériale des sciences de Saint Pétersbourg*, 7th series, 25: 1-147.

Pettijohn F.J. (1954). Classification of sandstones. *The Journal of Geology*, 62: 360-365.

Potievskaya P.D. (1964). Some fusulinids and small Foraminifers from the Bashkirian sediments of the Greater Donbass. *Trudy Geological Institute Nauk, Academy Nauka, Ukranian Sovietic Socialist Republic, Series on Stratigraphy and Paleontology*, 48: 31-59.

Rauzer-Chernousova D.M. (1949). On the ontogeny of some Palaeozoic foraminifera. *Trudy Paleontological Institut Akademy Nauk Union of Soviet Socialist Republic*, Moskva, 20: 339-353.

Rauzer-Chernousova D.M., Gryzlova N.D., Kireeva G.D., Leontovich G.E., Safonova T.P. & Chernova E.I. (1951). Middle Carboniferous fusulinids of the Russian Platform and Neighboring Regions. 380 pp. Academy of Sciences Union of Soviet Socialist Republics, Moscow.

Reitlinger E.A. (1961). Stratigraphy of the Middle Carboniferous (Krasnaja Poljana, boring well no 1) of the TransVolga. *Regional Stratigraphy*, 5: 218-260.

Riding R. (1979). *Donezella* bioherms in the Carboniferous of the southern Cantabrian Mountains, Spain. *Bulletin des Centres de Recherches Exploration-Production Elf-Aquitaine*, 3: 787-794.

Rodríguez-Castro I., Rodríguez S. & Fregenal-Martínez M. (2019). Depósitos de flujos en masa y carbón en la Formación Valdeteja (Bashkiriense) en Truébano (León, Cordillera Cantábrica). *In* Martínez-Navarro B., Palmqvist P., Espigares M.P. & Ros-Montoya S. (eds), Libro de Resúmenes XXX Jornadas de la Sociedad Española de Paleontología, Baza 2-5 de Octubre de 2019: 247-250.

Rodríguez-Garcia S. (1984). Corales rugosos del Carbonífero del Este de Asturias. *Colección Tesis Doctorales UCM*, 109/84: 1-594.

Said I., Rodríguez S., Berkhli M, Cózar P. & Gómez-Herguedas A. (2010). Environmental parameters of a coral assemblage from the Akerchi Formation (Carboniferous), Adarouch Area, central Morocco. *Journal of Iberian Geology*, 36: 7-19.

Samankassou E. (2001). Internal structure and depositional environment of Late Carboniferous mounds from the San Emiliano Formation, Cármenes Syncline, Cantabrian

Mountains, Northern Spain. *Sedimentary Geology*, 145: 235-252.

Samankassou E. (2003). Upper Carboniferous-Lower Permian Buildups of the Carnic Alps, Austria-Italy. *Society for Sedimentary Geology Special Publication*, 78: 201-217.

Vachard D. & Béckary S. (1988). Les «tacañas», coal balls mixtes du Carbonifère de Truébano (León, Espagne). *Bulletin de la Société Géologique de France,* 8: 1271-1278.

Vachard D. & Béckary S. (1991). Algues et foraminiferes Bachkiriens des coal balls de la Mine Rosario (Truebano, Leon, Espagne). *Revue de Paléobiologie*, 10: 315-357.

Vachard D. & Cózar P (2010). An attempt of classification of the Palaeozoic *incertae sedis* Algospongia. *Revista Española de Micropaleontología*, 42: 129-241.

Verwer K., Kenter J.A.M., Maathuis B. & Della Porta G. (2004). Stratal patterns and lithofacies of an intact seismic-scale Carboniferous carbonate platform (Asturias, NW Spain): A virtual outcrop model. *In* Curtis A. & Wood R. (eds), Geological Prior Information: Informing Science and Engineering. *Geological Society, London, Special Publication*, 239: 29-41.

Villa E. (1982). Foraminíferos de la Formación Valdeteja (Carbonífero, NW de España) en su área tipo. *Revista Española de Micropaleontología*, 14: 63-72.

Villa E., Sánchez de Posada L.C., Fernández L.P., Martínez-Chacón M.L. & Stavros C. (2001). Foraminifera and Biostratigraphy of the Valdeteja Formation Stratotype (Carboniferous, Cantabrian Zone, NW Spain). *Facies*, 45: 59- 86.

Wagner R.H., Winkler-Prins C.J. & Riding E. (1971). Lithostratigraphic units of the lower part of the Carboniferous in northern León, Spain. *Trabajos de Geología*, 4: 603-663.

Winkler Prins C.F. (1968). Carboniferous Productidina and Chonetidina of the Cantabrian Mountains (NW Spain): Systematics, Stratigraphy and Palaeocology. *Leidse Geologische Mededelingen*, 43: 41-126.

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New data on lower Permian rugose corals from the Southern Karavanke Mountains (Slovenia)

Olga Kossovaya*, Matevž Novak & Dieter Weyer

O. Kossovaya, Vserossiskiy Nauchno-issledovatelskiy Geologicheskiy Institute (VSEGEI), Sredny pr. 74, Saint Petersburg 199106, Russia; Kazanskiy Federalnyy Universitet, Kazan, Russia; olga_kossovaya@vsegei.ru **corresponding author*
M. Novak, Geološki zavod Slovenije, Dimičeva ul. 14, SI-1000 Ljubljana, Slovenia; matevz.novak@geo-zs.si
D. Weyer, Museum für Naturkunde (Leibniz-Institut) at Humboldt-University, Invaliden-Str. 43, D-10115 Berlin, Germany; dieter.weyer@t-online.de

KEY WORDS - Gregaria corals, Carinthiaphyllum*, Asselian-Sakmarian, Southern Alps.*

ABSTRACT - Studies of upper Palaeozoic corals from the Southern Alps (Karavanke Mountains in Slovenia and Carnic Alps along the Austrian/Italian border) started at the end of the 19th century. Since the mid-20th century, corals of the Karavanke Mountains have been studied in detail by several authors. Recently, several coral type localities and the coral groups occurring therein have been reinvestigated. This paper deals in particular with the study of Carinthiaphyllum *Heritsch, 1936 and all previously known data have been revised within this study. Most specimens of* Carinthiaphyllum *originate from museum collections and from new findings in the Dovžanova Soteska area of northern Slovenia. Additional material is represented by newly found samples from the locality of Mt. Boč in eastern Slovenia. The stratigraphic position and age of the* Carinthiaphyllum *occurrences are determined by fusulinid and conodont assemblages. Two species,* Carinthiaphyllum crasseseptatum *Gräf & Ramovš, 1965 and* C. ramovsi *n. sp., are described herein. New morphological features, including root-like protrusions and connecting stereoplasmic tubes, have been found for the first time in gregaria growth mode. Therefore, these new observations provide evidence of a solitary gregaria growth mode: individuals are invariably separated with contact and reciprocal support only by root-like, sometimes channeled tubes occurring as outgrowths of the archaeothecal wall. An emended diagnosis of* Carinthiaphyllum *is proposed herein. The studied collection is housed in the Museum für Naturkunde (Leibniz-Institut) at the Humboldt University in Berlin.*

INTRODUCTION

Studies of the upper Palaeozoic corals from the Southern Alps (Karavanke Mountains in Slovenia and Carnic Alps along the Austrian/Italian border) started at the end of the 19th century. The lower Permian rugose corals in particular are widespread in different parts of the Southern Karavanke Mountains. They also occur in southern Slovenia, near the town of Ortnek, which belongs to the External Dinarides (Fig. 1). Schellwien (1898a) mentioned three species found in upper Palaeozoic rocks in Dovžanova Soteska gorge (Devil's gorge, Teufelsschlucht in German language literature), Southern Karavanke Mts: *Caninia* aff. *kokscharowi* Stuckenberg, 1895, *Diphyphyllum* sp., and *Cyathaxonella* sp. Since the mid-20th century, corals of the Karavanke Mountains have been studied by several authors. In an historical overview, Heritsch (1933, p. 43) wrote (our translation from Slovenian): "Corals from the Trogkofel Limestone have never been described so far." To fill this gap, he described seven species from Dovžanova Soteska: *Sinophyllum pendulum* Grabau, 1928, *Lopholasma ilitschense* Soshkina, 1928, *Amplexocarinia geyeri* Heritsch, 1933, *Tachylasma aster* Grabau, 1922, *Caninophyllum gortanii* Heritsch, 1933, *Palaeosmilia hammeri* Heritsch, 1933, and *Lonsdaleia yokoyamai* Heritsch, 1933. Later the list of species was supplemented by *Carinthiaphyllum suessi* Heritsch, 1936. Summarizing previous works on Slovenian corals, Gräf & Ramovš (1965) reported twelve species of late Carboniferous to middle Permian age. Some species are identical with taxa described in 1936 by Heritsch from the Carnic Alps, namely: *Amandophyllum carnicum* (Heritsch, 1936), *A. ruedemanni* Heritsch, 1936, *A. smithi* Heritsch, 1936, *Carinthiaphyllum* cf. *suessi*, and *Wentzelophyllum*? *stillei* (Heritsch, 1936). The others were considered similar to Uralian faunas, i.e., *Amplexocarinia irginae* Soshkina, 1928, and *Ufimia exceptata* (Soshkina, 1928). The age of these species was determined as early Permian. From the Vitanje Hills in the eastern part of the Southern Karavanke Mts, Ramovš & Schouppé (1961) reported four species, namely: *Lophophyllidium minimum* (Heritsch, 1936), *Amplexocarinia heimoi* Heritsch, 1936, *Amandophyllum carnicum* (Heritsch, 1936), and *Gshelia* cf. *calophylloides* (Holtedahl, 1913). Recently, small ahermatypic, non-dissepimental corals of the new genus *Sloveniaxon* Kossovaya, Novak & Weyer, 2012 were described from the middle Asselian, uppermost level of the Dovžanova Soteska Formation (Kossovaya et al., 2012), and the large-sized "caninioid" *Preisingerella stegovnikensis* Kossovaya, Novak & Weyer, 2016 from the slope facies of the Asselian-Sakmarian Born Formation in the Stegovnik section (Southern Karavanke Mts) (Kossovaya et al., 2016, fig. 1).

The present revision of the *Carinthiaphyllum* fauna of the Karavanke Mts reveals three species, namely: *C. crasseseptatum* Gräf & Ramovš, 1965, *C. suessi*, and *C. ramovsi* n. sp. All coral localities under consideration, except for Ortnek, are in the Southern Karavanke Mts that belong to the Southern Alps.

The collection of *Carinthiaphyllum* specimens originates from the old samples and new findings in Dovžanova Soteska 3.5 km NNE of the town of Tržič in northern Slovenia. The parallel determination of fusulinid index-fossils is used for precise determination of ages of the main *Carinthiaphyllum* occurrences. A second collection is represented by samples from Mt. Boč

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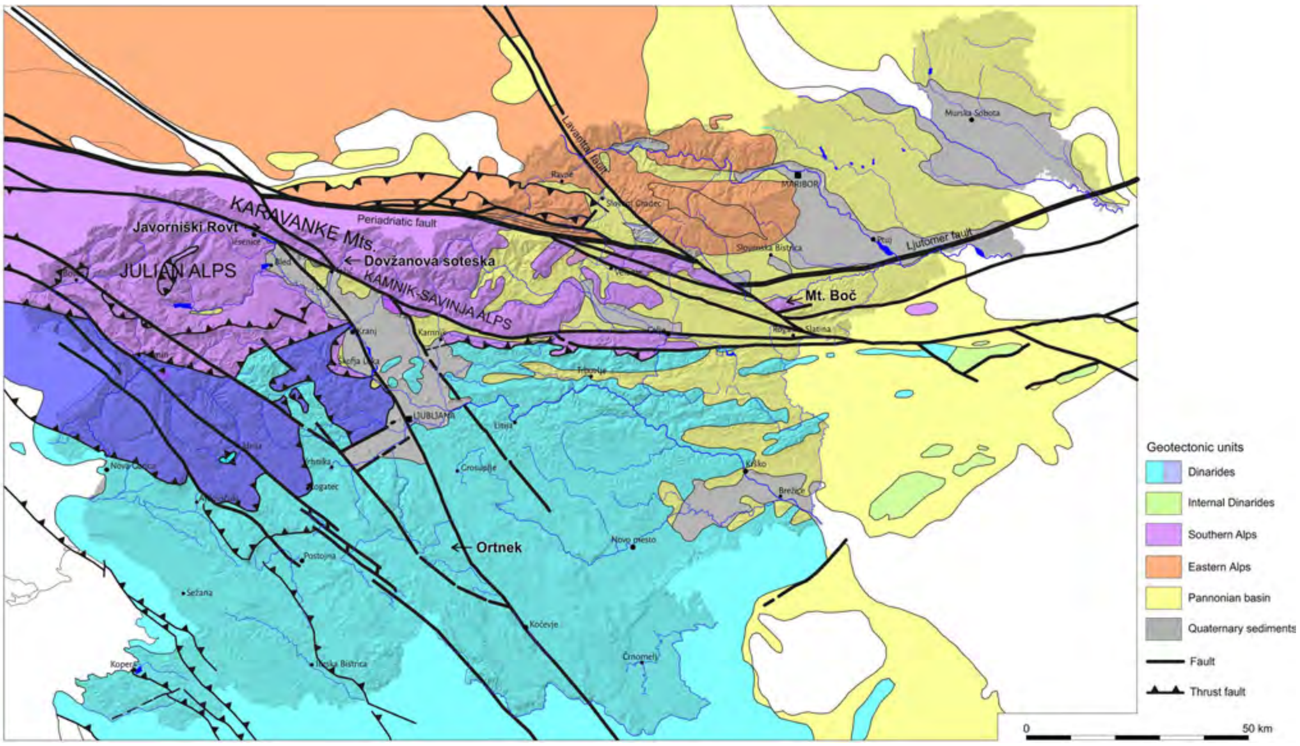


Fig. 1 - (color online) Geotectonic map of Slovenian territory (according to Placer, 2008) with lower Permian coral localities.

(Wotsch-Berg in German language literature) NNW of the town of Rogaška Slatina in eastern Slovenia (Fig. 1).

GEOLOGICAL AND STRATIGRAPHICAL SETTING

Slovenia is located at the junction of the Eastern Alps, Southern Alps, Dinarids, and the Pannonian Basin. The rocks of these geotectonic units belong to the Adriatic Lithospheric Microplate, which detached from the African Plate during the Mesozoic and collided with the Eurasian Plate during the Alpine Orogeny in Neogene times. The Southern Alps in Slovenia are represented by the Southern Karavanke Mts, which are the eastern prolongation of the Carnic Alps (Austria/Italy), where many corals have been described by Heritsch (1936) (Fig. 1).

Comprehensive summaries of the upper Palaeozoic lithostratigraphic units of the post-Variscan sequence are available in several publications (e.g., Venturini, 2006; Schönlaub & Forke, 2007; Novak & Skaberne, 2009; Schönlaub, 2014; Novak et al., 2019). With respect to previous publications on the lower Permian corals in Slovenia, it is important to note that for decades all coral-bearing limestones have been regarded to represent the Trogkofel Limestone of the Carnic Alps (Heritsch, 1938). This is the case with all localities: Dovžanova Soteska, Mt. Boč, and Ortnek. Recently found conodonts *Streptognathodus bellus* Chernykh & Ritter, 1997, *S.* aff. *nodulinearis* Reshetkova & Chernykh, 1986, *S.* aff. *isolatus* Chernykh, Ritter & Wardlaw, 1997, *Hindeodus minutus* (Ellison, 1941), and *Diplognathodus* together with the fusulinid species *Dutkevitchia complicata* (Schellwien, 1898b), *Rugosofusulina latispiralis* Forke, 2002, *Pseudoschwagerina* aff. *uddeni* (Beede & Kniker, 1924) in the Dovžanova Soteska gorge indicate an early to middle Asselian age for the Dovžanova Soteska Formation limestones (Buser & Forke, 1996; Forke, 2002; Novak, 2007). The overlying Born Formation has been first assigned by Kahler & Kahler (1937), Heritsch (1941), and Ramovš (1956) to the Upper *Pseudoschwagerina* Limestone (former name of the Zweikofel Formation) of the Carnic Alps, based on lithological similarities and the lower Permian fusulinids. The detailed mapping showed that this unit overlies the Dovžanova Soteska Limestone, which at that time was regarded as the Trogkofel Limestone and that therefore cannot be older. The problem has been solved by Buser (1974, 1980) with application of the concept of Clastic Trogkofel Beds with reworked fusulinid fauna, introduced by Ramovš (1968), as a lateral development of the Trogkofel Limestone. This concept proved to be misleading in all re-studied sections in the Karavanke Mts (Forke, 2002; Novak & Forke, 2005). The fusulinid assemblage of *Sphaeroschwagerina carniolica* (Kahler & Kahler, 1937), *Rugosofusulina* cf. *likana* Kochansky-Devidé, 1959, *Paraschwagerina mukhamedjarovica* Rauzer-Chernousova, 1949, and *Darvasites eocontractus* Leven & Scherbovich, 1980 indicates a late Asselian-Sakmarian age. Both formations probably represent a time-equivalent to predominantly clastic and fossil-barren beds of the Grenzland Formation in the Carnic Alps (Forke, 2002) (Fig. 2). Fusulinid assemblages of the Dovžanova Soteska and Born formations correspond to faunas of the *Sphaeroschwagerina moelleri-Schwagerina fecunda* fusulinid Zone and to the lower part of the *Sphaeroschwagerina sphaerica-Schwagerina firma* fusulinid Zone, which represent the middle and late Asselian age in the Southern Urals.

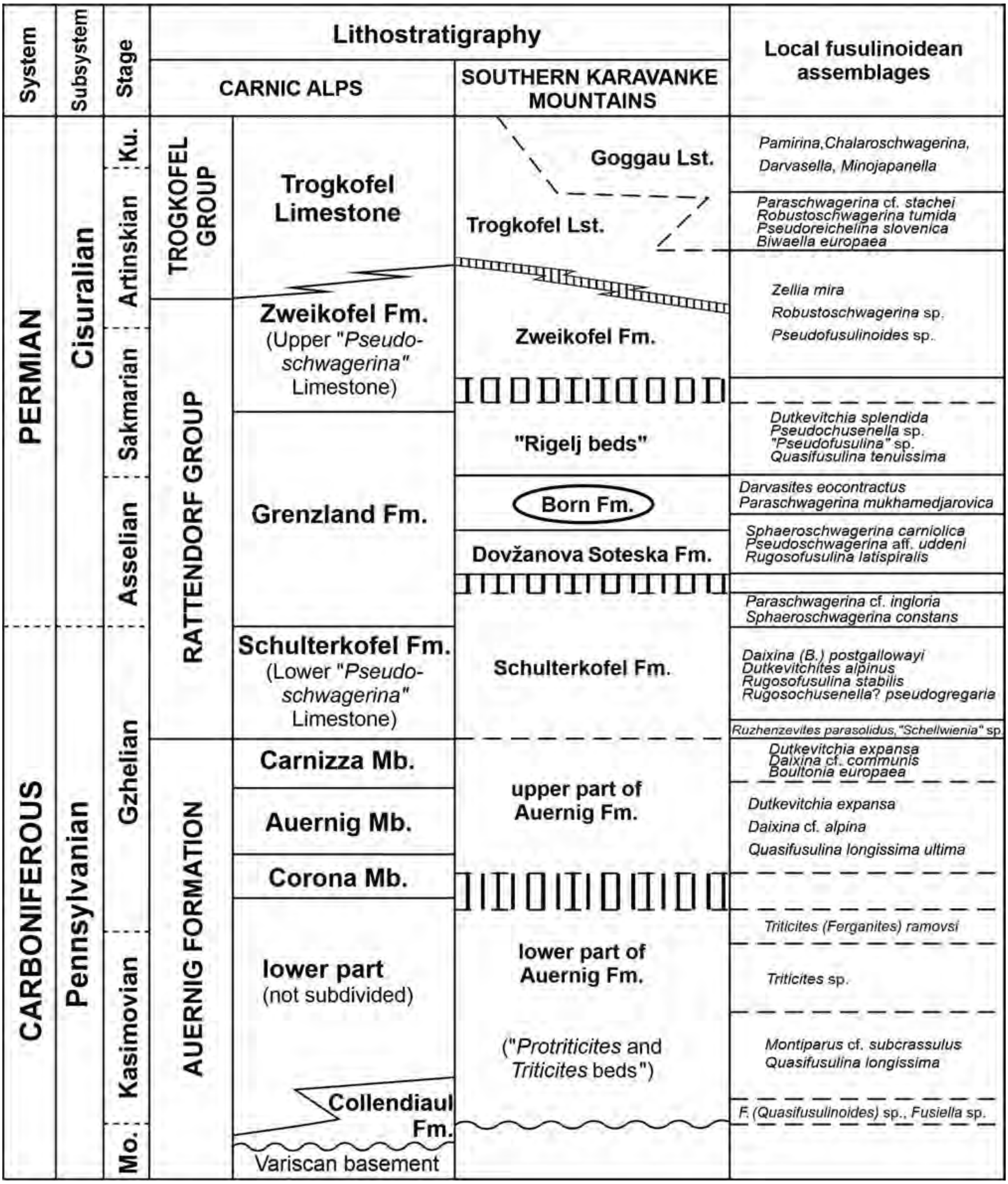


Fig. 2 - Pennsylvanian-lower Permian lithostratigraphic units in the Southern Karavanke Mts with local fusulinoidean assemblages and correlation with the Carnic Alps. All Slovenian corals discussed in this paper belong to the marked Born Formation. Mo., Moscovian; Ku., Kungurian.

Dovžanova Soteska section

Dovžanova Soteska (Devil's gorge) is known as a fossil-rich upper Carboniferous to lower Permian classical locality since Schellwien (1898a, b, 1900). Two levels with corals were recently studied at Dovžanova Soteska (Figs 3-5). The first level occurs in the uppermost part of the Dovžanova Soteska Formation within an 80 cm thick horizon of thin-bedded brownish-grey calcareous siltstone and marly limestone. They were deposited in the deepening phase of a reef facies formation (Novak, 2007). This deep water and slope facies is rich in small, non-dissepimental ahermatypic corals of *Sloveniaxon*

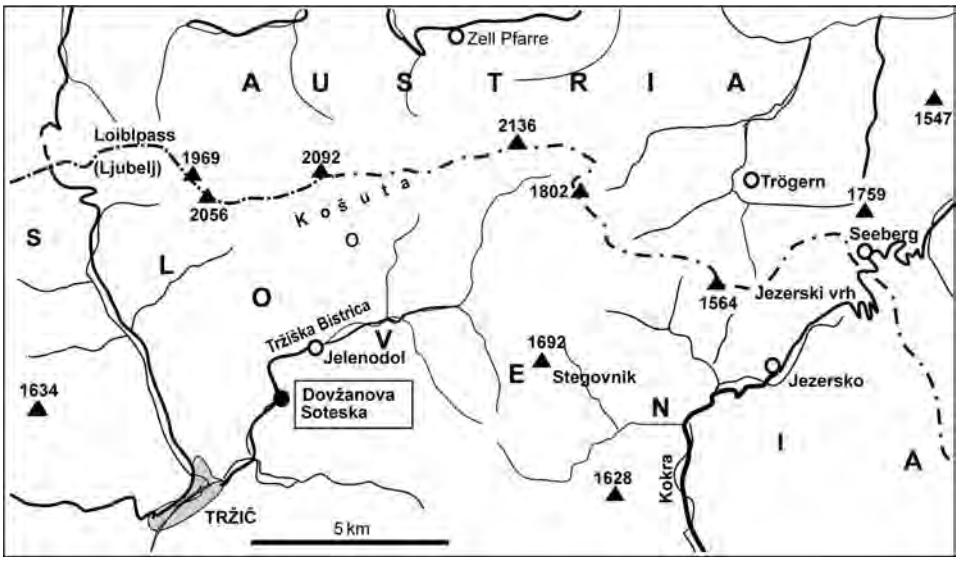


Fig. 3 - Locality map of Dovžanova Soteska gorge.

Kossovaya, Novak & Weyer, 2012. The early-middle Asselian age of the Dovžanova Soteska Formation is established by conodonts (Buser & Forke, 1996) and by the fusulinid assemblage of the *Pseudoschwagerina* aff. *uddeni-Rugosofusulina latispiralis* Zone (Forke, 2002; Novak, 2007).

The second horizon with corals occurs in the middle part of the overlying Born Formation, represented predominantly by dark-grey bedded limestones deposited in the open-marine inner platform. Corals occur in a patch reef facies on top of one of the rocky pyramids. It is built of massive, light grey boundstone, mostly composed of bioclasts (crinoid fragments and echinoid spines, bryozoans, fusulinid and smaller foraminifera), bound by *Tubiphytes* in partly dolomitized dismicritic matrix (Fig. 6a-b). It includes accumulations of "gregaria" corals, assigned here to *C. crasseseptatum* Gräf & Ramovš, 1965, and some small massive colonies.

Mt. Boč occurrence

The second new collection came from Mt. Boč, the tectonically dislocated part of the Southern Karavanke Mts north of Rogaška Slatina in eastern Slovenia. Along Labot (Lavanttal) and Donat faults, Boč and Plešivec massifs represent eastern prolongations of the Southern Karavanke geotectonic unit. Southeastern Karavanke shear zone is displaced along the dextral Labot (Lavanttal) fault for 10-18 km (Fodor et al., 1998; Vrabec & Fodor, 2006; Placer, 2008). One hundred to two hundred meters wide and several hundred meters long lenses of Permian-Mesozoic carbonates are incorporated within the shear zone and can be interpreted as strike-slip duplexes (Márton et al., 2002). The upper Palaeozoic rocks occur on the northern and southern slopes of the Boč anticline and as isolated elongate, strongly deformed tectonic lenses in the core of the Donat fault zone north of the town of Rogaška Slatina and eastwards to Žetale (Ramovš, 1959) (Fig. 5).

The lower Permian light-grey, thick-bedded to massive bioclastic limestone (wackestone to boundstone) (Fig. 6c-d) is only exposed in bands or scattered outcrops as a result of strong overprint by the Alpine tectonics and thick cover of weathering residue. Therefore, no lithostratigraphic succession can be traced in this area. The fusulinid assemblage is similar to that in the Born Formation in the stratotype section in the Dovžanova Soteska gorge, indicating the same age of the unit at Boč.

OCCURRENCES OF *CARINTHIAPHYLLUM* SPECIES IN SLOVENIA

Some specimens found in the Dovžanova Soteska gorge by previous investigations were considered as *Carinthiaphyllum kahleri* Heritsch, 1936 (Holzer & Ramovš, 1979). According to the primary description of Heritsch (1936), who studied the collection from the Carnic Alps, the maximum diameter in this species is 12.5 mm with 23 major septa (Tab. 1). In the specimens from Dovžanova Soteska described by Holzer & Ramovš (1979) the maximum diameter is 10 mm. The figure 1 in plate 2 of Holzer & Ramovš (1979) shows a trabecular septal microstructure and a specific thickening of the peripheral part of septa similar to "naotic" structures. Some septa come to the thick pseudocolumella (morphological term of Milne-Edwards & Haime, 1848, p. 78, revised by Berkowski & Weyer, 2012, p. 246). Corals assigned to *Carinthiaphyllum kahleri* by Holzer & Ramovš (1979) differ from the type specimens (Heritsch, 1936) by a lack of lonsdaleioid dissepiments, smaller diameter and reduced number of septa (Fig. 7).

Carinthiaphyllum suessi was described at first from Dovžanova Soteska. The main morphological features are the wide diameter (19-20 mm) and the high number of septa (27 × 2) (Heritsch, 1936) (Fig. 7). Specimens determined in open nomenclature as *C.* cf. *suessi* were found at Javorniški Rovt (Gräf & Ramovš, 1965). A comparison with the holotype of *C. suessi* showed that specimens of Gräf & Ramovš have a smaller diameter and a higher number of septa (11 mm-62 septa). The pseudocolumella in the calice is similar to that of the new species, described herein (Gräf & Ramovš, 1965, pl. 6,

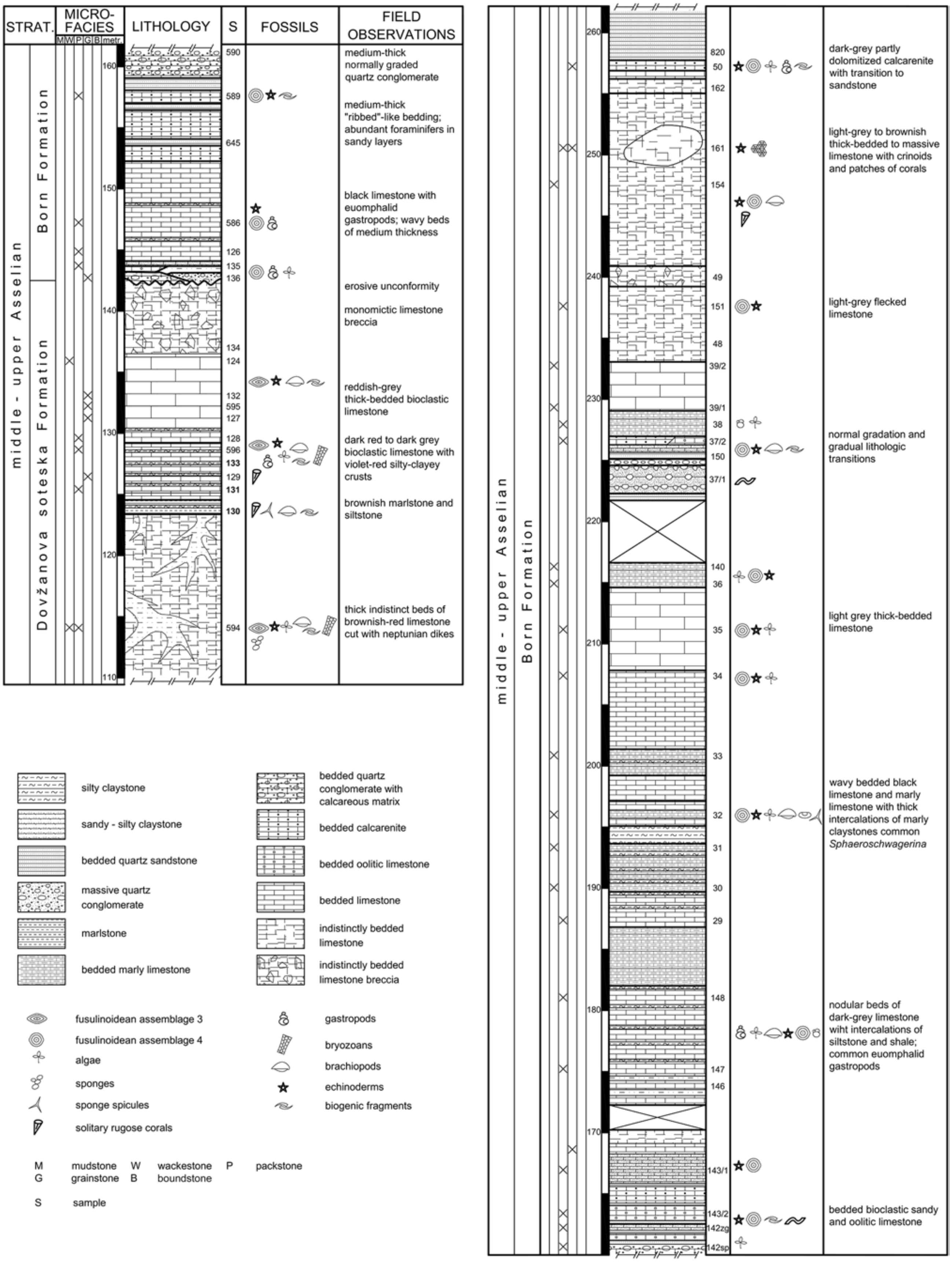


Fig. 4 - Lithostratigraphic section of Dovžanova Soteska gorge with two coral horizons.

fig. 2). Another occurrence was mentioned from Mt. Boč (Heritsch, 1941).

Carinthiaphyllum crasseseptatum Gräf & Ramovš, 1965 was found in an isolated limestone block at the

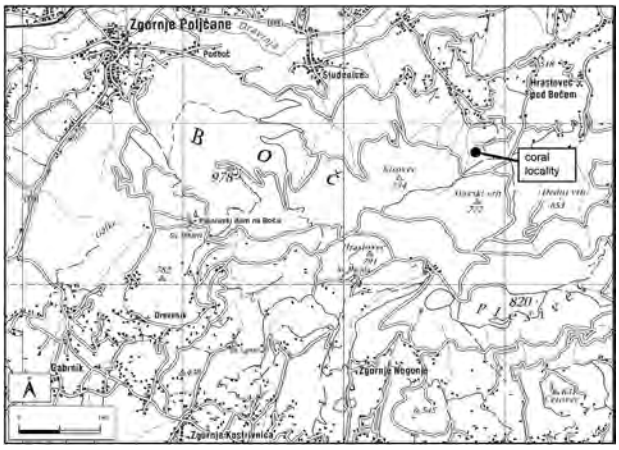


Fig. 5 - Locality map of Mt. Boč coral occurrence.

Ortnek locality. A few more typical morphological features are: a pseudocolumella of various thickness and structure with developed radial lamellae, numerous septa (27 + 27) at a diameter of 9 mm. Several major septa join the pseudocolumella (Fig. 7).

Thus, according to the reinvestigation of published and new collections, three species are established in the Karavanke Mountains. In addition to all already mentioned species, the association in the Carnic Alps includes two more species: *Carinthiaphyllum kahleri* Heritsch, 1936 and *Carinthiaphyllum carnicum* Heritsch, 1936 (Heritsch, 1941; Homann, 1971). *Carinthiaphyllum suessi* was also found in Greece (Schouppé, 1961).

TAXONOMIC REMARKS

The higher taxonomical position of the genus has changed since the first reference to Clisiophyllidae Nicholson, 1889 (in Nicholson & Lydekker, 1889) by Heritsch (1936), at first to Neockoninckophyllidae Fomichev, 1953 (Fomichev, 1953), and now to Geyerophyllidae Minato, 1955 (Minato, 1955; Minato & Kato, 1967, 1975; Cocke, 1970; Hill, 1981; Rodriguez, 1985; Rodriguez & Bamber, 2012). A few main features such as clinotabulae and connection of pseudocolumella with cardinal septum are typical for the genera included in this family. The detailed study of young stages was demonstrated for *Geyerophyllum* Heritsch, 1936 (Cocke & Cocke, 1968), *Darwasophyllum* Pyzhyanov, 1964, *Carinthiaphyllum* (Minato & Kato, 1967 and herein), and for *Amygdalophylloides* Dobrolyubova & Kabakovich, 1948. Most of the genera included in this family have a solitary growth mode, and some demonstrated gregaria

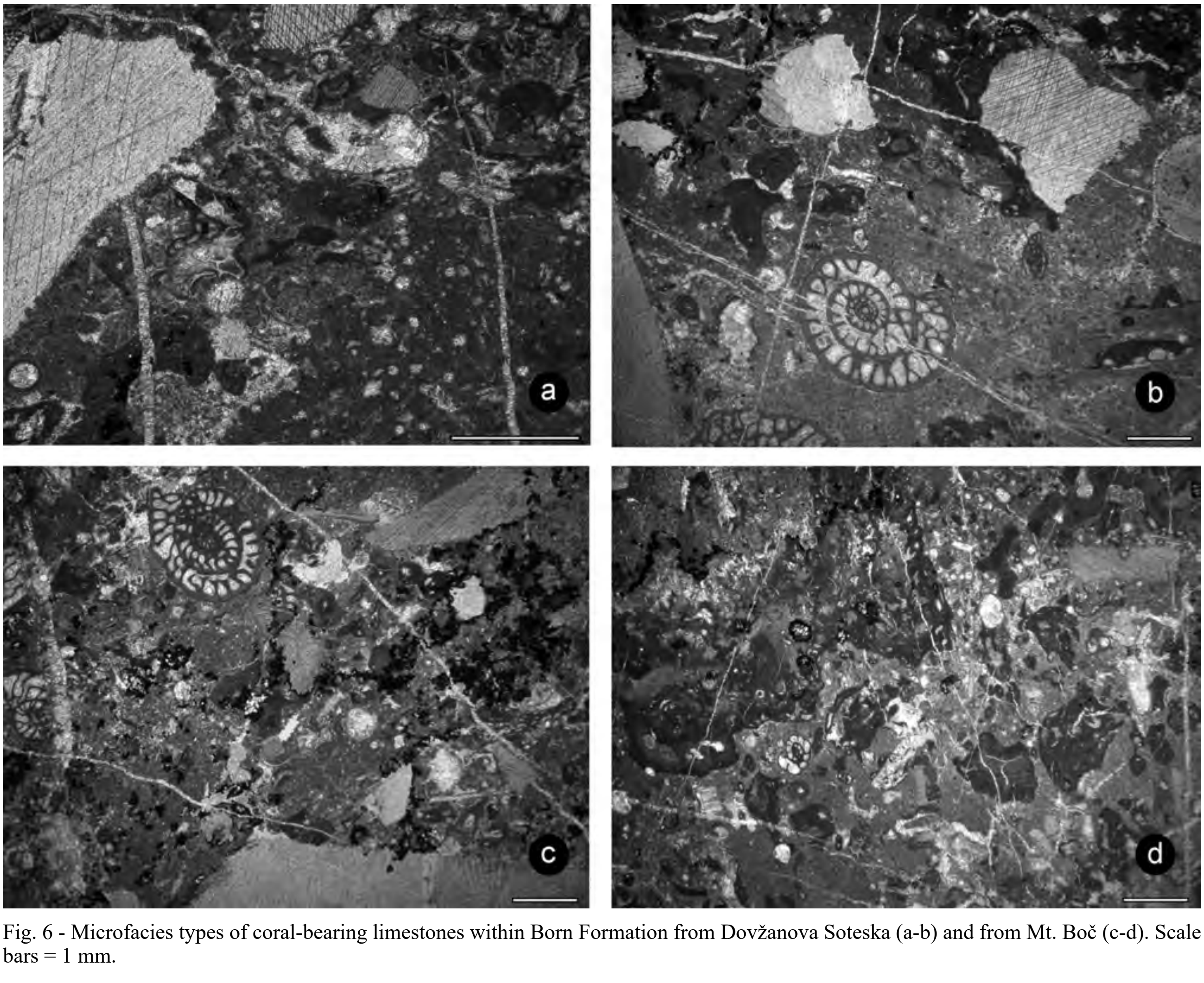


Fig. 6 - Microfacies types of coral-bearing limestones within Born Formation from Dovžanova Soteska (a-b) and from Mt. Boč (c-d). Scale bars = 1 mm.

Locality	Co-occurring species	Age
Dovžanova Soteska	*Carinthiaphyllum crasseseptatum* Gräf & Ramovš, 1965 new collection, *Carinthiaphyllum suessi* Heritsch, 1936	upper Asselian
Mt. Boč	*Carinthiaphyllum ramovsi* n. sp. new collection, *C. suessi* Heritsch (1941)	upper Asselian
Javorniški Rovt	*Carinthiaphyllum ramovsi* n. sp. (re-definition of *C.* cf. *suessi* Heritsch, illustrated in Gräf & Ramovš, 1965)	upper Asselian - lower Sakmarian
Ortnek	*Carinthiaphyllum crasseseptatum* Gräf & Ramovš, 1965	upper Asselian-Sakmarian

Tab. 1 - Stratigraphic distribution and occurrences of *Carinthiaphyllum* species in Slovenia.

growth, for example *Darwasophyllum* Pyzhyanov, 1964 (Rodriguez & Bamber, 2012). Cocke (1970) accepted a double growth mode (both solitary and colonial) for *Geyerophyllum* Heritsch, 1936, depending on different environmental conditions. Interpretation of the growth mode of *Carinthiaphyllum* changed a few times from solitary (Heritsch, 1936), to fasciculate (Minato & Kato, 1967; Rodriguez, 1985), fasciculate or solitary (Hill, 1981), fasciculate or solitary/gregaria (Rodriguez & Bamber, 2012). The first to proclaim a gregaria growth mode for *Carinthiaphyllum* was Fedorowski (1980); he showed the *Carinthiaphyllum* corals growing one on another. Accumulations of corals in transverse sections give an impression similar to fasciculate colony (Fedorowski, 1980, pl. 26, fig. 2); he and other authors estimated the gregaria growth mode as of generic value.

The growth mode of *Carinthiaphyllum yezoense* Minato & Rowett, 1967 from the Lower Pennsylvanian of Hokkaido is unclear; in spite of lack of budding, it was considered as a fasciculate colony. The species has many morphological differences from the type species and is to be referred to *Carinthiaphyllum* with question. Distant co-occurrences of "corallites" and their probable parallel growth is considered as fasciculate growth mode and hypothesized as a case of asexual reproduction (Minato & Rowett, 1967a, b).

The new material of *Carinthiaphyllum* from the Karavanke Mountains demonstrates the distinct gregaria growth mode (see later) for the genus with some additional morphological features.

DESCRIPTION OF SPECIES

Family Geyerophyllidae Minato, 1955

Genus *Carinthiaphyllum* Heritsch, 1936

Type species *Carinthiaphyllum kahleri* Heritsch, 1936.

Species included - Carinthiaphyllum kahleri Heritsch, 1936 (Carnic Alps, lower Permian, Homann, 1971), *C. carnicum* Heritsch, 1936 (lower Permian, Carnic Alps, Minato & Kato, 1967; Homann, 1971), *C. suessi* (Karavanke Mts, lower Permian, Heritsch, 1941; Greece, Schouppé, 1961), *C. crasseseptatum* Gräf & Ramovš, 1965 (Karavanke Mts, lower Permian), *C. ramovsi* n. sp. (Karavanke Mts, lower Permian), *C.* sp. (Texas, USA, lower Permian, Fedorowski, 1980), *C. heritschi* Pyzhyanov, 1966 (Zaalai Range, Kyzyl Su River, Tadzhikistan, lower Permian), *C. maklayi* Pyzhyanov, 1966 (Darvaz Range, Obi-Hungou River, Tadzhikistan, lower Permian), *C.*? *elegans* Wu & Zhao, 1989 (Weining Formation, Lower Pennsylvanian), *C.*? sp. (Fomichev, 1953, Donets Basin, upper Gzhelian), *C.*? *exquisitum* Wu & Zhao, 1974 (Bashkirian, China), *C.*? *yezoense* Minato & Rowett, 1967 (Moscovian, Japan), *C. bayanbulagense* Guo, 1983 (Pennsylvanian, China), *C. subdenroides* Guo, 1983 (Pennsylvanian, China), *C. xiangchengense* Wu & Zhang, 1985 (Carboniferous, China), *C. provectum* Yu Xueguang, 1991 (Carboniferous, China), *C. eostrotionideum*

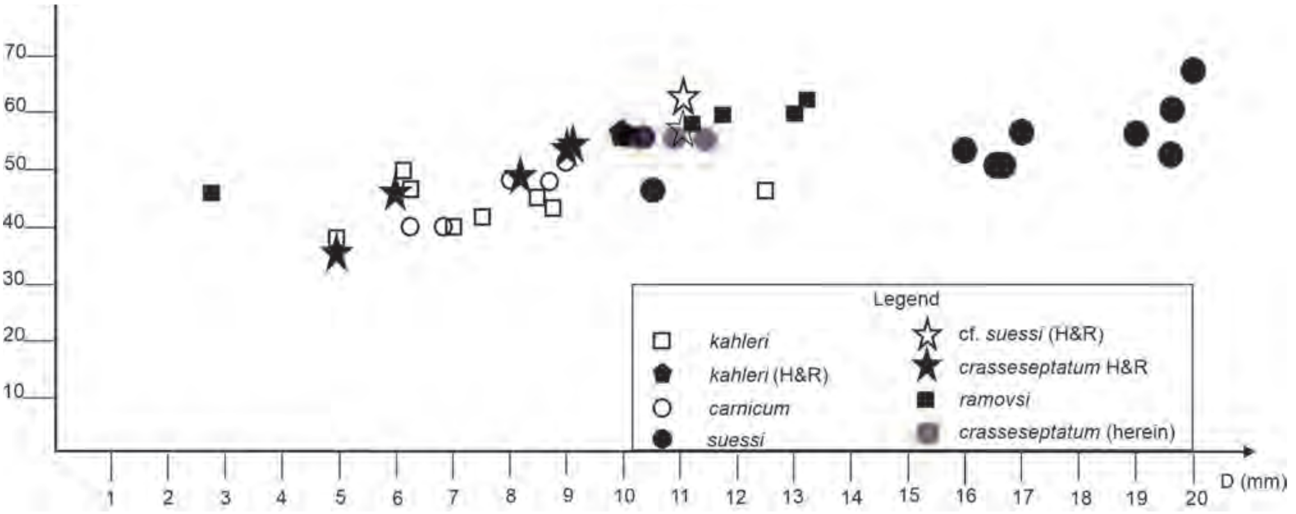


Fig. 7 - Correlation between septal number and diameter for *Carinthiaphyllum* found in the Mediterranean Province: *C. kahleri*, *C. carnicum*, *C. suessi*, *C. crasseseptatum*, *C. ramovsi*. (H & R): measurements were done from the publication of Holzer & Ramovz (1979).

Zhu & Zhao, 1992 (uppermost Carboniferous - lowermost Permian, China), *C. igoi* Niikawa, 1981 (Moscovian, Japan).

Non *Carinthiaphyllum multicystatum* Kossovaya, 1986 (upper Kasimovian-Gzhelian, Samarskaya Luka, Russian Platform). In the opinion of one of the authors (Kossovaya) this species belongs to *Geyeronaotia* Rodriguez, 1984.

Discussion - The original diagnosis of Heritsch (1936) included: 1) the columella (continuation of counter septum) with a thin, mostly irregularly curved median plate. Surrounded cuts of thin plates followed orientation of septa, but they are never connected with them. Isolated tangential cuts are interpreted as tabellae. The columella is thickened by stereoplasm attached to the plates (=radial lamellae), giving the impression of a lophophylloid columella; 2) the middle region of septa may be free of dissepiments, or these reach up to the ends of major septa. Sections near to the calice show a free space between columella and the septal ends; 3) the peripheral zone has compact dissepiments in several rows. Sometimes locally at the margin there are big tangential vesicles (lonsdaleioid dissepiments), which are never constantly developed.

The connection of the pseudocolumella to the cardinal septum was mentioned by Fomichev (1953, p. 399). A further diagnosis of the genus *Carinthiaphyllum* was proposed by Pyzhyanov (1966), before the clinotabulae were accepted as a diagnostic feature of the genus (Minato & Kato, 1967). His main ideas can be summarized as follows: solitary corals with three-zonal structure. The central zone is occupied by a thick pseudocolumella connected at young stages with cardinal and counter septa and later with cardinal only. The pseudocolumella consists of central and radial lamellae. The inner part of the tabularium is occupied by split tabulae inclined to columella (= clinotabulae). Just near the columella, tabulae can be graded or sometimes rise to pseudocolumella. At the periphery of the coral, there are a few rows of interseptal dissepiments. The inner wall is rare and thin.

Minato & Kato (1967) re-described *Carinthiaphyllum carnicum* Heritsch, 1936 (based on the Heritsch collection, housed at the University of Graz, Austria, and on their own small collection from the type region), and proposed the main changes in the diagnosis of *Carinthiaphyllum*. The first detailed study of the early stages demonstrated the connection of the pseudocolumella with the cardinal septum, not with the counter septum. The generic diagnosis by Minato & Kato (1967, p. 11) is as follows: "Fasciculate corals with a long cardinal septum, the axial end of which usually is expanded to form a prominent, solid columella in neanic to ephebic stages. The columella may be, however, somewhat modified to form an axial structure with a median plate, a few septal lamellae, and some irregular axial tabellae-like structures in the latest ontogenetic stage. Septa are of two orders, pinnately arranged, especially in the early ontogenetic stage, but tend to show more or less radial symmetry in the mature stage. The fine structure of septa is fibro-normal to diffuso-trabecular. Dissepiments are concentrically disposed between septa in transverse sections. Lonsdaleoid dissepiments occur only rarely in late stages. Tabulae are mostly inclined axially and include steeply or gently inclined clinotabulae." The presence of clinotabulae was also mentioned for the first time.

The most disputable feature considered in this diagnosis is the fasciculate mode of coral growth. In the first description of Heritsch (1936) the growth form was interpreted as solitary. The controversy started with Minato & Kato (1967, 1975), who declared that the close position of "corallites" in spite of lack of visible budding can be considered as proof of a fasciculate colony.

Microstructure - The morphological term trabicula was revised by Weyer (2014, p. 116) selecting for Rugosa as "morpho-terminological type" the species *Palaeocyclus porpita* (Linné, 1767), going back to the original spelling of Milne-Edwards & Haime (1848: trabiculina; 1850: trabicula). The version "trabecula" was introduced by Pratz (1882, without any discussion on this change in spelling), and later he was often cited (incorrectly) as the author of the term. In the Latin language, both variants are correct: trabicula and trabecula as diminutive of "traps, trapis".

The morphological term diffuso-trabecular (in German: "diffus-trabekulär") was proposed by Schindewolf (1942, p. 25), mentioning and illustrating only Scleractinia as examples. It is unclear if these are real trabicular spines (minitrabiculae sensu Roniewicz, 1984) or half-moon shaped growth segments (German "Stirnzonen": Schouppé & Stacul, 1955, 1959, revised in Weyer, 2014 as typical lamellar = fibronormal septal microstructure).

There are quite a few publications recording a diffuso-trabecular microstructure, e.g., in such unrelated genera as *Euryphyllum* (Kato, 1976), *Carcinophyllum* (Niikawa, 1979), *Yamatophyllum* (Ezaki & Kato, 2014). In spite of differences in the septal microstructure of all these genera, there is a row of trabiculae.

According to Holzer & Ramovš (1979, p. 7), the septal microstructure of "*Carinthiaphyllum kahleri* Heritsch, 1936" (= *C. suessi* in our identification) is a trabicular construction with lateral lamellar stereoplasmic thickening (terminology of Schouppé & Stacul, 1962, fig. 3). The microstructure in mature stages of our studied species of *Carinthiaphyllum* shows several rows of trabiculae, clearly visible in the peripheral zone near the archaeothecal wall - corresponding to the term multitrabicular (as "multitrabecular") of Kato (1963). This term is better defined than "diffusotrabicular". Weyer (1981, 1984) called the multi-spinous septal margins at the uppermost calicular rim (with broad septal sockets) multitrabicular, changing deeper in the calice to a coarse monacanth microstructure typical for Neaxoninae Hill, 1981 = Petraiidae Koninck, 1872.

Revised diagnosis - After our present revision, the main features of *Carinthiaphyllum* Heritsch are: solitary or gregaria growth mode, pseudocolumella connected with the cardinal septum, pseudocolumella of compact structure or with well-developed axial lamellae, trabicular/multitrabicular septal microstructure of septa, sometimes lonsdaleioid dissepiments or "naotic structure" of septa at periphery of the calice. Clinotabulae present.

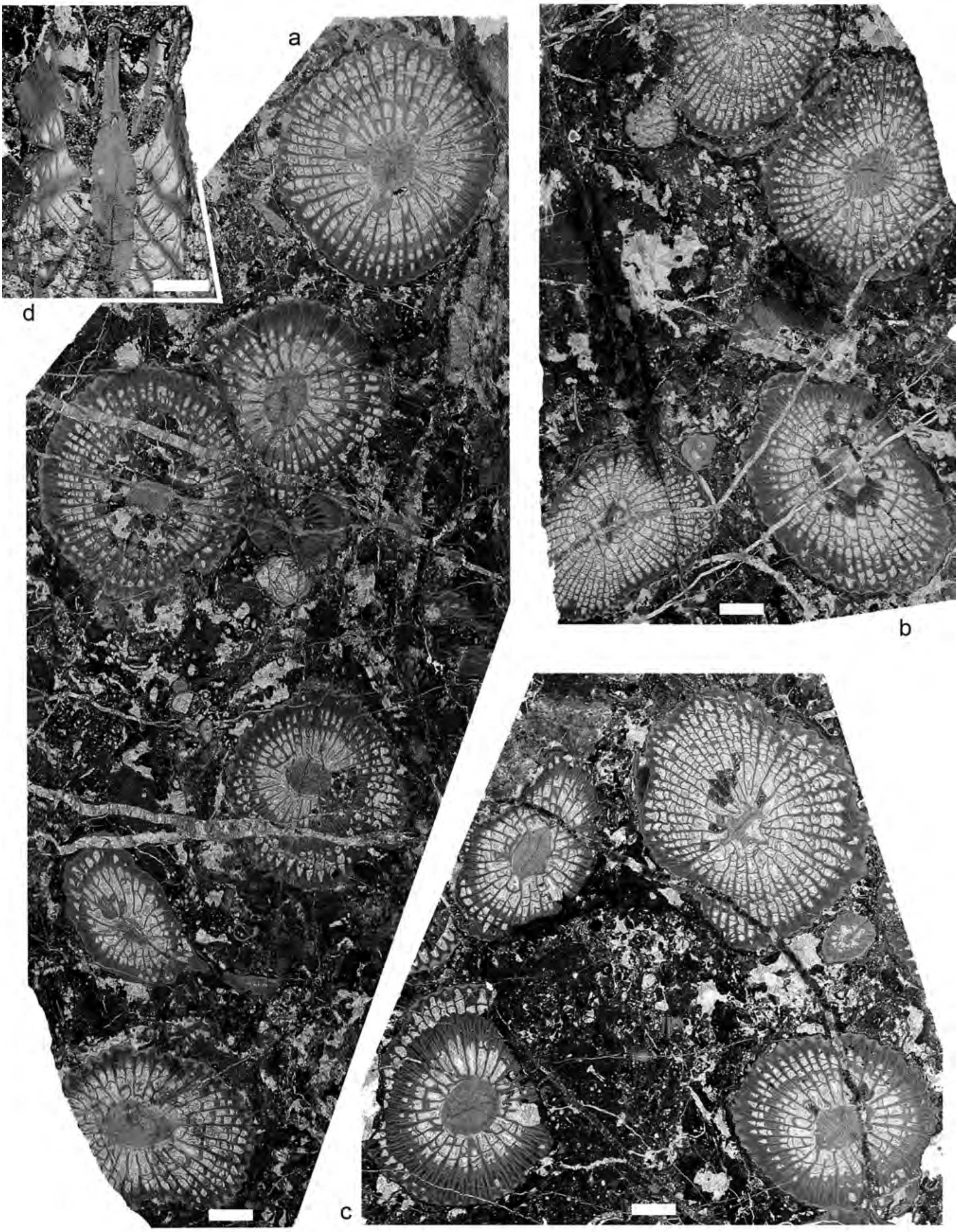


Fig. 8 - *Carinthiaphyllum crasseseptatum* Gräf & Ramovš, 1965, upper Asselian (middle Born Formation), locality Dovžanova Soteska NNE of Tržič. a-c) Transverse sections of gregaria, nrs MB.K.8073.-1., 8072.-3., 8071.-3. d) Longitudinal section, nr. MB.K.8074.-2. All scale bars = 2 mm.

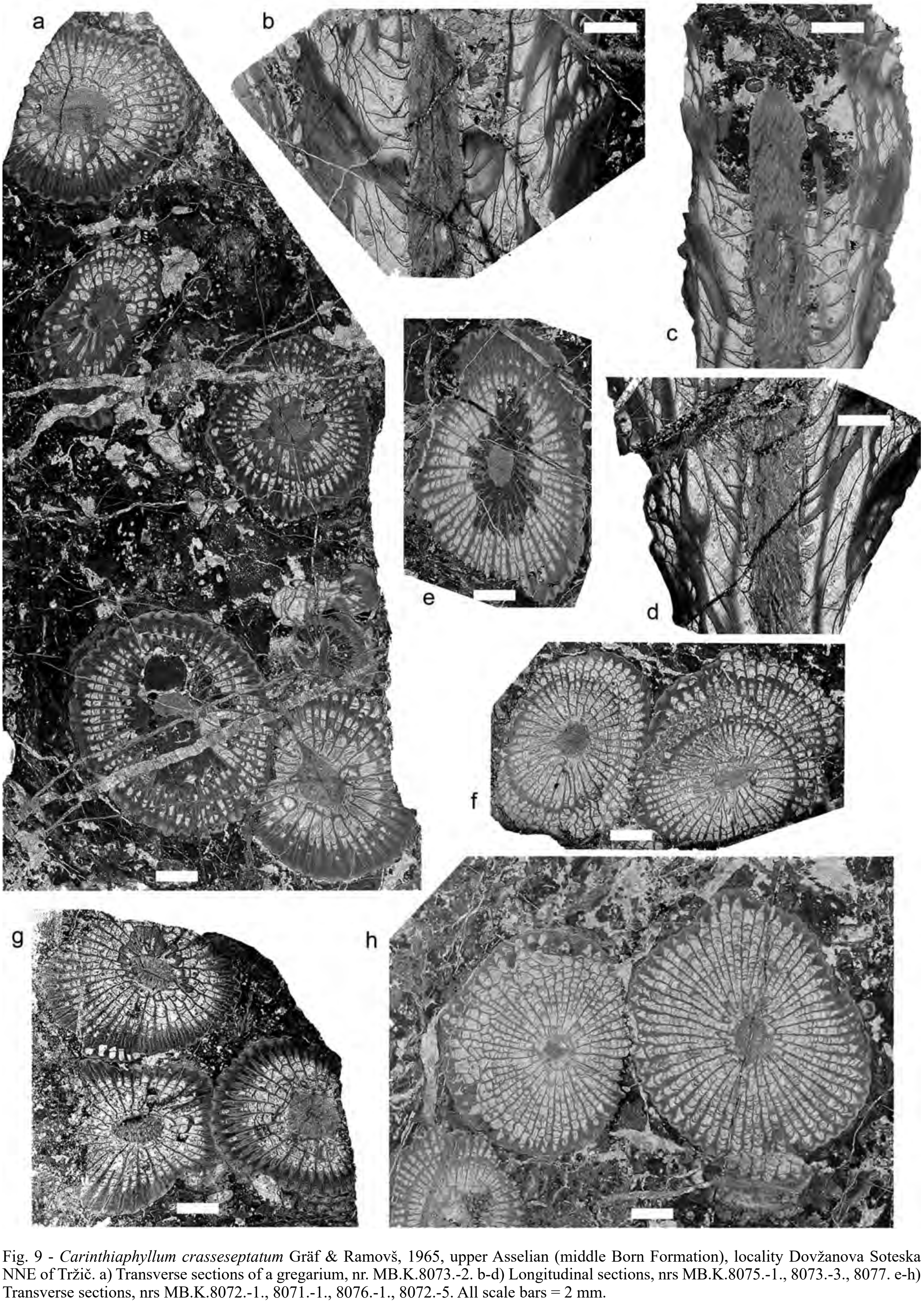


Fig. 9 - *Carinthiaphyllum crasseseptatum* Gräf & Ramovš, 1965, upper Asselian (middle Born Formation), locality Dovžanova Soteska NNE of Tržič. a) Transverse sections of a gregarium, nr. MB.K.8073.-2. b-d) Longitudinal sections, nrs MB.K.8075.-1., 8073.-3., 8077. e-h) Transverse sections, nrs MB.K.8072.-1., 8071.-1., 8076.-1., 8072.-5. All scale bars = 2 mm.

Carinthiaphyllum crasseseptatum Gräf & Ramovš, 1965 (Figs 8-11)

1965 *Carinthiaphyllum crasseseptatum* n. sp. Gräf & Ramovš, p. 169-170, Pls 8-10.
1972 *Carinthiaphyllum crasseseptatum* - Ramovš, Pl. 3, fig. 2.
1979 *Carinthiaphyllum kahleri* Heritsch - Holzer & Ramovš, Pl. 25.

Holotype - Specimen shown by Gräf & Ramovš (1965, pl. 8), housed in the Geological and Palaeontological department of Ljubljana University, locality Ortnek, Slovenia.

Description - Solitary (gregaria) with small corals. Septa of two orders. Major septa are long, some of them are connected with the pseudocolumella (Fig. 9a, f, h). Cardinal septum is long, connected with pseudocolumella (Figs 8a, 10d). Counter septum is equal in length with the other major septa. The peripheral part of major septa near the outer wall is thickened and has a triangular shape (Figs 8-9, 10a-b, 11). The length of minor septa changes from 1/2 to 2/3 of major septa according to the growth of corals (compare Fig. 9a, c). Pseudocolumella is very variable; its shape either oval compact (Figs 8, 9a) with tightly arranged radial lamellae (Fig. 9d), or consists of several radial lamellae and a median lamella (Figs 9b-c, 10f). This median lamella is well visible in all corals. Lonsdaleioid dissepiments are rare and occur in the mature stage (Fig. 9g). Interseptal dissepiments are rather numerous. The peripheral parts of septa show growth lines resembling "naotic structures" (Figs 8c, 9h, 10a-b, 11). The clinotabulae are deeply inclined (Fig. 9b, d). Tabulae situated between clinotabulae and pseudocolumella are flat. Microstructure multitrabicular at the upper margin of calice (visible in the broad triangular septal bases forming the archaeothecal wall), but monacanth in the interior thinner septa (Fig. 10a-c).

Measurements - Diameter 9 mm - 24 major septa; 10.2 mm - 30 major septa; 12 mm - 29 major septa. The original description of Gräf & Ramovš (1965) shows diameter 9 mm - 27 major septa (Fig. 7).

Discussion - Corals assigned to *C. kahleri* by Holzer & Ramovš (1979) are included in the synonymy of *C. crasseseptatum.* They have maximum diameter 10 mm, with total septal number 56. Size and septal numbers, the peripheral parts of septa and the microstructure as shown by Holzer & Ramovš (1979) are identical with our material. The same "naotic-like" structures of the peripheral parts of septa are typical for *C. crasseseptatum*

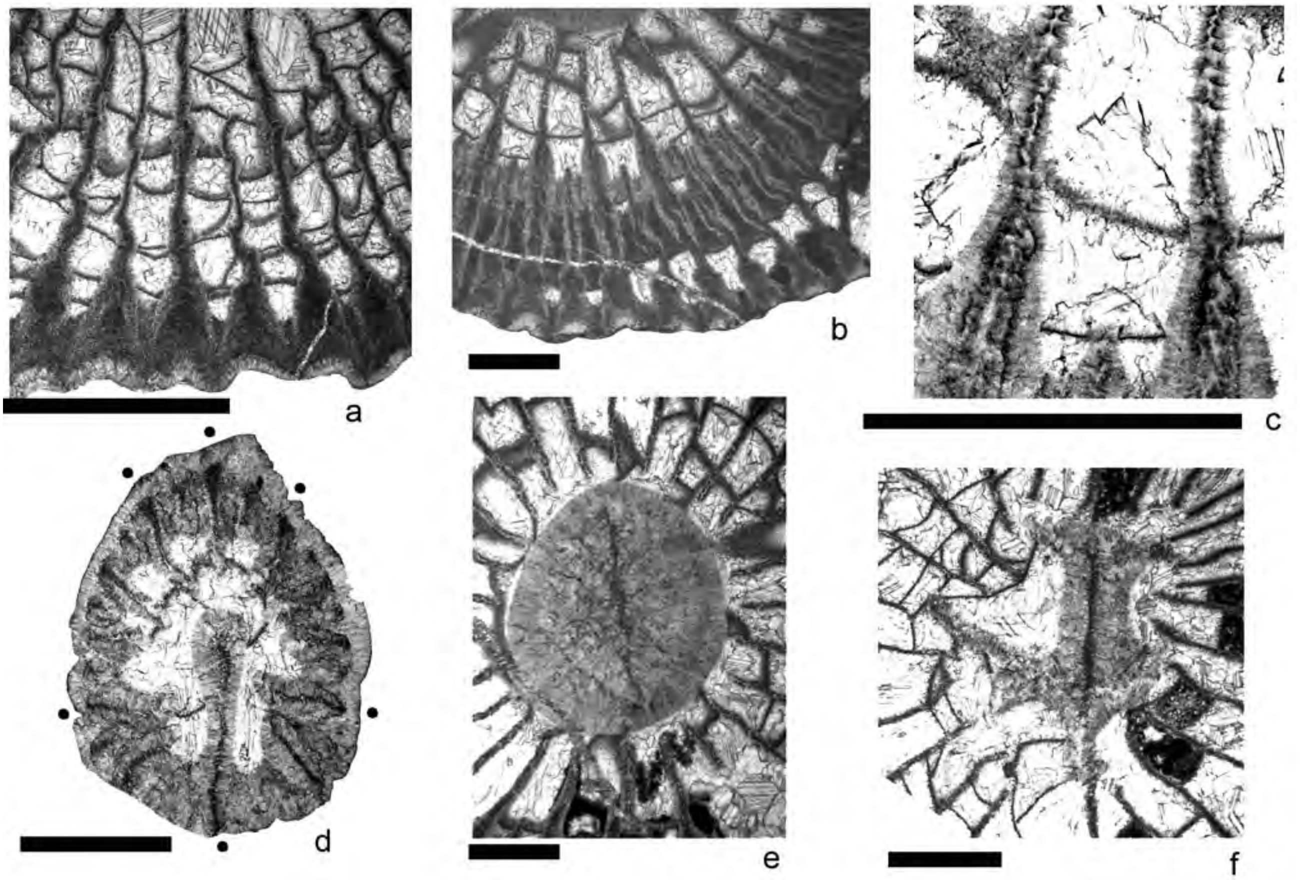


Fig. 10 - *Carinthiaphyllum crasseseptatum* Gräf & Ramovš, 1965, middle/upper Asselian (middle Born Formation), locality Dovžanova Soteska NNE of Tržič. nr. MB.K.8071.3. (see also Fig. 8a). a-c) Trabicular septal microstructures, often overprinted by growth lines ("Stirnzonen"), multitrabicular in the peripheral broader septal sockets, monacanth in the interior thinner septal parts. d) Juvenile transverse section (joined cardinal septum and pseudocolumella). e) Compact oval adult pseudocolumella (bordered by an axial tabula). f) Smaller adult pseudocolumella with longer free-ending septal lamellae. All scale bars = 1 mm.

Fig. 11 - *Carinthiaphyllum crasseseptatum* Gräf & Ramovš, 1965, middle/upper Asselian (middle Born Formation), locality Dovžanova Soteska NNE of Tržič. Transverse sections of eight corals in a gregarium, nr. MB.K.8072. Scale bar = 2 mm.

and were mentioned in the original text (Gräf & Ramovš, 1965, pl. 8, p. 169). The topotype specimens of *C. kahleri* differ by a larger number of septa, slightly larger diameter (12.5-11.0 mm - 23 [x2] septa, and 13.0-11.5 mm - 23 [x2] septa according to Heritsch, 1936).

Material - Several samples include numerous corals with cross sections clearly visible on weathered surfaces. Samples were collected from the top of the middle "rocky pyramids" (named Kušpegarjevi turni = Kušpegar towers) at the locality Dovžanova Soteska, NNE of Tržič, Slovenia, in the reef facies, upper Asselian. The collection is housed in Berlin (Museum für Naturkunde, nrs MB.K.8071.-8078., 62 thin sections).

Carinthiaphyllum ramovsi n. sp.
(Figs 12-14)

1965 *Carinthiaphyllum* cf. *suessi* Heritsch - Gräf & Ramovš, Pl. 5, fig. 2.

Holotype - Specimen MB.K.8067a., (five transverse and five longitudinal sections - in four sections also containing the paratype nr. MB.K.8067b.). Locality Mount Boč north of Rogaška Slatina, Karavanke Mts, Fig. 12a-e, upper Asselian.

Derivation of the name - In memory of Anton Ramovš (1924-2011), famous geologist in Ljubljana, for his stratigraphic and palaeontological studies of the Palaeozoic of Slovenia.

Diagnosis - Small gregaria corals possessing major and minor septa, which are thinner than the wider interseptal spaces (Fig. 12). Broad septal sockets at the wall are extremely short; major septa are thin in the dissepimentarium, slightly thickened in the tabularium. Cardinal septum is connected with pseudocolumella (Figs 12-14). Thick pseudocolumella consists of numerous radial lamellae and median lamella (Fig. 12e). Axial tabula is developed and connected with radial lamellae. Their peripheral ends enter the tabularium (Fig. 14c-d). Clinotabulae present (Fig. 13c-d). Dissepiments are interseptal and lonsdaleioid (rare) (Fig. 12a, d, f). Root-like structures and archaeothecal protrusions are common (Fig. 12f).

Description - Small gregaria corals possessing major and minor septa. Major septa are long; some of them are connected with pseudocolumella. No fossula is visible. The counter septum is equal or slightly shorter than the other major septa (compare Fig. 13a and 13b). In Fig. 12d the counter septum is much shorter than most other major septa. The minor septa length is 2/3 of major septa. The thickness of all septa is rather equal along the length of septa (in transverse section). The outer wall has wavy inner margin and a well-visible trabicular structure in the broad septal sockets (Fig. 13f). In the early ontogenetic stages, the inner part of the cardinal septum is connected with the pseudocolumella (Fig. 14). In the mature stage major septa are joined with concentric axial tabulae surrounding the pseudocolumella (Fig. 13). The latter consists of numerous, rather densely packed radial lamellae and the median lamella (Figs 12a, d, 13b, e). The number of radial lamellae corresponds to the number of major septa. Some outer parts of the radial lamellae go out of the outer margin of the pseudocolumella and are clearly visible in transverse and longitudinal sections (Fig. 13); in the latter, they join the axial tabula or sometimes even reach beyond it into the tabularium. The dissepimentarium consists of six rows of nearly vertical small interseptal, slightly convex dissepiments. Lonsdaleioid dissepiments appear at late mature stages. Clinotabulae are deeply inclined. Tabulae are concave and occur rather rarely. Septa and axial lamellae have a trabicular microstructure.

Measurements - Maximum diameter of coral reached 13.3 mm with 62 septa (Tab. 2).

Ontogenesis - The earliest observed stage demonstrates the connection of cardinal and counter septa; both lateral septa are also present (Fig. 14a). The cardinal septum is extremely thick. Next two sections show the thickening of the inner end of the cardinal septum and the beginning of the pseudocolumellar growth (Fig. 14b); they have 21 and 23 major septa (Fig. 14b-c), and the counter septum lost the connection with the pseudocolumella.

Discussion - The new species differs from the type species *Carinthiaphyllum kahleri* Heritsch, 1936 by the complex axial structure and a larger diameter with higher numbers of septa. *C. suessi* is distinctly larger (Fig. 7). The lack of strongly thickened peripheral septal sockets with "naotic-like" structures and the presence of a more complex axial structure distinguish the new species from *Carinthiaphyllum crasseseptatum*.

Reproduction - *Carinthiaphyllum ramovsi* n. sp. has a gregaria growth mode with juvenile corals settling on the outer wall of a nearly mature coral (sometimes with root-like protrusions) (Figs 13b, 14e-f). The septa of the "substrate" corals do not connect with those of juvenile corals; there is never a wall interrupted by any connecting pores. In mature stage, neighbouring corals may touch each other some time for support, when growing upwards nearby. Special outgrowth root-like structures were observed only in this species. The additional stereoplasmic protrusion was segregated by the archaeotheca of the "substrate" coral for a connection with the juvenile neighbors. The protrusion exists temporarily and was not observed between mature stages.

Material - One small limestone sample with 12 transverse coral thin sections; nr. MB.K.8067.-8068. is housed in the Museum für Naturkunde in Berlin.

GREGARIA MODE OF CORAL GROWTH

The term gregaria growth form of solitary corals was proposed by Fedorowski (1980) for the case of accumulated corals, appearing like a fasciculate colony, but with no visible features of buddings. According to this author "two facts are striking: 1) only larvae of the same species settled together, 2) specimens are differentiated

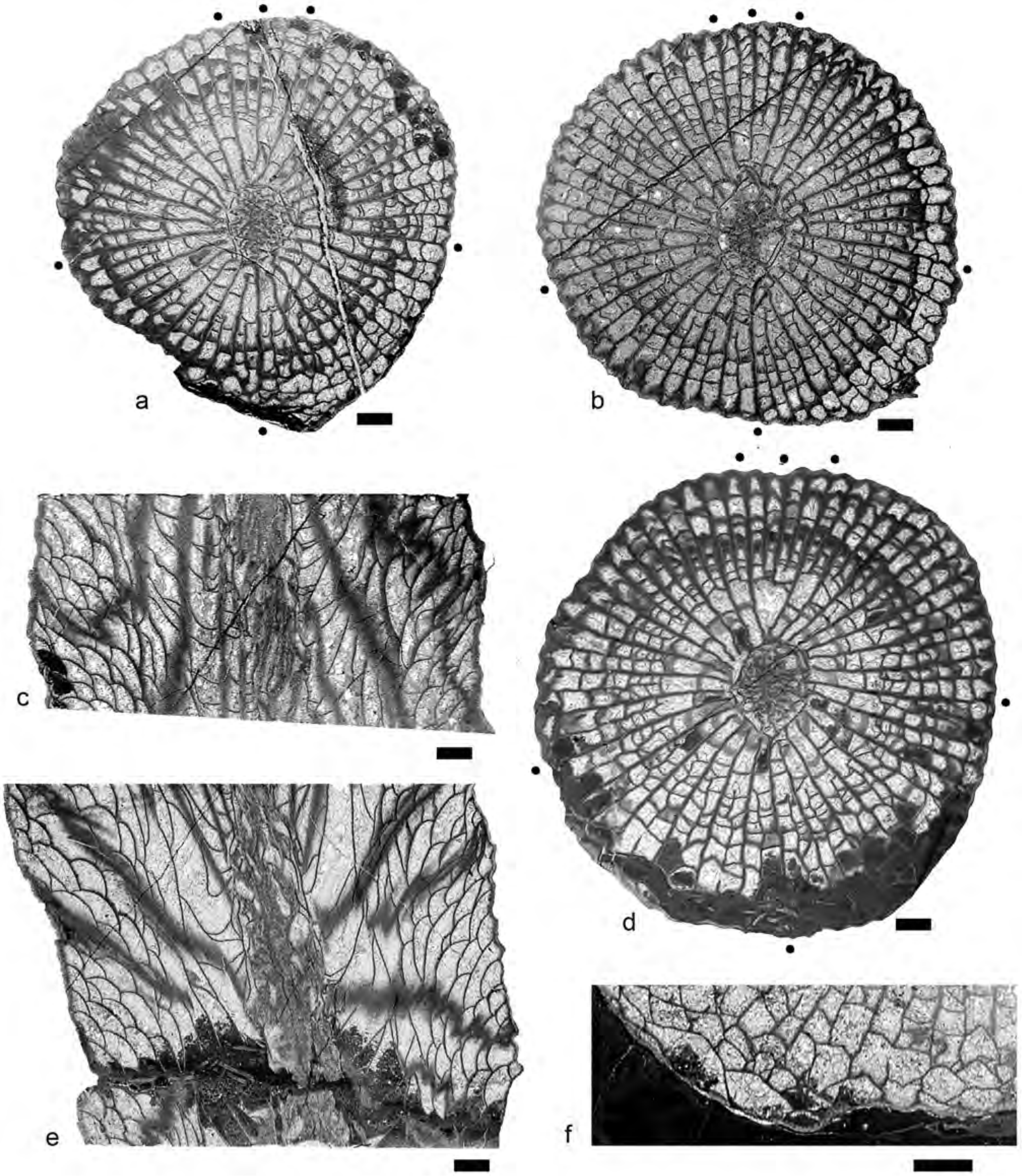
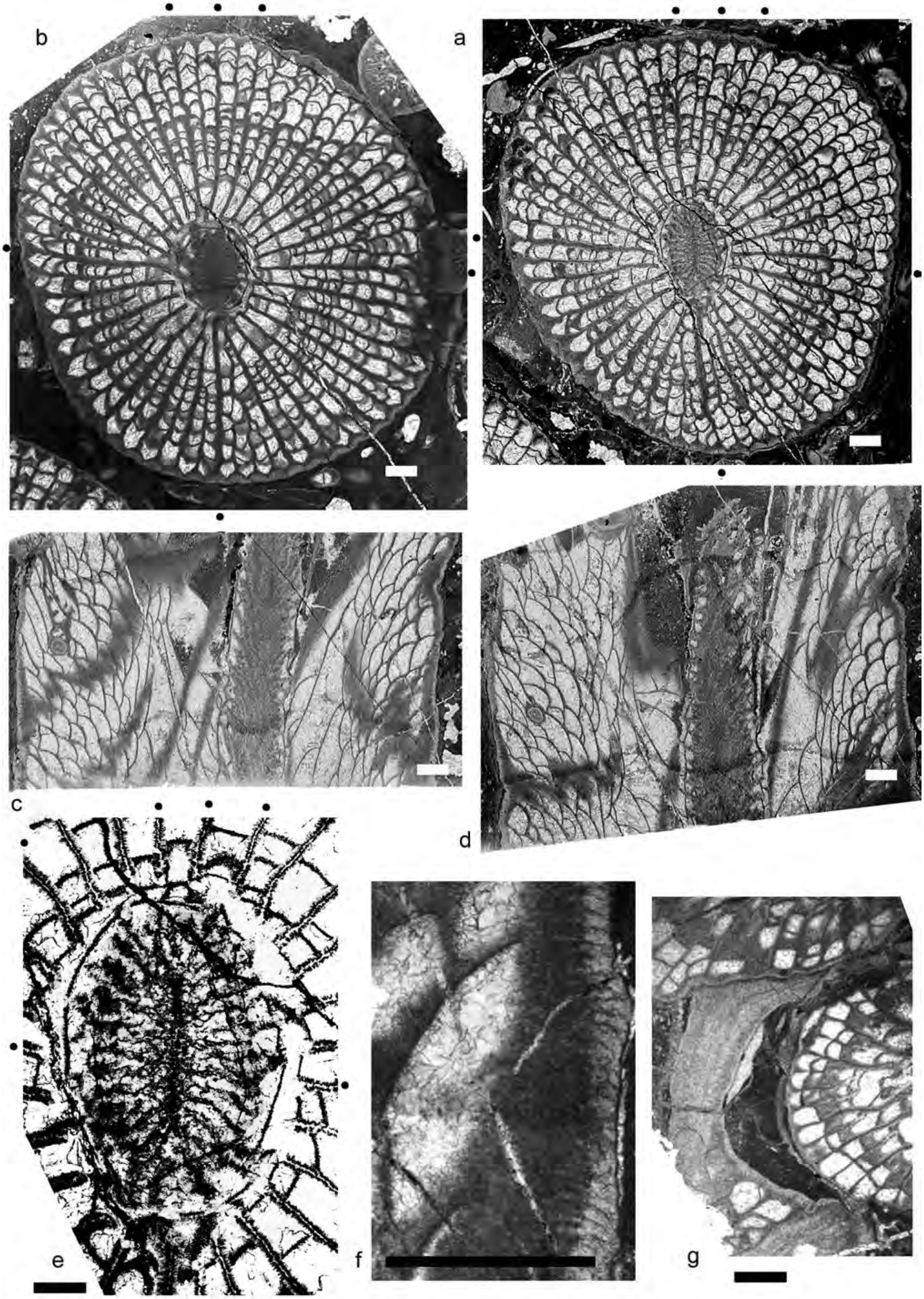


Fig. 12 - *Carinthiaphyllum ramovsi* n. sp., upper Asselian, locality Mount Boč north of Rogaška Slatina. Abbreviations (for all figures) - N: number of all septa; n: number of major septa; D: diameter; C: cardinal septum; c: counter septum; L: lateral septum; numbers are the major septa in four quadrants. Sequence of transverse and longitudinal (parallel to the cardinal-counter plane) subtabular sections (six protosepta marked). a-d) Holotype nr. MB.K.8067; septal formula for transverse section (a) (from left to right): C-6-L-9-c-8-L-6 (n-33; N-59; D-11, 2); septal formula for transverse sections (b) and (d): C-6-L-9-c-8-L-7 (n-34, N-60, D-11, 7-13 mm). c-e) Longitudinal sections. f) Specimen nr. MB.K.8068 with normal and occasional lonsdaleioid dissepiments. All scale bars = 1 mm.

Fig. 13 - *Carinthiaphyllum ramovsi* n. sp., upper Asselian, locality Mount Boč north of Rogaška Slatina. a-b) Subtabular transverse sections of paratype nr. MB.K.8067; septal formula for section (a) C-7-L-8-c-8-L-7 (n-34, N-61, D-12, 7 mm); septal formula for section (b) C-7-L-8-c-8-L-8 (n-35, N-62, D-13.3 mm). c-d) Longitudinal sections of paratype nr. MB.K.8067 near the calicular base (at right angle to the cardinal-counter plane) with well-developed clinotabulae. e) Pseudocolumella magnified fragment of the figure (b) with regularly arranged septal lamellae in paratype nr. MB.K.8067. f) Multitrabicular septal microstructure within archaeotheca in paratype nr. MB.K.8067, magnified detail of the figure (d). g) Nr. MB.K.6087c; transverse section with archaeothecal tube-like outgrowth touching two neighbouring corals of the gregarium. All scale bars = 1 mm.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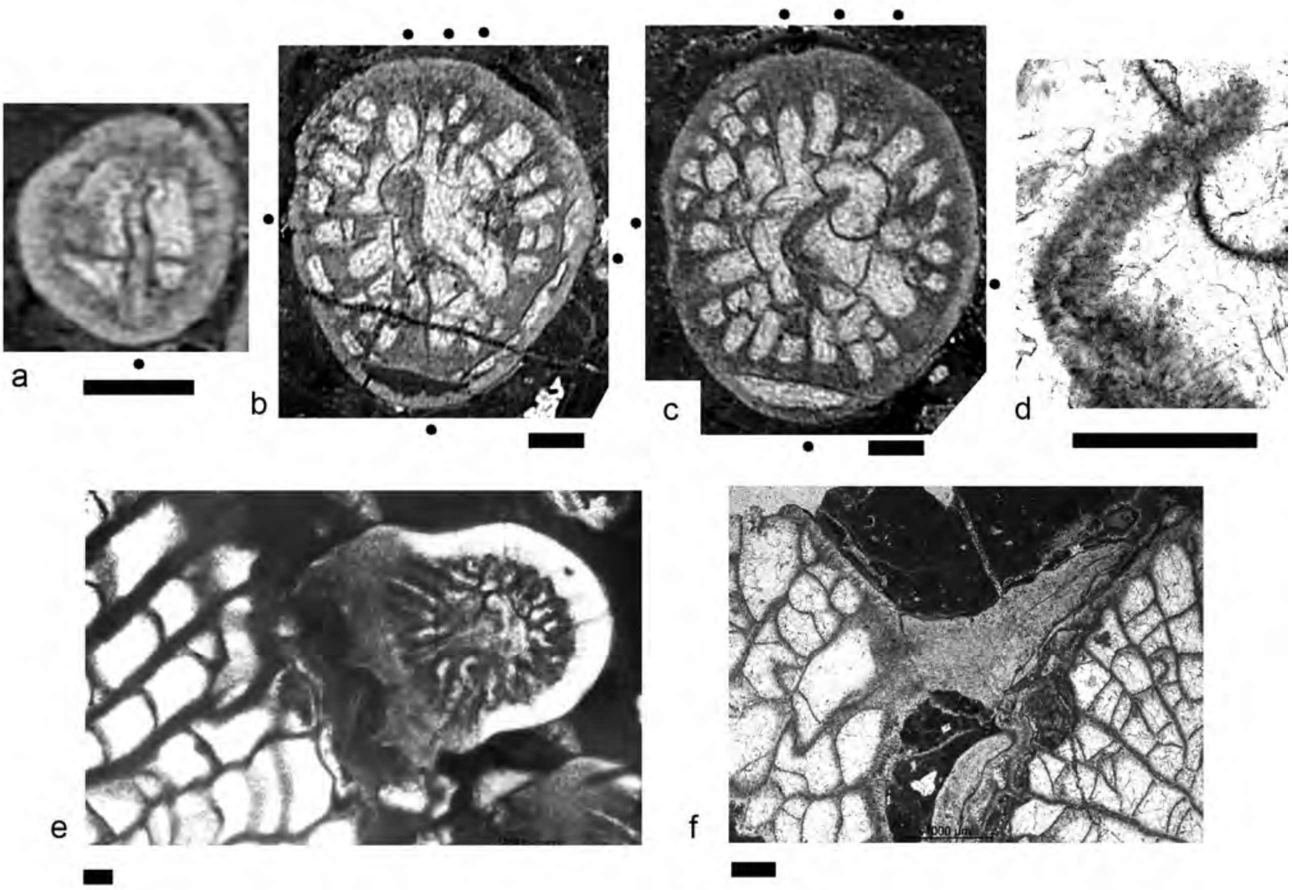

Fig. 14 - *Carinthiaphyllum ramovsi* n. sp., upper Asselian, locality Mount Boč north of Rogaška Slatina. a) Extreme juvenile transverse section nr. MB.K.8068.2a (D 1.05 mm) with prominent cardinal septum only. b-c) Succeeding subtabular transverse sections nr. MB.K.8068.2 with initial pseudocolumella, originating from the cardinal septum, still without further septal lamellae; septal formula for section (c) C-6-L-6-c-6-L-5 (n 27, N 46, D 2.8 mm). d) Section nr. MB.K.8068.2c; pseudocolumella of thin with nearly vertically arranged trabiculae. e) Section nr. MB.K.8068.2; juvenile coral, attached to an adult one, using three archaeothecal outgrowths. f) Section nr. MB.K.8068.2; left coral with tube-like outgrowth, attached to the adult right specimen. All scale bars = 0.5 mm.

in ontogenetic development (which) makes clear that gregaria were acting as comparatively long-lasting larvae settlements" (Fedorowski, 1980, p. 435).

Earlier this phenomenon was interpreted in most cases as fasciculate colonies without observed budding. The consideration of the growth form of corals used as a generic feature demands a detailed look in every case. A first feature of probable gregaria mode is the occurrence of many juvenile stages (just with wall and still very few septa), which did not develop into mature stages. Second feature: no budding is visible. Third criterion can be the appearance of the additional root-like outgrowths or other modification of supporting protrusions. In some cases, such tubes are channeled, but without any fusion of soft parts between the neighboring corals. In our material only one *C. crasseseptatum* specimen had a protrusion, where a channel was seen. Also, in the numerous protrusions of *Carinthiaphyllum ramovsi* n. sp. real fusion was not observed.

The origination of rhizoids is not a unique phenomenon. A good example was shown for solitary corals, surrounded by tabulate *Halysites* colonies. The development of rhizoid strategy is used by *Cystiphyllum visbyense* Wedekind, 1927 for support, using both living and dead parts of *Halysites* colonies. In this case (Ireviken cliff on Gotland Island, upper Llandovery), the rhizoids are constructed by tubes with an empty channel (Berkowski & Zapalski, 2018).

The gregaria growth form was studied in *Darwasophyllum* Pyzhyanov, 1964 (Rodriguez & Bamber, 2012), showing extremely similar features observed here in *Carinthiaphyllum*. The high number of juvenile forms of the same species points to some restrictions for planula distribution, probably some barrier or current. *Lytvophyllum*? *hongi* (Wilson, 1982) is not a pseudocolony (as suggested by Stevens, 2008), but has to be assigned to gregaria. Gregaria accumulation is distributed rather widely in late Palaeozoic times, and in future many corals considered as fasciculate could be revised as gregaria.

The meaning of gregaria is quite close to "pseudocolonial" according to the definition of pseudocolony "as a cluster of individual corallites of the same species that grow close to one another, giving the impression of being produced by offsetting" (Fedorowski, 1978). Spassky & Kravtsov (1974) used pseudocolony in a different sense for cases of intracalicular circumperipheral budding, resulting in many juvenile buds around the big parent coral (like the lectotype of the upper Silurian

Figure	Diameter (mm)	N	n	Ns- number of minor septa
13a	11.2	59	33	26
13b	13.3	62	35	31
12b	11.7	60	34	26
12d	13.0	60	34	26
14b	2.7	46	27	19
14c	2.8	48	28	20

Tab. 2 - Measurements of *Carinthiaphyllum ramovsi* n. sp. (septa are counted morphogenetically as major septa (= protosepta, metasepta) and minor septa (= catasepta). Abbreviations: N - number of all septa; n - number of major septa.

Entelophyllum prosperum (Počta, 1902), refigured in Prantl, 1940, pl. 1, fig. 6). However, the term pseudocolony had another definition earlier, being commonly used among Scleractinia corals - dominating for phaceloid colonies derived from one planula, but lacking later integration of soft parts (Roniewicz & Stolarski, 1999). Thus, Scleractinian pseudocolonies are formed via asexual budding - that is the basic difference against gregaria with their only sexual type of reproduction.

CONCLUSIONS

The revision of *Carinthiaphyllum*, distributed in the lower Permian of the Karavanke Mountains and the Dinarides (Slovenia), is based on new and previously obtained material. It allowed the generic diagnosis to be emended, to more clearly define the species and to separate the new species *Carinthiaphyllum ramovsi* n. sp. The gregaria mode of reproduction was documented for *C. ramovsi* n. sp. and, probably, is one of the typical features for the genus *Carinthiaphyllum* Heritsch, 1936 and family Geyerophyllidae Minato 1955.

The ages of the three species under consideration were determined according to new results on fusulinids and conodonts. Thus, the interval of distribution of *Carinthiaphyllum suessi* and *C. ramovsi* is considered as upper Asselian - lower Sakmarian, and the age of *C. crasseseptatum* is late Asselian - Sakmarian. The brief analysis of the geographical distribution shows that Carboniferous *Carinthiaphyllum* species were characteristic for the eastern part of the Palaeotethys, but Permian ones are typical for the western part of the Palaeotethys Ocean. This supports the assumptions about some isolation of the western Palaeotethys in the Permian.

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REFERENCES

Beede J.W. & Kniker H.T. (1924). Species of the genus *Schwagerina* and their stratigraphic significance. *University of Texas Bulletin*, 2433: 1-96.

Berkowski B. & Weyer D. (2012). *Hamaraxonia*, a new pseudocolumellate genus of Middle Devonian deep-water Rugosa (Anthozoa) from Morocco. *Geologica Belgica*, 15: 245-253.

Berkowski B. & Zapalski M.K. (2018). Large dwellers of the Silurian *Halysites* biostrome: rhizosessile life strategies of cystiphyllid rugose corals from the Llandovery of Gotland. *Lethaia*, 51: 581-595.

Buser S. (1974). Neue Feststellungen im Perm der westlichen Karawanken. *Carinthia II*, 84: 27-37.

Buser S. (1980). Basic geologic map SFR Yugoslavia 1:100,000. Explanatory notes on the sheet of Celovec (Klagenfurt). *Zvezni geološki zavod*, Beograd: 1-62.

Buser S. & Forke H.C. (1996). Lower Permian conodonts from the Karavanke Mts. (Slovenia). *Geologija*, 37-38 [1994/95]: 153-171.

Chernykh V.V. & Ritter S.M. (1997). *Streptognathodus* (Conodonta) Succession at the Proposed Carboniferous-Permian Boundary Stratotype Section, Aidaralash Creek, Northern Kazakhstan. *Journal of Paleontology*, 71: 459-474.

Chernykh V.V., Ritter S.M. & Wardlaw B.R. (1997). *Streptognathodus isolatus* n. sp. (Conodonta): Proposed index for the Carboniferous-Permian boundary. *Journal of Paleontology*, 71: 16-164.

Cocke J.M. (1970). Dissepimental Rugose corals of Upper Pennsylvanian (Missourian) rocks of Kansas. *Paleontological Contribution University of Kansas*, 54: 1-67.

Cocke J.M. & Cocke N.C. (1968). Classification and distribution of Missourian (Upper Pennsylvanian) Geyerophyllid Corals from Kansas. *Transaction of the Kansas Academy of Science*, 71: 38-48.

Dobrolyubova T.A. & Kabakovich N.V. (1948). Nekotorye predstaviteli Rugosa srednego i verkhnego karbona podmoskovnogo basseyna. [Some representatives of Rugosa from the Middle and Upper Carboniferous of the Moscow Basin]. *Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR* (*Transaction of the Palaeontological Institute Academy of Sciences USSR*), 14: 1-37. [in Russian]

Ellison S.P. Jr. (1941). Revision of Pennsylvanian conodonts. *Journal of Paleontology*, 15: 107-143.

Ezaki Y. & Kato M. (2014) Phylogenetic and palaeobiological implications of a new Carboniferous rugose coral with unusual trait combinations from the Akioshi Terrane of Japan. *Journal of Systematic Paleontology*, 12: 481-492.

Fedorowski J. (1978). Some aspects of coloniality in Rugose corals. *Palaeontology,* 21: 177-224.

Fedorowski J. (1980). Some aspects of coloniality in corals. *Acta Palaeontologica Polonica*, 25: 429-437.

Fodor L., Jelen B., Marton E., Skaberne D., Čar J. & Vrabec M. (1998). Miocene-Pliocene tectonic evolution of the Slovenian Periadriatic Line and surrounding area: Implications for Alpine-Carpathian extrusion models. *Tectonics*, 17: 690-709.

Fomichev V.D. (1953). Korally Rugosa i stratigrafiya sredne- i verkhnekamennougol'nykh i permskikh otlozheniy Donetskogo basseyna. [Rugosa corals from the Middle and Upper Carboniferous and from the Permian of the Donez basin]. *Trudy, Vsesoyuznyy Nauchno-Issledovatel'skiy Geologicheskiy Institut (VSEGEI)*: 1-622. [in Russian]

Forke H.C. (2002). Biostratigraphic Subdivision and Correlation of Uppermost Carboniferous/Lower Permian Sediments in the Southern Alps: Fusulinoidean and Conodont Faunas from the Carnic Alps (Austria/Italy), Karavanke Mountains (Slovenia), and Southern Urals (Russia). *Facies*, 47: 201-276.

Grabau A.W. (1922). Palaeozoic corals of China: Part 1, Tetraseptata. *Palaeontologica Sinica*, *series B*, 2-1: 1-74.

Grabau A.W. (1928). Palaeozoic corals of China. Part 1. Tetraseptata II. *Paleontologica Sinica*, *series B,* 2-2: 1-175.

Gräf W. & Ramovš A. (1965). Rugose Korallen aus dem Jungpaläzoikum Sloweniens (NW Jugoslawien). *Geologija*, 8: 160-189.

Guo Sheng-zhe (1983). Middle and Upper Carboniferous Rugose Corals from Southern Dahinganling (Mts. Great Khingan). *Acta Palaeontologica Sinica*, 22: 220-230. [in Chinese with English summary]

Heritsch F. (1933). Rugose Korallen aus dem Trogkofelkalk der Karawanken und der Karnischen Alpen. *Prirodoslovne Razprave*, 2: 42-55.

Heritsch F. (1936). Korallen der Moskauer-, Gshel- und Schwagerinen-Stufe der Karnischen Alpen. *Palaeontographica A*, 83: 99-162.

Heritsch F. (1938). Die stratigraphische Stellung des Trogkofelkalkes. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*, 79/B: 63-186.

Heritsch F. (1941). Nachweis des Oberen Schwagerinenkalkes (Unteres Perm) im Gebiete des Wotsch-Berges bei Pöltschach, südlich von Marburg a.d. Drau. *Zentralblatt für Mineralogie, Geologie, und Paläontologie B,* 9: 274-279.

Hill D. (1981). Part F. Coelenterata. Supplement 1. Rugosa and Tabulata. *In* Teichert C. (ed.), Treatise on Invertebrate Paleontology. The geological Society of America: The University of Kansas Press, Lawrence, 1-2: 1-762.

Holtedahl O. (1913). Zur Kenntnis der Karbonablagerungen des westlichen Spitzbergens. II. Allgemeine stratigraphische und tektonische Beobachtungen. *Skrifter utgit av Videnskapsselskapet i Kristiania, I, matematisk-naturvidenskabelig Klasse*, 1912, 2: 1-91.

Holzer H.L. & Ramovš A. (1979). Neue rugose Korallen aus dem Unterperm der Karawanken. *Geologija*, 22: 1-20.

Homann W. (1971) Korallen aus dem Unter- und Mittelperm der Karnischen Alpen. *Carinthia II, Sonderheft*, 28: 97-143.

Kahler F. & Kahler G. (1937). Beiträge zur Kenntnis der Fusuliniden der Ostalpen: Die Pseudoschwagerinen der Grenzlandbänke und des oberen Schwagerinenkalkes. *Palaeontographica A*, 87: 1-44.

Kato M. (1963) Fine skeletal structures in the Rugosa. *Journal of the Faculty of Science, Hokkaido University*, *Series IV*, 11: 571-630.

Kato M. (1976). A Permian rugose coral *Euryphyllum* from Kashmir. *Journal of Faculty of Science, Hokkaido University, Series IV*, 17: 357-364.

Kochansky-Devidé V. (1959). Karbonske i permske fuzulinidne foraminifere Velebita i Like. Donji perm. *Palaeontologia Jugoslavica*, 3: 1-62. [in Croatian with German summary]

Koninck L.G. (1872). Nouvelles Recherches sur les Animaux Fossiles du Terrain Carbonifère de la Belgique. Première Partie. *Mémoires de l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique*, 39: 1-178.

Kossovaya O.L. (1986). Klass Anthozoa. Podklass Rugosa (Tetracorallia). *In* Murav'ev I.S. & Grigor'eva A.D. (eds), Atlas fauny verkhnego karbona i nizhney permi Samarskoy Luki, 62-69, 145-146; Kazan' (izdatel'stvo Kazanskogo universiteta). [in Russian]

Kossovaya O.L., Novak M. & Weyer D. (2012). *Sloveniaxon*, a new genus of ahermatypic Rugosa (Anthozoa) from the basal Permian (Asselian) of Slovenia. *Geologica Belgica*, 15: 361-369.

Kossovaya O.L., Novak M. & Weyer D. (2016). Large-sized Early Permian "caninioid" corals from the Karavanke Mountains, Slovenia. *Journal of Paleontology*, 90: 1049-1067.

Leven E.Ya. & Shcherbovich S.F. (1980). Komplex fuzulinid sakmarskogo yarusa Darvaza. *Voprosy mikropaleontologii, AN SSSR*, 23: 71-85. [in Russian]

Linné C. (1767). Systema Naturae. *Editio duodecima reformata*, I (2): 533-1327.

Márton E., Fodor L., Jelen B., Márton P., Rifelj H. & Kevrić R. (2002). Miocene to Quaternary deformation in NE Slovenia: complex paleomagnetic and structural study. *Journal of Geodynamics*, 34: 627-651.

Milne-Edwards H. & Haime J. (1848). Recherches sur les polypiers. Premier Mémoire: Observations sur la structure et le développement des polypiers en général. *Annales des Sciences Naturelles (Paris), série 3, zoologie*, 9: 37-89.

Milne-Edwards H. & Haime J. (1850-1855). A Monograph of the British Fossil Corals. *The Palaeontographical Society (London), Monographs*: 1-322.

Minato M. (1955). Japanese Carboniferous and Permian corals. *Journal of the Faculty of Science, Hokkaido University*, 9: 1-222.

Minato M. & Kato M. (1967). On the coral genus *Carinthiaphyllum* Heritsch with description of *Carinthiaphyllum carnicum* Heritsch from Carnic Alps. *Journal of the Faculty of Science, Hokkaido University*, 4: 313-320.

Minato M. & Kato M. (1975). Geyerophyllidae Minato, 1955. *Journal of the Faculty of Science, Hokkaido University*, 17: 1-21.

Minato M. & Rowett C.L. (1967a). New Palaeozoic fossils from Southern Hokkaido, Japan. *Journal of the Faculty of Science, Hokkaido University*, 4: 322-332.

Minato M. & Rowett C.L. (1967b). Modes of reproduction in rugose corals. *Lethaia*, 1: 175-183.

Nicholson H.A. & Lydekker R. (1889). A manual of palaeontology, 1. 885 pp. Blackwood & Sons, Edinburg, London.

Niikawa I. (1979). *Carcinophyllum* from Ichinotani Formation in Fukuji, Cantral Japan. *Journal of the Faculty of Science, Hokkaido University*, *Series 4*, 19: 235-240.

Niikawa I. (1981). Rugose Coral from Fukuji, Central Japan. Part I. Carboniferous. *Journal of General Education Department, Niigata University*, 11: 131-161.

Novak M. (2007). Depositional environment of Upper Carboniferous - Lower Permian in Karavanke Mountains (Southern Alps, Slovenia). *Geologija*, 50: 247-268.

Novak M. & Forke H.C. (2005). Updated fusulinid biostratigraphy of Late Palaeozoic rocks from the Karavanke Mts. (Slovenia). *In* Hubmann B. & Piller W.E. (eds), Jahrestagung der Paläontologischen Gesellschaft: Beitragskurzfassungen. *Berichte des Institutes für Erdwissenschaften Karl-Franzens-Universität Graz*, 10: 90-91.

Novak M., Forke H.C. & Schönlaub H.P. (2019). The Pennsylvanian-Permian of the Southern Alps (Carnic Alps/Karavanke Mts.), Austria/Italy/Slovenia - fauna, facies and stratigraphy of a mixed carbonate-siliciclastic shallow marine platform along the northwestern Palaeotethys margin: Field Trip C3. *In* Herbig H.-G., Aretz M., Amler M.R.W. & Hartenfels S. (eds), 19th International Congress on the Carboniferous and Permian, Cologne, July 29-August 2, 2019, field guides. *Kölner Forum für Geologie und Paläontologie*, 24: 251-302.

Novak M. & Skaberne D. (2009). Upper Carboniferous and Lower Permian. *In* Pleničar M., Ogorelec B. & Novak M. (eds), The Geology of Slovenia. Geological Survey of Slovenia (Ljubljana): 99-136.

Placer L. (2008). Principles of the tectonic subdivision of Slovenia. *Geologija*, 51: 205-217.

Počta P. (1902). Anthozoaires et Alcyonaires. *In* Barrande J., Système Silurien du Centre de la Bohême. Partie I. Recherches Paléontologiques. VIII.2. I-VIII: 1-347.

Prantl F. (1940). *Xylodes* Lang & Smith (Rugosa) in the Czechoslovakian Silurian. *Rozpravy, České Akademie Ved a Umení, Třida II*, 50: 1-31.

Pratz E. (1882) Über die verwandtschaftlichen Beziehungen einiger Korallengattungen mit hauptsächlicher Berücksichtigung ihrer Septalstructur. *Palaeontographica*, 29: 81-124.

Pyzhyanov I.V. (1964). Novyy rod chetyrekhluchevykh korallov iz srednekamennougol'nykh otlozheniy Darvaza. [A new genus of tetracorals from the Middle Carboniferous of the Darvaz]. *Trudy Upravleniya Geologii i Okhrany Nedr pri Sovete Ministrov Tadzhikskoy SSR (Gosudarstvennyy Geologicheskiy Komitet*

SSSR), paleontologiya i stratigrafiya (Moskva), 1: 169-177. [in Russian]

Pyzhyanov I.V. (1966). Nekotorye predstaviteli Rugosa iz nizhnepermskikh otlozheniy Severnogo Pamira. [Some Rugosa from the Lower Permian of the northern Pamir]. *Trudy Upravleniya Geologii Soveta Ministrov Tadzhikskoy SSR, paleontologiya i stratigrafiya (Moskva)*, 2: 265-297. [in Russian]

Ramovš A. (1956). Razvoj paleozoika na Slovenskem. *In* Duhovnik J. & Ramovš A. (eds), 1. Jugoslovanski geološki kongres, Bled 23.-27. 5. 1954, *Predavanje in poročila*: 27-34.

Ramovš A. (1959). Paleozojske in mezozojske kamenine v donački dislokacijski coni. (Palaeozoic and Mesozoic Rocks in the Donačka Gora Dislocation Zone). *Geografski vestnik*, 31: 97-120.

Ramovš A. (1968). Biostratigraphie der klastischen Entwicklung der Trogkofelstufe in den Karawanken und Nachbargebieten. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 131: 72-77.

Ramovš A. (1972). Mittelpermische Klastite und deren marine Altersäquivalente in Slowenien, NE Jugoslawien. *Verhandlungen der Geologischen Bundesanstalt (Wien)*, 20: 35-45.

Ramovš A. & Schouppé A. (1961). Karbon und Perm im Vitanje-Gebirge, Ostkarawanken, NW-Jugoslawien. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 7: 346-374.

Rauzer-Chernousova D.M. (1949). Nekotorye psevdofuzuliny i parafuzuliny bashkirskogo priuralja. *Trudy IGN AN SSSR*, 105 (ser. Geol., 35): 118-162. [in Russian]

Reshetkova N.P. & Chernykh V.V. (1986). New conodonts from Asselian deposits on the west slope of the Urals. *Paleontologicheski Zhournal*, 4: 108-112. [in Russian]

Rodriguez S. (1984). Corales Rugosos del Carbonífero del Este de Asturias. *Tesis Doctoral, Universidad Complutense de Madrid (Departamento de Paleontología, Facultad de Ciencias Geológicas)*, 109/84: 1-528.

Rodriguez S. (1985). The taxonomic status of Geyerophyllid corals. *Acta Geologica Polonica*, 35: 277-278.

Rodriguez S. & Bamber E.W. (2012). Gregarious versus colonial habit in the rugose coral family Geyerophyllidae Minato, 1955. *Geologica Belgica*, 15: 355-358.

Roniewicz E. (1984) Microstructural evidence of the Distichophylliid affinity of the Caryophylliina (Scleractinia). *Palaeontographica Americana*, 54: 515-518.

Roniewicz E. & Stolarski J. (1999). Evolutionary trends in the epithecate scleractinian corals. *Acta Palaeontologica Polonica*, 44: 131-166.

Schellwien E. (1898a). Bericht über die Ergebnisse einer Reise in die karnischen Alpen und die Karawanken. *Sitzungsberichte der königlich Preussischen Akademie der Wissenschaften zu Berlin, mathematisch-physikalische Klasse*, 44: 693-700.

Schellwien E. (1898b). Die Fauna des karnischen Fusulinenkalkes, Teil II: Foraminifera. *Palaeontographica*, 44: 237-282.

Schellwien E. (1900). Die Fauna der Trogkofelschichten in den Karnischen Alpen und den Karawanken. 1. Teil. Die Brachiopoden. *Abhandlungen der kaiserlich-königlichen Geologischen Reichsanstalt Wien*, 16: 1-122.

Schindewolf O.H. (1942). Zur Kenntnis der Polycoelien und Plerophyllen. Eine Studie über den Bau der „Tetrakorallen" und ihre Beziehungen zu den Madreporarien. *Abhandlungen des Reichsamts für Bodenforschung (Berlin), Neue Folge*, 204: 1-324.

Schönlaub H.P. (2014). Karnische Alpen/Carnic Alps -Post-Variscan Sequence. *In* Hubmann B., Ebner F., Ferretti A., Kido E., Krainer K., Neubauer F., Schönlaub H.P. & Suttner T.J., The Palaeozoic Era (them), 2nd Edition. *In* Piller W.E. (ed.), The Lithostratigraphic Units of the Austrian Stratigraphic Chart 2004 (Sedimentary Successions), Vol. I, *Abhandlungen der Geologischen Bundesanstalt Wien*, 66: 82-90.

Schönlaub H.P. & Forke H.C. (2007). Die post-variszische Schichtfolge der Karnischen Alpen. Erläuterungen zur Geologischen Karte des Jungpaläozoikums der Karnischen Alpen 1: 12500. *Abhandlungen der Geologischen Bundesanstalt Wien*, 61: 3-157.

Schouppé A. (1961). Nachweis von Unterperm in Attika dirch *Carinthiaphyllum suessi* Heritsch 1936. *Annales Géologiques des Pays Helléniques (Athen)*, 12: 122-128.

Schouppé A. & Stacul P. (1955). Die Genera *Verbeekiella* Penecke, *Timorphyllum* Gerth, *Wannerophyllum* n.gen. und *Lophophyllidium* Grabau aus dem Perm von Timor. *Palaeontographica*, *Supplement-Band*, 4: 95-196.

Schouppé A. & Stacul P. (1959). Säulchenlose Pterocorallia aus dem Perm von Indonesisch-Timor (mit Ausnahme der Polycoeliidae). Eine morphogenetische und taxonomische Untersuchung. *Palaeontographica*, *Supplement-Band*, 4: 197-359.

Schouppé A. & Stacul P. (1962). Das Stereoplasma der Pterocorallia, seine Genese und Struktur. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 114: 24-57.

Soshkina E.D. (1928). Lower Permian (Artinskian] corals of the western slope of the northern Urals [Nizhnepermskie (artinskie) korally zapadnogo sklona Severnogo Urala]. *Byulleten' Moskovskogo Obshchestva Ispytateley Prirody, novaya seriya,* 36: 339-393. [in Russian]

Spassky N.Y. & Kravtsov A.G. (1974). Budding types of Tetracorals. [Tipy pochkovania chetyrekhluchevykh korallov]. *In* Sokolov B.S. (ed.), Ancient Cnidaria, Trudy Instituta Geologii i Geofiziki SO AN SSSR, Novosibirsk (Nauka), 21: 165-169. [in Russian]

Stevens C.H. (2008). Permian colonial Rugose corals from the Wrangellian Terrane in Alaska. *Journal of Paleontology*, 82: 1043-1050.

Stuckenberg A.A. (1895). Korally i mshanki kamennougol'nykh otlozheniy Urala i Timana. [Korallen und Bryozoen der Steinkohlenablagerungen des Ural und des Timan]. *Trudy Geologicheskago Komiteta [Mémoires du Comité Géologique, S.-Peterburg]*, 10: 1-244. [in Russian]

Venturini C. (2006). Evoluzione geologica delle Alpi Carniche. Edizione del Museo Friulano di Storia Naturale (Udine), 48: 1-208.

Vrabec M. & Fodor L. (2006). Late Cenozoic Tectonics of Slovenia Structural Styles at the Northeastern Corner of the Adriatic Microplate. *In* Pinter N., Grenerczy G.Y., Weber J., Stein S. & Medek D. (eds), The Adria Microplate: GPS Geodesy, Tectonics and Hazards. Nato Science Series: IV: Earth and Environmental Sciences (Springer): 151-168.

Wedekind R. (1927). Die Zoantharia Rugosa von Gotland (bes. Nordgotland), Nebst Bemerkungen zur Biostratigraphie des Gotlandium. *Sveriges Geologiska Undersökning*, 19: 1-94.

Weyer D. (1981). Bathyale Rugosa (Anthozoa) aus pelagischem Oberems (Unterdevon) im Thüringischen Schiefergebirge. *Abhandlungen und Berichte für Naturkunde und Vorgeschichte (Kulturhistorisches Museum Magdeburg)*, 12 [1980]: 23-73.

Weyer D. (1984). *Neaxon cheilos* n.sp. aus dem Unterfamenne von Schleiz im Thüringer Schiefergebirge (Anthozoa, Rugosa; Oberdevon). *Abhandlungen und Berichte für Naturkunde und Vorgeschichte (Kulturhistorisches Museum Magdeburg)*, 12 [1982]: 3-16, 77-83.

Weyer D. (2014). *Thurispina* nov. gen. (Anthozoa, Rugosa) from the Upper Famennian of Thuringia (Germany). *Freiberger Forschungshefte*, 548: 109-151.

Wilson E.C. (1982). Wolfcampian Rugose and Tabulate Corals (Coelenterata: Anthozoa) from the Lower Permian McCloud Limestone of Northern California. *Contributions in Science, Natural History Museum of Los Angeles County,* 337: 1-90.

Wu Wang-shi & Zhang Yan-sheng (1985). Carboniferous Rugose Corals from eastern Xizang and western Sichuan. *In* Stratigraphy and Palaeontology in West Sichuan and East Xizang, China. Sichuan Geological Survey, Nanjing Institute of Geology and Palaeontology, Academia Sinica (eds.). Chengdu (Sichuan Science and Technology Press). Part 4: 103-162. [in Chinese with English summary]

Wu Wang-shi & Zhao Jia-ming (1974). Carboniferous Corals, Permian Corals. *In* A handbook of the stratigraphy and palaeontology of southwest China. Nanjing Institute of Geology and Palaeontology, Academia Sinica (ed.) Beijing Science Press: 206-299. [in Chinese]

Wu Wang-shi & Zhao Jia-ming (1989). Carboniferous and early Permian Rugosa from western Guizhou and eastern Yunan, southwestern China. *Palaeontologia Sinica*, 177, New Series B, 24: 1-230. [in Chinese with English summary]

Yu Xue-guang (1991). New genus and species of Carboniferous Tetracorals from Jiangsu and Anhui. *Acta Palaeontologica Sinica*, 30: 420-438. [in Chinese with English summary]

Zhu Zheng-gang & Zhao Jia-ming (1992). Late Carboniferous and earliest Permian rugose corals from Jiangxi. *Acta Palaeontologica Sinica*, 31: 657-677. [in Chinese with English summary]

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Intraspecific competition in Guadalupian fasciculate rugose coral clusters (Hawasina Nappes, Oman Mountains)

Oliver Weidlich

O. Weidlich, Technical University Berlin, Institute of Applied Geosciences, Ernst-Reuter-Platz 1, D-10587 Berlin, Germany; o_weidlich@yahoo.co.uk

KEY WORDS - Live-live interactions, intra-clonal aggression, Praewentzelella regulare.

ABSTRACT - Guadalupian (middle Permian) reef blocks of the Al Jil and Bai'd formations (Hawasina Nappes, Oman Mountains) contain rugose corals. Praewentzelella regulare*, a fasciculate coral, is found in clusters, with more than 80% of the colonies in growth position. The good preservation of microstructure and minimal taphonomic alteration (e.g., lack of postdepositional tilt or transport of colonies) allow to discuss whether or not live-live interactions for space, particularly intraspecific competition, has been preserved. The evaluation is based on the distribution of coral colonies mapped in the field, three-dimensional reconstruction of coral growth using serial cuts of a block and microfacies evaluation of thin sections.*

A rarely observed phenomenon of intraspecific competition is described herein and the term "intra-clonal aggression" is proposed for interactions between sedentary organisms of the same species leading to the distortion of skeletal elements of one colony.

INTRODUCTION

In modern reef ecosystems, competition for substrate, light, space or nutrients are key factors controlling the distribution of sedentary organisms and the spatial dynamics of calcified scleractinian corals vs non-calcified algae (Sandin & McNamara, 2012). Regarding competition for space, understanding factors defining competitive outcomes among neighbors is relevant for predicting changes in the composition of reef organisms in time and space. Scleractinian corals, for example, developed different expansion strategies depending on their prevailing morphology (Sandin & McNamara, 2012). Sensu Connell (1976), competition among reef corals is direct in the case of physical contact of the soft tissues or indirect if expansion continues without touching each other.

In a more generic sense, inter- and intraspecific live-live interactions for space comprise: 1) stand-off or distance avoidance; 2) aggression between neighboring reef builders; 3) overgrowth and overtopping of the neighboring colony; and 4) peripheral growth of one colony around another (Rinkevich & Loya, 1983; Logan, 1984; Fagerstrom et al., 2000; West et al., 2011; Liow et al., 2016). Assumed live-live interactions are not the topic of this paper, but set the broader frame and are considered in the discussion. In the fossil record, the recognition of live-live interactions, or more specifically competition for space, is difficult to prove as neighboring reef builders preserved in rocks have not necessarily grown at the same time. Fagerstrom et al. (2000) analysed extant reef communities and concluded that live-live interactions observed in modern reefs are useful indicators to interpret Paleozoic communities despite taxonomic differences. These authors summarised many examples of live-live interactions of fossil reef builders. Götz (2003) paid special attention to interactions between rudists and corals in a Upper Cretaceous biostrome. More recently, interactions interpreted as fusion of probable clones were presented by Stanton et al. (2016: *Chaetetes* sp.), Fagerstrom & West (2011: stromatoporid) and West et al. (2011: *Chaetetes* sp., fistuliporiid bryozoans).

The rugose coral *Praewentzelella regulare* Flügel in Weidlich & Flügel (1995), found in well preserved Guadalupian reef blocks of the Oman Mountains (Figs 1-2), was investigated with emphasis on live-live interactions, particularly intraspecific competition for space. The body of data presented here includes: 1) quantitative outcrop data of coral coverage and distribution patterns of corallites (area analysed covers 0.7 m^2); 2) serially cut slabs of one reef block (out of four) allow to detect spatial trends in vertical coral growth and clone interaction; 3) complementary petrographic microfacies observations from thin sections.

GEOLOGICAL SETTING OF RUGOSE CORAL-BEARING BLOCKS

In the Oman Mountains, deposits of Permian age with rugose corals are found in: 1) (par)autochthonous Arabian platform carbonates (e.g., Jebel Akhdar and Saih Hatat); 2) mixed carbonate-siliciclastic slope deposits of the Arabian platform lumped as Sumeini Group; 3) deposits of a basin North of the Arabian Plate with relicts of collapsed seamounts (Hawasina Complex) (Fig. 1). In the Hawasina Basin, Guadalupian reef blocks with rugose corals are found, with the Ba'id area as most prolific sample location for *Praewentzelella regulare* (Fig. 2). There, isolated seamounts situated in the Hawasina Basin have been proposed as a source for the reef blocks, whereas the slope of the Arabian platform has been discarded as provenance area (Blendinger, 1988). The Bai'd area is located to the south of the autochthonous Arabian platform and is tectonically located below the Semail ophiolite. The area of interest forms an anticline

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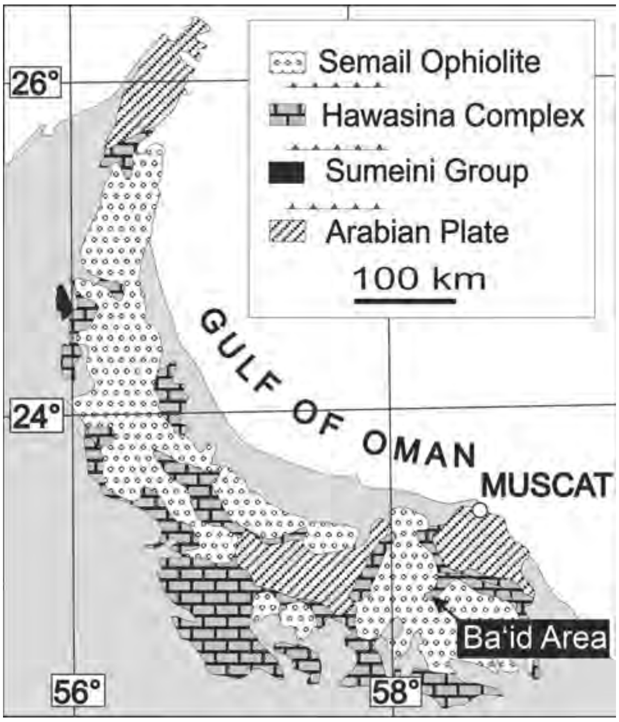

Fig.1 - Simplified geological map of the Oman Mountains showing the location of the Ba'id area.

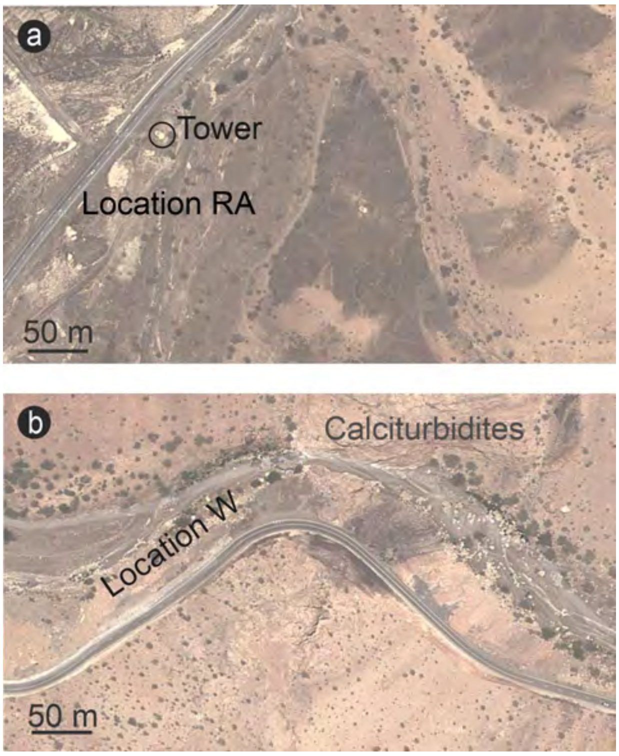

Fig. 2 - (color online) Satellite images of locations in the Ba'id area. a) Location RA (23°06'21.0"N 58°18'25.6"E). b) Location W (23°06'43.2"N 58°19'33.5"E); from Google Maps.

with a roughly N-S trending axis that exposes imbricate slices of the Hawasina sedimentary and volcanic units. The Wadi Wasit in the center of the Ba'id tectonic window provides unique exposures of Permian and Triassic Al Jil and Ba'id formations. Pillevuit et al. (1997) described a 250 m thick middle Permian volcano-sedimentary sequence, containing basal pillow basalts, radiolarian-bearing cherts, volcaniclastic breccias, gravity flow deposits with Permian platform carbonates, reef boulders and deep-water sediments. The Guadalupian reef blocks represent cosmopolitan reef-types, notably sponge reefs and algal/cement reefs which flourished for approximately 30 million years, while rugose coral reefs flourished for a few million years.

The rugose corals of reef blocks collected in the Ba'id area are represented by seven genera, including *Yokoyamella*, *Monothecalis*, *Wentzelella*, *Wentzelloides*, *Multimurinus*, *Lonsdaleiastraea*, *Praewentzelella*; Tabulata are represented by *Multithecopora*. These taxa are typical of the Tethyan realm, where rugose corals were extraordinarily diverse during the Guadalupian (Wang et al., 2018).

MATERIAL AND METHODS

Rugose coral-bearing reef blocks of the Al Jil and Ba'id formations were collected between 1990 and 2008 at the western flank of Jebel Rahbah (Loc RA: 23°06'21.0"N 58°18'25.6"E, Fig 2b, see sample RA2) and in Wadi Wasit (Loc W: 23°06'43.2"N 58°19'33.5"E, Fig. 2a, see samples W30 and W31-8). More recently, these coral bearing outcrops were revisited during the 12th International Symposium on Fossil Cnidaria and Porifera in Oman (Pre-conference FT 1; see also Baud et al., 2010). Hitherto unpublished observations were updated and are now to be published for the first time.

The database consists of a mapped reef block (0.7 m^2), six samples from different blocks and 12 thin sections. Sample W-30 was cut into seven slabs perpendicular to coral growth with the aim to analyse the vertical growth.

The figured specimens are stored at the Dipartimento di Scienze Chimiche e Geologiche, Università di Modena e Reggio Emilia, Italy. Repository numbers are as follows: IPUM 29855, thin section RA2; IPUM 29856, thin section W30; IPUM 29857, thin section W31-8.

DATA

H.W. Flügel (in Weidlich & Flügel, 1995, p. 236) provided the following original description for *Praewentzelella regulare*: "Mature calices attain a diameter of 30 mm with 28 to 32 major septa. The number of minor septa between two major septa is always odd, fluctuating between 1 and 13. The septa are peripherally thickened into a septal wall. The wall is approximately 1 mm thick. The axial zone is complex with a diameter of 4.5 to 5 mm. Median lamellae are dilated and occasionally connected. Up to 15 sections of tabellae occur between the radial lamellae. The tabularium is well developed. The boundaries between the columella and the dissepimentarium are distinct." Flügel concluded that *P. regulare* had a fasciculate growth with closely spaced calices.

Field mapping of a *P. regulare* reef block cut perpendicular to growth exhibits that 80% of the corals are

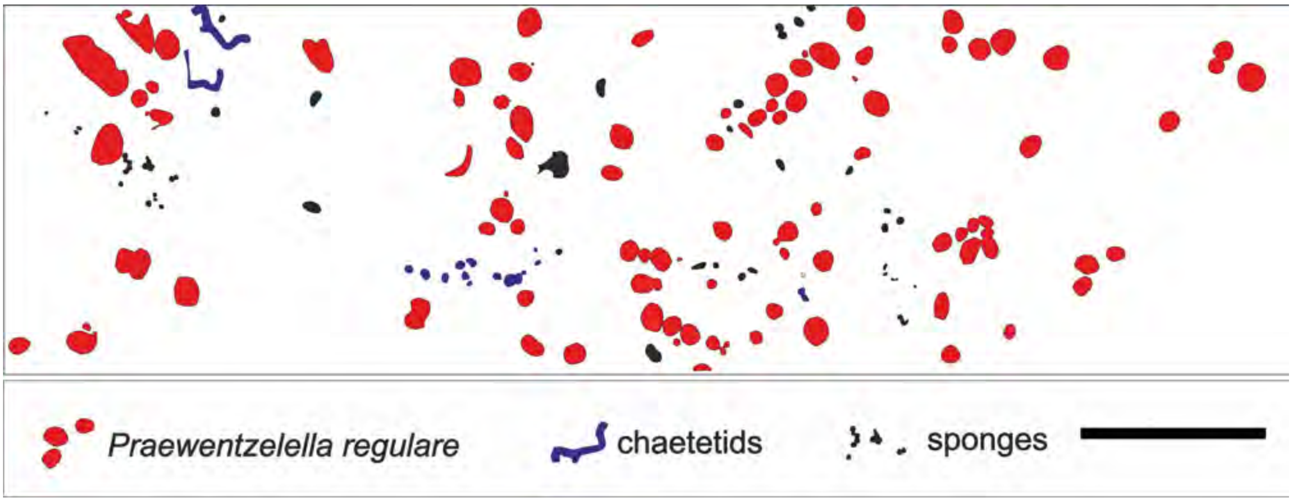

Fig. 3 - (color online) Field map of *Praewentzelella regulare* (location W); after Weidlich & Flügel (1995). View perpendicular to growth direction. Circular to elliptical calyx outlines indicate that more than 80% of the corals are in growth position; after Weidlich & Flügel (1995). Scale bar is 20 cm.

in growth position; coral coverage attains 20% over an area of 0.7 m^2 (Fig. 3). *Praewentzelella regulare* is associated with sphinctozoans (e.g., *Sollasia ostiolata* Steinmann, 1882; *Parauvanella paronai* Senowbari-Daryan & Di Stefano, 1988; *Colospongia* sp.; *Thaumastocoelia* sp.; and chaetetids [*Chaetetes* sp.]).

Polished slabs and thin sections exhibit a biogenic framework stabilising the corals built by calcareous algae (*Ungdarella* sp. and *Parachaetetes* sp.) and fenestellid or dendroid bryozoans. *Archaeolithoporella hidensis* Endo, 1959, *Tubiphytes obscurus* Maslov, 1956, *Tubiphytes cylindricus* Senowbari-Daryan & Flügel, 1993 and microbes provide additional strength by forming distinct crusts. Primary growth framework pores are rimmed by marine phreatic cements and filled with peloidal mud of microbial origin. Brachiopod shells, crinoid ossicles, bioclasts from solenoporacean algae and thalli of dasycladacean algae (*Imperiella* sp.) form bioclastic wacke- to grainstones. Reef dwelling foraminifers are represented by *Climacammina* sp., *Tetrataxis* sp., *Dunbarula* sp. and *Kahlerina* sp.

Some calices of *P. regulare* are partly silicified. The incomplete replacement started from the center of calices. The boundary between the silicified and non-silicified parts is lined by mega-quartz crystals which are idiomorphic towards the unsilicified peripheral coral skeleton. Despite this overprint, most corals are well preserved exhibiting the microstructure of the skeleton in detail.

Within clusters of *P. regulare* with minimal taphonomic overprint, three patterns of assumed intraspecific live-live interactions can be recognised:

1. No obvious live-live interaction or possibly distance avoidance (Fig. 4)

OBSERVATION - Calices with no visible interaction; the distance between the calices exceeds 4 mm. Calices are

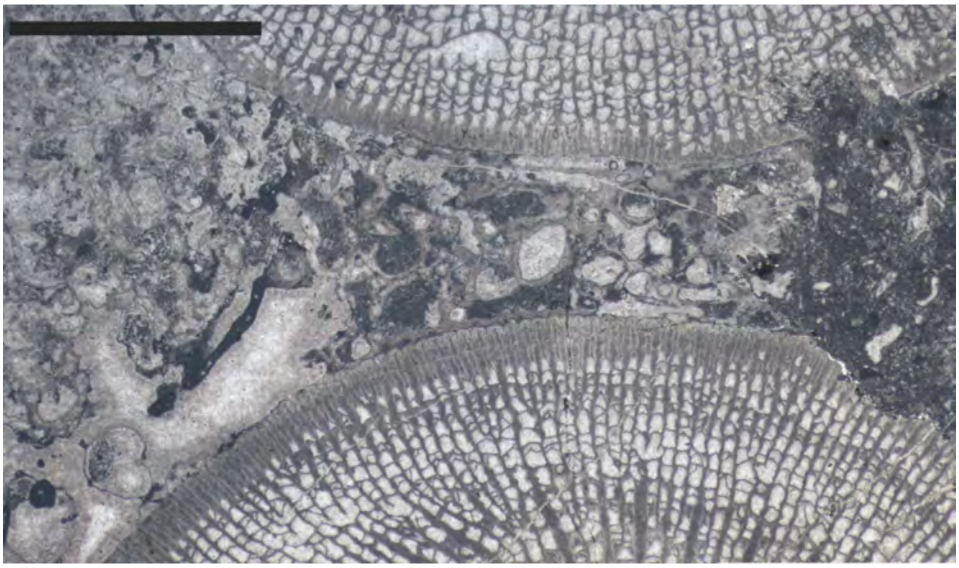

Fig. 4 - (color online) Photomicrograph of two calices without observable live-live interaction. Sample W31-8 (Location W, thin section IPUM 29857). Scale bar is 5 mm.

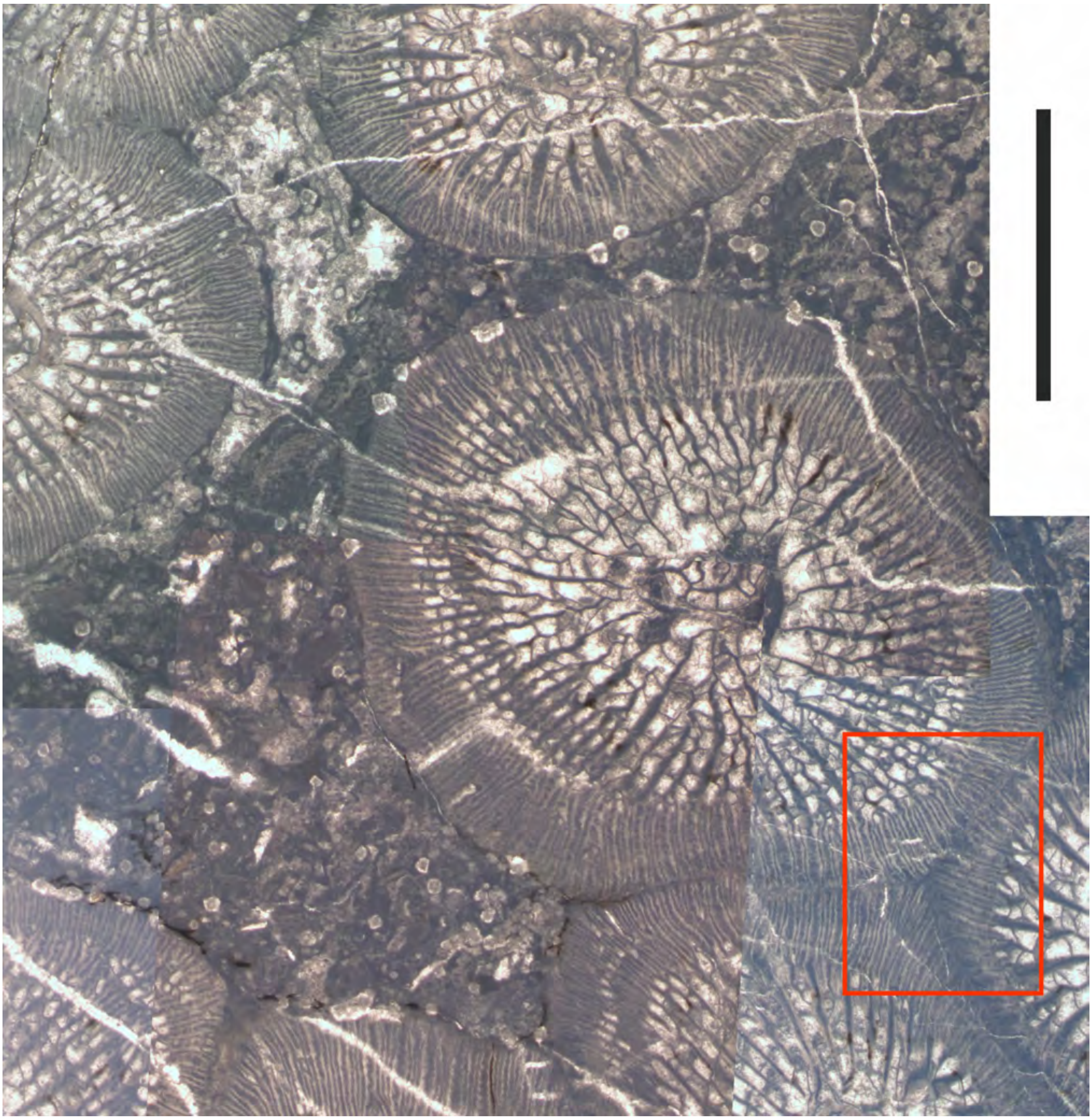

Fig. 5 - (color online) Overview of *Praewentzelella regulare* perpendicular to growth direction. Red rectangle is outline of Fig. 6. Sample RA2 (Location RA, thin section IPUM 29855). Scale bar is 5 mm.

circular in cross section and lack any distortion of the microstructure. Skeletal elements are well developed, especially the septal wall is regular and lacks deformation.

INTERPRETATION - Absence of live-live interactions is obvious; it can be speculated, however, that these corals kept a given distance, while growing at the same time.

2. Contact between corallites of one colony (Figs 5-6)

OBSERVATION - Individual calices touch each other. Major and minor septa of the neighboring calices are slightly bent, indicating contemporaneous calix growth while space for growth was limited. Despite contemporaneous calyx growth, fusion of calices did not happen. Thin section analysis suggests that the calices developed thick septal walls without skeletal distortion.

INTERPRETATION - Considering the fasciculate coral as a special form of dendroid growth strategy, it is concluded that touching calices belong to one colony.

3. Aggression and avoidance between corallites of two colonies (Figs 7-9)

OBSERVATION - The serial slabs highlight the development of two contemporaneously growing *P.*

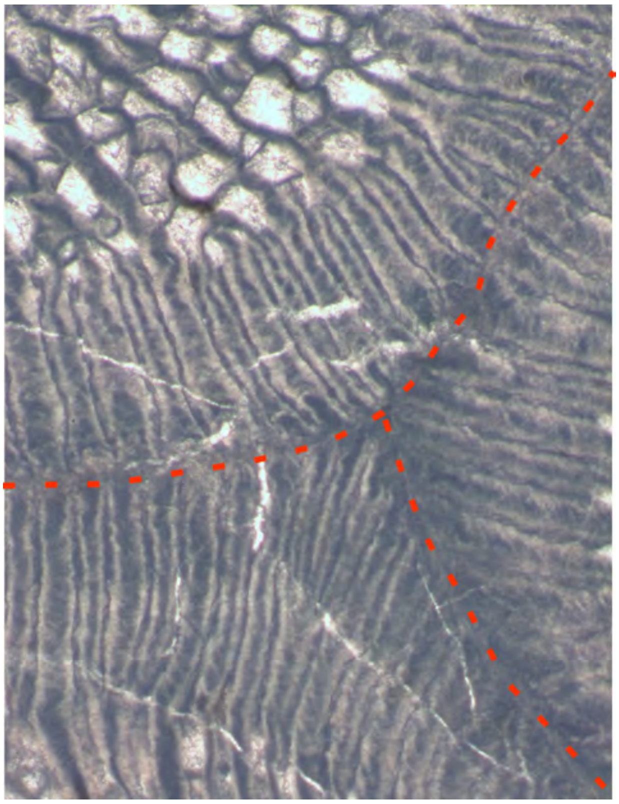

Fig. 6 - (color online) Close-up view of Fig. 5. Dashed line indicates boundary between calices.

regulare colonies with juvenile growth stage in slabs 1-2 and adult stages with the development of fasciculate colony growth in slabs 3 to 5 (Figs 7 and 9a). If the adult corals come closer than 5 mm (left coral is specimen B, right coral is specimen A, Fig. 7), significant deformation of one calyx (specimen A) becomes obvious. The outline of specimen A changes from circular to slightly bean-shaped caused by the limited growth of the septa wall. Finally, as documented in slabs 6 and 7, the distance between the calices increases and the septal wall is developed again. It is likely that the deformation of specimen A ceased with increasing distance. Thin-section analysis exhibits the following pattern (Fig. 8): in the case of distances > 4 mm, no deformation of the skeleton is observed; smaller distances between corallites, e.g., less than 3 mm, lead to deformation of one calyx, as indicated by irregularities of the septal wall and changes in the formation of dissepiments.

Interpretation - The observed pattern is interpreted as competition for space between two colonies. This phenomenon has been rarely described and the term "intra-clonal aggression" is proposed to describe this type of interaction between sedentary organisms of the same species.

DISCUSSION

Taphonomic biases such as transport, post-mortem damage and mixing of sediments or organisms are sometimes perceived as insurmountable problems for the paleoecologic interpretation of organisms and communities (Leighton & Schneider, 2004). With regard to the discussion of assumed live-live interactions in reef communities, minimal taphonomic and diagenetic overprint is vital. The preservation of microstructure is relevant as the distortion of skeletal elements acts as indicator of aggression between coral clones (Rinkevich & Loya, 1983, 1985). It has been demonstrated with this data set that *P. regulare* colonies exhibit minimal postmortal degradation due to a stable biogenic framework. The diagenetically stable skeleton of the calcitic Rugosa recorded distortions of the microstructure of nearby clones. Thus, description of live-live interactions is possible and subject to discussion.

The observations presented provide evidence for two types of intra-specific live-live interactions of *P. regulare*:

1. Live-live interactions, leading to physical contact of corallites of one colony (microstructures indicate contemporaneous corallite growth) without distortion of skeletal elements. This pattern has been widely observed among reef builders and may even lead to the fusions of clones as described for chaetetids or stromatoporoids (Fagerstrom et al., 2000; Stanton et al., 2016).
2. Aggressive live-live interaction, causing physical damage of skeletal elements and distance avoidance of two different colonies growing next to each other. There exist few published data, but Rinkevich & Loya (1983, 1985) documented and described in detail how the growth of the scleractinian *Stylophora pistilla*ta Esper (1797) changes from normal growth to retreat growth of one specimen, if calices dominant and subordinate clones grow at the same time.

CONCLUSIONS

This contribution analyses the spatial pattern of the rugose coral *Praewentzelella regulare* under consideration of the preservation potential of coral competition for space in the rock record. It provides evidence for intra-specific live-live interactions or, more specifically, for intraspecific competition between specimens of *P. regulare* based on field data, slabs and thin sections. Minimal taphonomic and diagenetic alteration of the corals provide a suitable data set for the discussion of assumed live-live interactions.

Two types of intraspecific live-live interactions are described:

1. Corallites which touch each other during lifetime and lack distortion of skeletal elements are interpreted as part of one colony (genetically identical clone). This observation has been made many times before and is typical of colonial corals when they grow next to each other.
2. Aggressive live-live interaction among rugose corals is believed to cause distorted skeletal elements of corallites of one colony and, at the end, maintains a given distance avoidance between the coral colonies again. This aggressive interaction causes macro- and microscopic deformation of one corallite as seen in thin sections. As this phenomenon has rarely been described in the literature, the term "intra-clonal aggression" is proposed

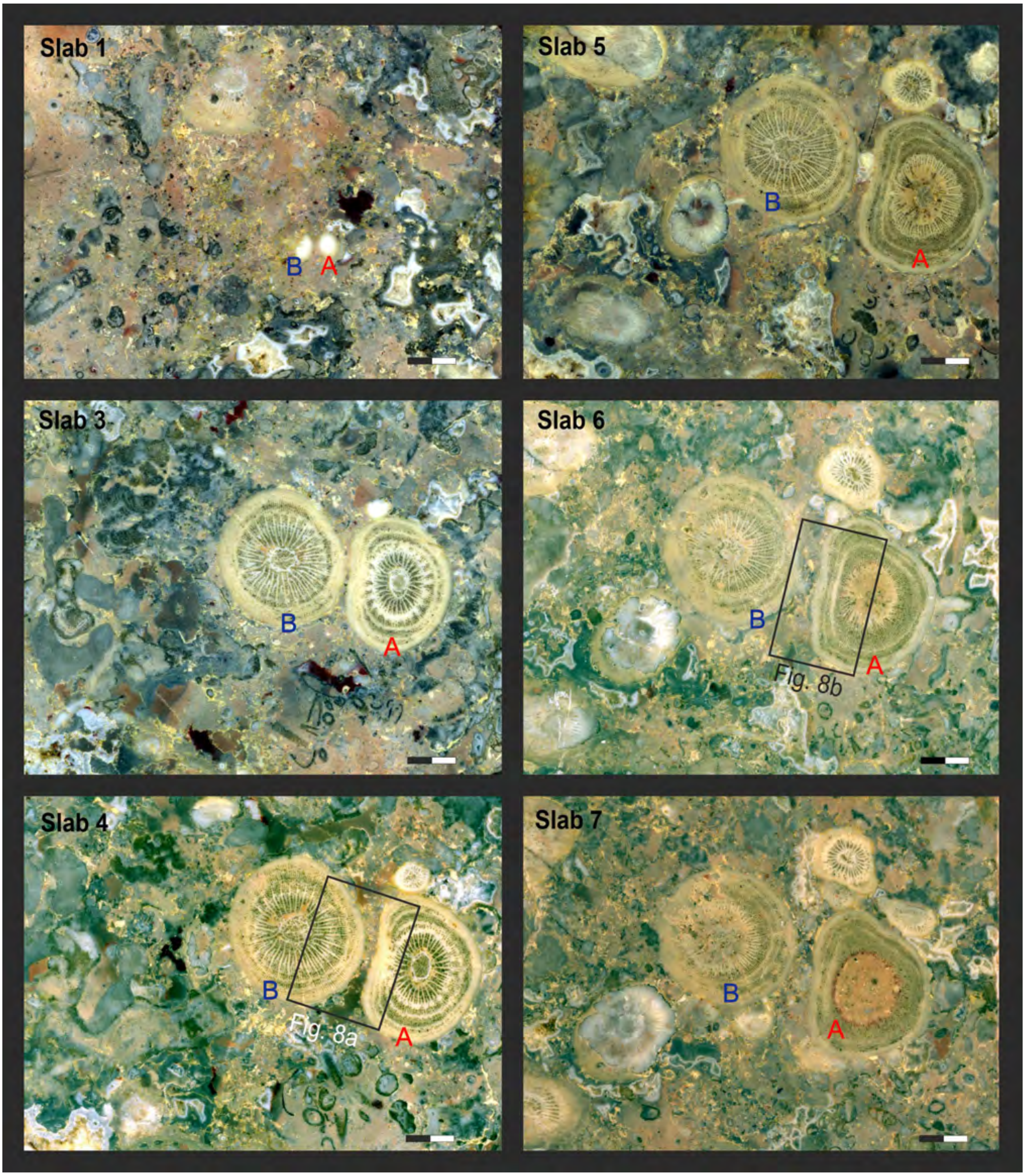

Fig 7 - (color online) Slabs showing the growth of *Praewentzelella regulare*, slab 1 represents juvenile growth and slabs 3-7 adult growth stages. Sample W30 (location W, thin section IPUM 29856). Rectangles refer to outlines of photomicrographs of Fig. 8. Scale bars are 1 cm.

to describe this aggressive interaction between sedentary organisms of the same species.

Observation of intra-clonal aggression provides the basis for further questions to be considered:

1. Van Veghel et al. (1996) investigated intra- versus interspecific interactions in modern coral reefs and observed that the majority of interactions were interspecific. Is this applicable to Guadalupian rugose corals in reefs as well?

2. Did rugose corals "invent" the principle of chemical interference (allelopathy), which is common for modern scleractinians (e.g., Bak & Borsboom, 1984)?

3. Did rugose coral develop sweeper tentacles as observed in modern corals (Hidaka & Yamazato, 1984)?

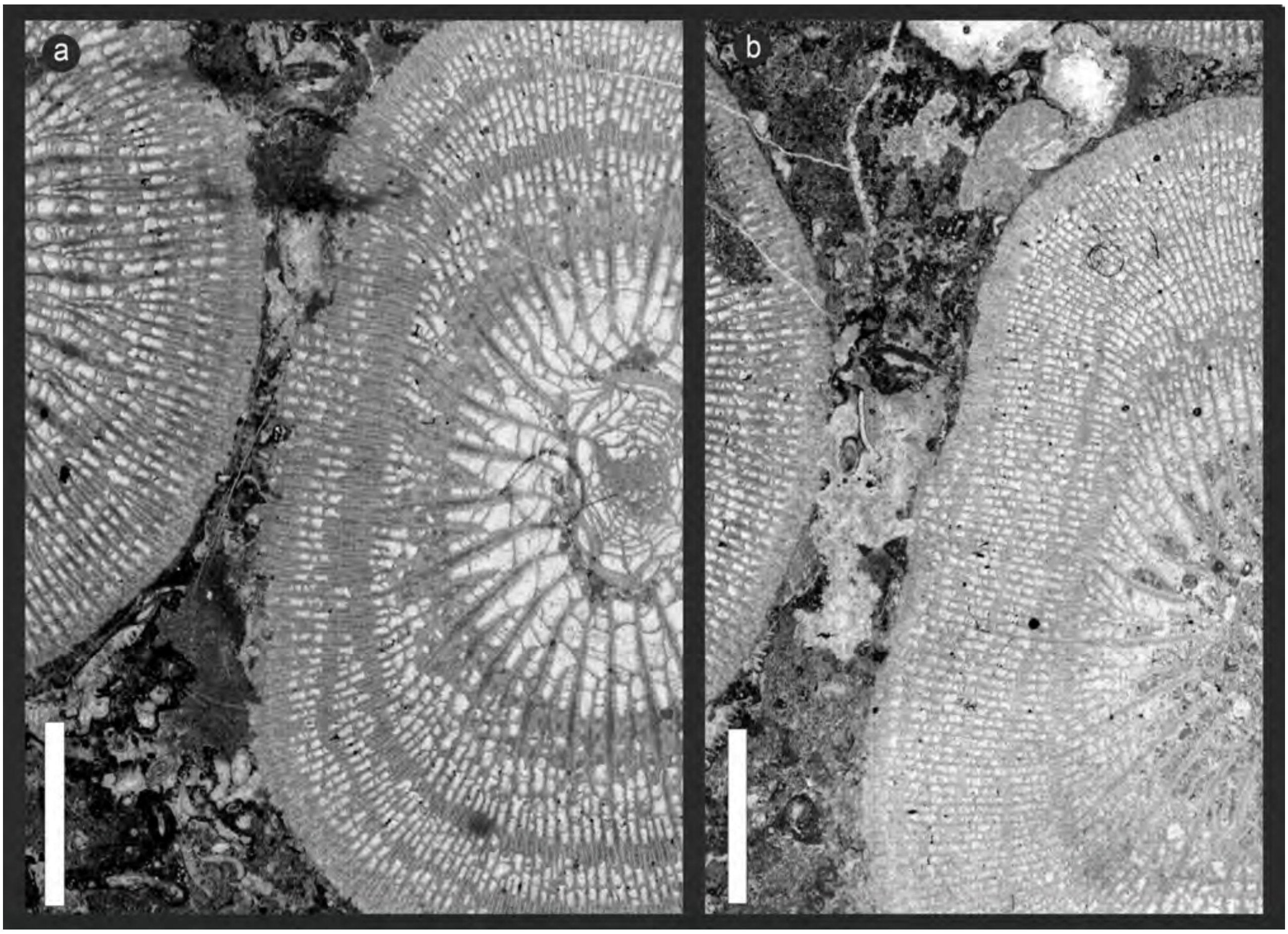

Fig. 8 - Representative thin section of two calices, one showing deformations, sample W30 (IPUM 29856); (a) slab 4, (b) slab 6. On the left, specimen B; on the right, specimen A. Scale bar is 3 mm.

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This paper is dedicated to Prof. Dr. Michaela Bernecker, former president of the International Association for the study of Fossil Cnidaria & Porifera.

REFERENCES

Bak R.P.M. & Barsboom J.L.A. (1984). Allelopathic interaction between a reef coelenterate and benthic algae. *Oecologia*, 63: 194-198.

Baud A., Henderson C.M., Krystyn L., Richoz S. & Beauchamp B. (2010). The Permian-Triassic transition in the Wadi Wasit area, stop1. *In* Baud A. & Bernecker M. (eds), IGCP 572 Field Guide Book 2: The Permian-Triassic transition in the Oman Mountains: 48-54.

Blendinger W. (1988). Permian to Jurassic deep-water sediments of the Eastern Oman Mountains: Their significance for the evolution of the Arabia margin of south Tethys. *Facies*, 19: 1-32.

Connell J.H. (1976). Competitive interactions and the species diversity of corals. *In* Mackie G.O. (ed.), Coelenterate ecology and behavior, Springer: 5158.

Endo R. (1959). Stratigraphical and paleontological studies of the Later Paleozoic calcareous algae in Japan. XIV. Fossil algae from the Nyugawa valley in the Hida massif. *Scientific Reports Saitama University, Series B*, 3/2: 177-207.

Esper, E.J.C. (1797). Fortsetzungen der Pflanzenthiere in Abbildungennach der Natur mit Farben erleuchtet nebst Beschreibungen. *Erster Theil (Nürnberg)*: 1-230.

Fagerstrom J.A. & West R. (2011). Roles of clone–clone interactions in building reef frameworks: principles and examples. *Facies*, 57: 375-394.

Fagerstrom J.A., West R., Kershaw S. & Cossey P.J. (2000). Spatial competition among clonal organisms in extant and selected Paleozoic reef communities. *Facies*, 42: 1-24.

Götz S. (2003). Biotic interaction and synecology in a Late Cretaceous coral-rudist biostrome of southeastern Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 193: 125-138.

Hidaka M. & Yamazato K. (1984). Intraspecific interactions in a scleractinian coral, *Galaxea fascicularis:* Induced formation of sweeper tentacles. *Coral Reefs*, 3: 77-85.

Leighton L.R. & Schneider C.L. (2004). Neighbor proximity analysis, a technique for assessing spatial patterns in the fossil record. *Palaios*, 19: 396-407.

Liow L.H., Di Martino E., Voje K.L., Rust S. & Taylor P.D. (2016). Interspecific interactions through 2 million years: are competitive outcomes predictable? *Proceedings of the Royal Society B, Biological Sciences*, 283: 1-7.

Logan A. (1984). Interspecific aggression in hermatypic corals from Bermuda. *Coral Reefs*, 3: 131138.

Maslov V.P. (1956). Fossil calcareous algae of the U.S.S.R. *Trudy Geologitschesski Institut an SSR*, 160: 1-301.

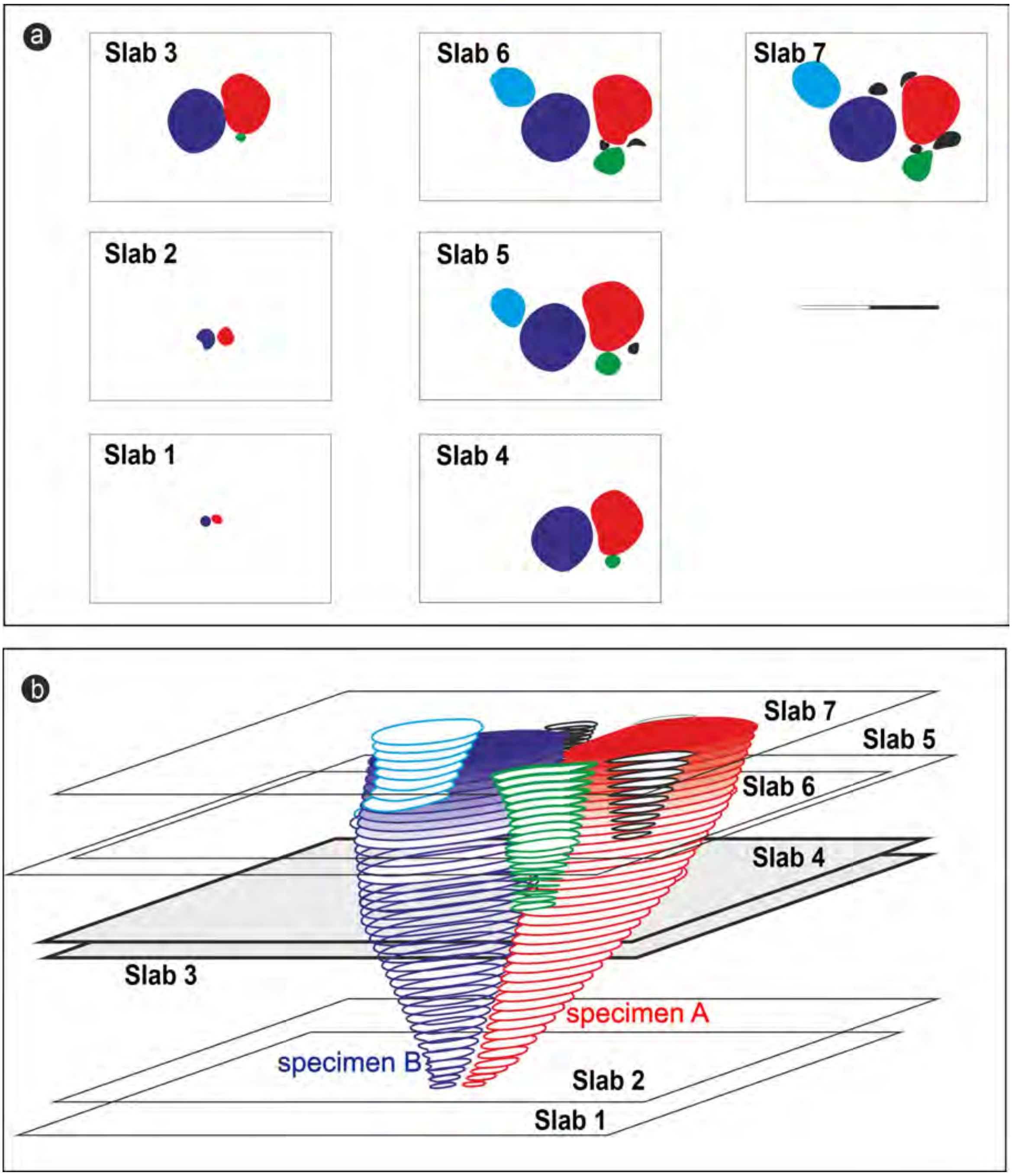

Fig. 9 - (color online) Line drawings (a) and three-dimensional reconstruction (b) of two *Praewentzelella colonies*, see Fig. 7 for photographs of the slabs. a) Line drawings showing sequential live-live interaction. Specimen A was dominated and, probably, harmed by specimen B; scale is 3 cm. This is suggested by irregular outline of the calyx, abnormal growth lines and deformed septal wall (visible in thin-sections, see Fig. 8).

Pillevuit A., Marcoux J., Stampfli G. & Baud A. (1997). The Oman Exotics: a key to the understanding of the Neotethyan geodynamic evolution. *Geodinamica Acta*, 10: 209-238.

Rinkevich B. & Loya Y. (1983). Intraspecific competitive networks in the Red Sea coral *Stylophora pistillata*. *Coral Reefs*, 1: 161172.

Rinkevich B. & Loya Y. (1985). Intraspecific competition in a reef coral: effects on growth and reproduction. *Oecologia*, 66: 100-105.

Sandin S.A. & McNamara D.E. (2012). Spatial dynamics of benthic competition on coral reefs. *Oecologia*, 168: 1079-1090.

Senowbari-Daryan B. & Di Stefano P. (1988). Microfacies and sphinctozoan assemblage of some Lower Permian breccias from the Lercara Formation (Sicily). *Rivista Italiana di Paleontologia e Stratigrafia*, 94: 3-34.

Senowbari-Daryan B. & Flügel E. (1993). *Tubiphytes* Maslov, an enigmatic fossil: classification, fossil record and significance through time. Part 1: discussion of Late Paleozoic material. *In* Barattolo F., De Castro P. & Parente M. (eds): Studies on fossil benthic algae. *Bollettino della Società Paleontologica Italiana*, *Special Volume 1*: 353-382.

Stanton J.R., Lambert L.L., Webb G.E. & Lustig L.D. (2016). *Chaetetes* morphology, environment, and taxonomy. *Facies*, 62: 28-49.

Steinmann G. (1882). Pharetronen-Studien. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*: 139-191.

Van Veghel M.L.J., Cleary D.F.R. & Bak R.P.M. (1996). Interspecific interactions and competitive ability of the polymorphic reef-building coral *Montastrea annularis*. *Bulletin of Marine Science*, 58: 792-803.

Wang X., Yao L. & Lin W. (2018): Permian rugose corals of the world. *In* Lucas S.G. & Sgen S.Z. (eds), The Permian Timescale. *Geological Society London, Special Publication*, 450: 165-184.

Weidlich O. & Flügel H.W. (1995). Upper Permian (Murghabian) Rugose corals from Oman (Ba'id area, Saih Hatat): Community structure and contributions to reefbuilding processes. *Facies*, 33: 229-263.

West R., McKinney F.K., Fagerstrom J.A. & Vacelet J. (2011). Biological interactions among extant and fossil clonal organisms. *Facies*, 75: 351-374.

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Exceptional development of dissepimental coenosteum in the new Eocene scleractinian coral genus *Nancygyra* (Ypresian, Monte Postale, NE Italy)

Francesca R. Bosellini*, Jarosław Stolarski, Cesare Andrea Papazzoni & Alessandro Vescogni

F.R. Bosellini, Dipartimento di Scienze Chimiche e Geologiche, Università degli Studi di Modena e Reggio Emilia, Via Campi 103, I-41125 Modena, Italy; francesca.bosellini@unimore.it **corresponding author*

J. Stolarski, Institute of Paleobiology, Polish Academy of Sciences, Twarda 51/55, PL-00-818 Warsaw, Poland; stolacy@twarda.pan.pl

C.A. Papazzoni, Dipartimento di Scienze Chimiche e Geologiche, Università degli Studi di Modena e Reggio Emilia, Via Campi 103, I-41125 Modena, Italy; papazzoni@unimore.it

A. Vescogni, Dipartimento di Scienze Chimiche e Geologiche, Università degli Studi di Modena e Reggio Emilia, Via Campi 103, I-41125 Modena, Italy; alessandro.vescogni@unimore.it

KEY WORDS - Aphroid colony, dissepiments, Euphylliidae, coral diversity, EECO, lower Eocene.

ABSTRACT - In colonial corals, the polyps are interconnected with a common tissue called coenosarc. Polyps and coenosarc secrete distinct skeletal structures: corallites and coenosteum, respectively. Ratio of corallite to coenosteum development may vary resulting in two extreme architectural patterns of coral colonies: corallite-dominated (e.g., cerioid) and coenosteum-dominated (e.g., aphroid) colonies. A large suite of examples of these patterns can be identified among extant and fossil corals, including Paleozoic rugosan corals. Herein we describe the new early Eocene colonial scleractinian coral genus Nancygyra *that forms exceptional coenosteum-dominated colonies. The colonies were found in Ypresian limestones at Monte Postale (Lessini Mountains, Veneto, NE Italy), very close to the Pesciara di Bolca Fossil-Lagerstätte, where coralgal buildups have been recently recognised and described. The corallum is massive and consists of corallites of variable size (typically few millimeters in lesser calicular diameter) dispersed and protruding from a very extensive and dense dissepimental coenosteum. The coenosteum forms ca. 60-80% of the corallum volume and is made of vesicular convex dissepiments. The new coral is tentatively assigned to Euphylliidae (known in the fossil record since the Paleocene) whose modern representatives develop similar extensive coenosteum with sticking-out corallites (*Galaxea*) and form coralla with well-developed walls and thickened axial margins of septa (*Euphyllia*). Among stratigraphically older scleractinian corals, similar extent of dissepimental coenosteum development is shown by some Mesozoic amphiastreids and rhipidogyriids.*

INTRODUCTION

In colonial corals, the polyps are interconnected with a common tissue called coenosarc. In certain types of colonies, e.g., plocoid or aphroid colonies, the coenosarc is particularly developed. Polyps and distinct skeletal coenosarc secrete different structures: corallites and coenosteum, respectively (Fig. 1). The coenosteum, also known as peritheca or coenenchyme, is the skeleton between corallites and in "robust" corals (as defined in Fukami et al., 2008) its structure can be costate, vesicular, spinose, or solid. If the coenosteum is narrow and regular, it may form a "double wall" (Budd & Stolarski, 2011; Budd & Bosellini, 2016). Coenosteum is most frequently composed of dissepiments and tabulae (e.g., in zooxanthellate *Galaxea*), rarely as massive thickening deposits (e.g., in azooxanthellate *Lophelia*). Ratio of corallite to coenosteum development may vary resulting in two extreme architectural patterns of coral colonies: corallite-dominated (e.g., in cerioid colonies) and coenosteum-dominated (e.g., in aphroid colonies). A large suite of examples of these patterns can be identified among extant and fossil corals, including Paleozoic rugosan corals (Fig. 2).

During a recent research on the early Eocene (Ypresian) coral buildups of the Monte Postale (Lessini Mountains, Veneto, NE Italy) (Vescogni et al., 2016), sampling of corals revealed the occurrence of a new colonial scleractinian coral that forms exceptional coenosteum-dominated colonies. The discovery of this coral, that we aim herein to describe and interpret, may provide new information on the composition of the still poorly known early Eocene reef coral fauna, developed during a time-window containing few coral reefs (Scheibner & Speijer, 2008; Zamagni et al., 2012) when Cenozoic Earth surface temperature reached its warmest state (EECO) (Zachos et al., 2001, 2008).

GEOLOGICAL BACKGROUND

The Monte Postale site is located in the Lessini Mountains (Veneto region, NE Italy), very close to the Pesciara di Bolca Fossil-Lagerstätte (Fig. 3a). The Lessini Mountains are characterised by a complex geological setting derived from the evolution of the Trento Platform, a large, shallow-water carbonate platform that during the Early Jurassic was one of the main structural components of the Southern Alps (Fig. 4). Since the Middle Jurassic, this platform suffered a progressive drowning, and starting from the Paleogene the Alpine collision led to a block-faulting of the area, with several blocks that were uplifted to a different degree (Bosellini et al., 1981; Winterer & Bosellini, 1981). In the early Eocene some of these blocks reached the photic zone and started to act as centers of carbonate production, eventually coalescing together to form the Lessini Shelf (Fig. 4) (Bosellini, 1989).

The Eocene limestones are grouped into an informal unit indicated as "Calcari Nummulitici" (nummulitic limestones) that includes a wide spectrum of carbonate

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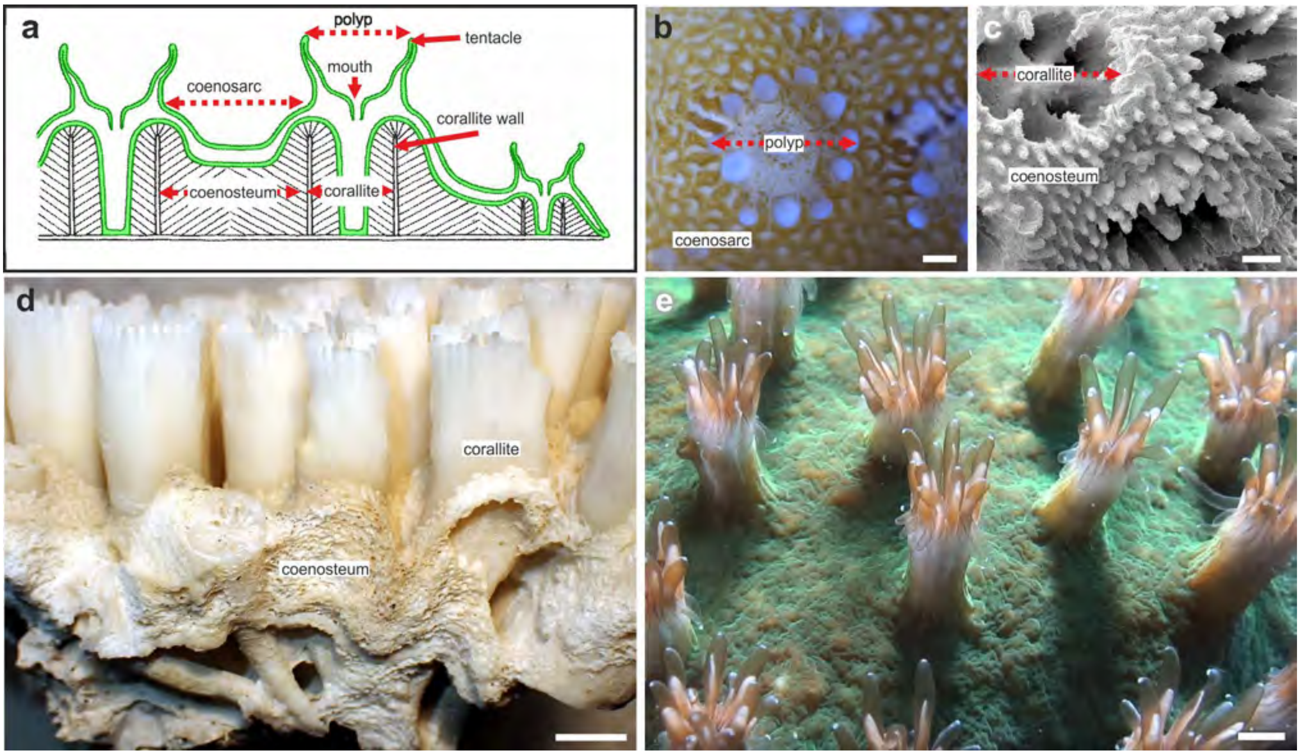

Fig. 1 - (color online) Coenosteum. a) Model of longitudinally sectioned colonial coral with main skeletal and soft tissue structures: polyps are interconnected with a common tissue called coenosarc. Polyps secrete corallite skeleton whereas coenosarc secretes coenosteum. b-c) Tissue cover and corresponding skeleton showing corallite and coenosteum in zooxanthellate scleractinian *Stylophora pistillata* Esper, 1797. d) Plocoid colony of zooxanthellate *Galaxea fascicularis* (Linnaeus, 1767) with well-developed vesicular coenosteum (specimen broken longitudinally) and corallites sticking-out of surface of the colony. e) Polyp-tissue relationship in plocoid colony of zooxanthellate *Galaxea paucisepta* Claereboudt, 1990: tissue with expanded polyps and greenish coenosarc (courtesy Bruce Carlson, CC BY, specimen from Solomon Islands, Morovo Lagoon near Wickham Island: https://www.youtube.com/watch?v=-WdMunCwN6o). c: SEM micrograph. Scale bars: b-c: 250 µm, d: 5 mm; e: 2 mm.

facies: larger foraminifera, coral and molluscs limestones, coralline algae breccias, marly limestones with freshwater fossils (Bosellini et al., 1967; Carraro et al., 1969; De Zanche et al., 1977). In the Monte Postale area the "Calcari Nummulitici" are mainly represented by shallow-water carbonates. In this zone the occurrence of isolated blocks of coral limestone has been firstly reported by Barbieri & Medizza (1969), while Trevisani (2015) mentioned the presence of in situ larger foraminifera-calcareous algal buildups. Vescogni et al. (2016) provided the first detailed description and facies analysis of the Monte Postale coralgal bioconstructions and Papazzoni et al. (2017), by the integration of larger foraminifera and calcareous nannofossils biostratigraphy, dated these limestones as late Ypresian (SB11 Zone of Serra-Kiel et al., 1998). During the early Oligocene, the Lessini Shelf became a rimmed platform, with the presence of a well-preserved reef tract along its southweastern margin (Frost, 1981; Bosellini & Trevisani, 1992; Bosellini et al., 2020). Upper Oligocene to lower Miocene sediments are represented by sandstone and limestone successions, followed by a few meters of Burdigalian marly clays that constitute the last marine deposits in the Lessini area (Bosellini et al., 1967; Bassi et al., 2007, 2008; Bassi & Nebelsick, 2010).

The upper Ypresian Monte Postale coralgal buildups (Vescogni et al., 2016) display a maximum thickness of five meters, forming a discontinuous rim along the northern side of the Monte Postale, arranged as a northward-convex arc about 20-30 m wide and 200 m in length (Fig. 3b). The coralgal boundstone facies is dominated by a scleractinian association of 17 genera and by solenoporaceans algae (Fig. 5). In particular, three main growth forms characterise the coral fauna, with no evident zonation in their distribution: platy colonies dominate the assemblage (*Actinacis*, *Siderofungia*), usually associated with small, massive growth forms (*Actinacis*, *Paraleptoria*, *Goniopora*) and to a minor amount with branching colonies (ramose and phaceloid: *Stylophora*, *Acropora*, *Cladocora*, *Caulastraea*). Scleractinians and solenoporaceans algae grew in close association with a well-developed encrusting structure, mainly composed of calcareous algae and encrusting foraminifera, sometimes forming up to 80 cm thick polygenic, laminar bindstones. Within the coralgal buildups bioclastic deposits are also abundant, mainly represented by *Alveolina* grainstones and by rudstones derived from the breakage of the reef-building organisms. Sediment textures and presence of abundant dasycladacean algae and *Alveolina* indicate for the Monte Postale coralgal buildups a high-energy, shallow-water depositional environment.

MATERIAL AND METHODS

Coral colonies investigated in this paper were collected in the field and formerly indicated as

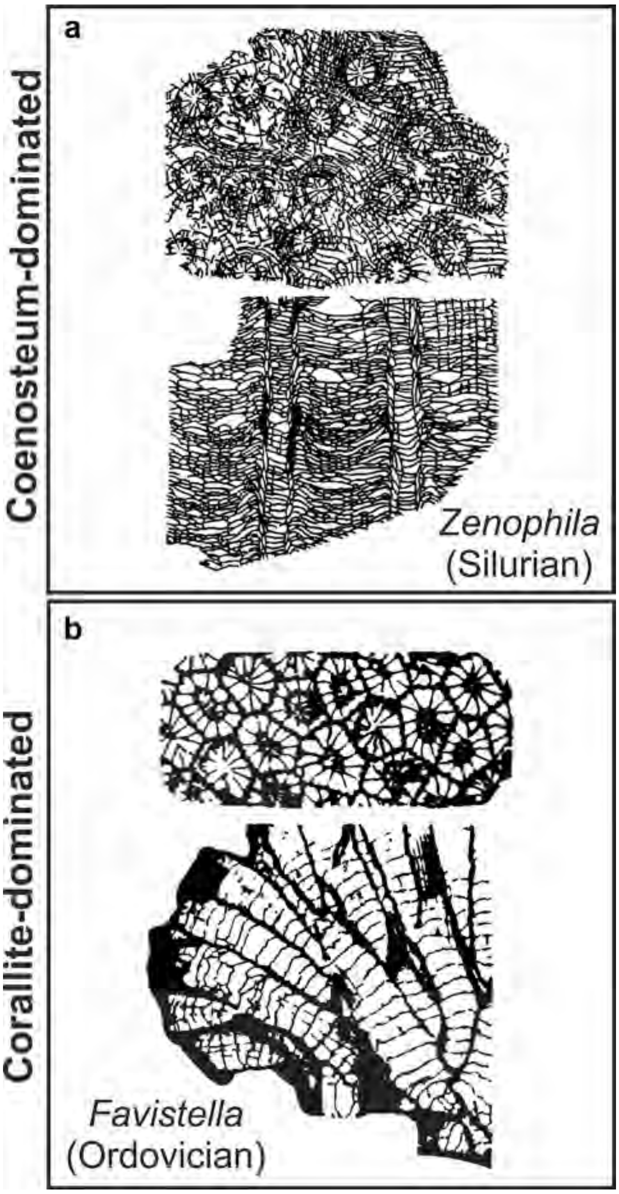

Fig. 2 - Coenosteum-dominated (a) vs corallite-dominated (b) coral colonies. Here exemplified by two rugose corals (Silurian *Zenophila* and Ordovician *Favistella*).

“undetermined corals” in Vescogni et al. (2016). These are five massive colonies that have been cut for polished slabs and thin sections. Polished sections parallel to corallite growth have been used to trace transects and calculate the coenosteum/corallite ratio (Fig. 6). Thin sections have been prepared to describe morphological characters and check preservation of microstructural details.

The thin-sections were first examined with a Nikon Eclipse 80i transmitted light microscope fitted with a DS-5Mc cooled camera head, next with hot cathode microscope HC1-LM at the Institute of Paleobiology, Polish Academy of Sciences. The following parameters of cathodoluminescence microscope were used: electron energy of 14 keV and a beam current density of 0.1 $\mu A\ mm^{-2}$. The observed orange to red luminescence was characteristic of secondary calcite with high Mn^{2+} concentrations (the main activator of luminescence in carbonates) (Marshall, 1988). Calcitic mineralogy of the sectioned coralla was further confirmed by immersion for ten minutes in Feigls’s solution: no black staining was observed which is typical of aragonite (Friedman, 1959).

Studied specimens are housed at the Department of Chemical and Geological Sciences, University of Modena and Reggio Emilia (Italy).

Repository abbreviations

IPUM: Inventario Paleontologia Università di Modena, Italy.

SYSTEMATIC PALEONTOLOGY

Order Scleractinia Bourne, 1900
Family Euphylliidae Alloiteau, 1952

Genus *Nancygyra* n. gen. Bosellini & Stolarski
Type species *Nancygyra dissepimentata* n. gen. n. sp.

Etymology - It is our pleasure to name this genus after the scleractinian coral specialist Professor Dr. Ann (Nancy) Budd.

Diagnosis - Massive aphroid colony with corallites protruding from an extensive and dense dissepimental coenosteum as in *Galaxea*. Budding intracalicular. It differs from *Galaxea* in developing two first orders of septa with thickened (rhopaloid) axial margin.

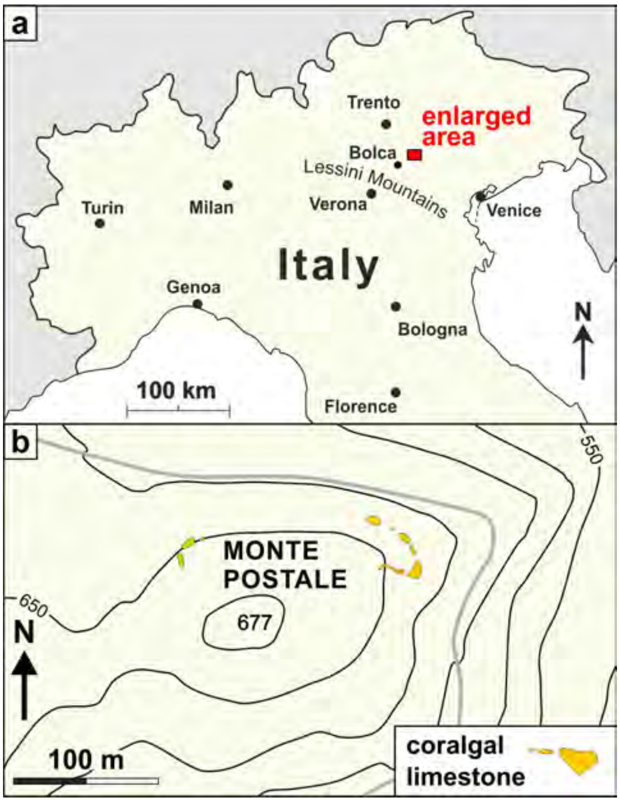

Fig. 3 - (color online) Location map. Map of the study area (a) with close-up of the Monte Postale area and location of the coral outcrops (b).

Fig. 4 - Paleogeographic reconstruction of the Lessini Shelf during the Paleogene (modified from Bosellini, 1989).

Composition - Type species only.

Nancygyra dissepimentata n. sp. Bosellini & Stolarski
(Figs 6-7)

Etymology - After the abundant dissepiments that characterise the coenosteum.

Type locality - Lower Eocene (upper Ypresian, 48.5-51 Ma) of the Monte Postale (Lessini Mountains, Verona, NE Italy).

Holotype - IPUM 28983.

Paratypes - IPUM 28984, IPUM 28985, IPUM 28986, IPUM 28987.

Diagnosis - As for the genus.

Material - Five colonies (IPUM 28983, IPUM 28984, IPUM 28985, IPUM 28986, IPUM 28987).

Diagnosis - As for the genus.

Description - Massive aphroid (neighboring corallites united by dissepiments only) colonies with monocentric intracalicular budding. Corallites mostly elliptical in outline, sometimes circular, with diameter ranging from 3 to 4 mm in smaller corallites and from 4 to 6 mm in larger ones (Figs 6-7). Unequal septa arranged in three, typically incomplete orders with septa of first two cycles with thickened (rhopaloid) inner margin. Columella absent. Wall well defined and thick.

Corallites protrude 7 to 10 mm from an extensive concave dense coenosteum made by vesicular convex dissepiments. These are quite irregularly arranged and spaced around sparse corallites. The coenosteum represents approximately the 50% of the colony structure.

The skeleton is entirely recrystallised to sparry calcite (Fig. 7a-c, f). The possible traces of original intra-skeletal microstructural boundaries were found inside the thick corallite wall (Fig. 7f). Similar sparry calcite is developed in the region originally occupied by the coral skeleton and in intracalicular space. These calcite crystals show zoned bright to dully red cathodoluminescence (Fig. 7g, regions marked "1"). Original skeletal boundaries show less bright luminescence (Fig. 7g, regions marked "2") whereas secondary deposits (cements) that form around the skeletal boundaries (Fig. 7g, regions marked "3") are non-luminescent.

DISCUSSION

Nancygyra n. gen. forms aphroid, lightweight coralla with a vesicular coenosteum similar to *Galaxea* but with corallites having more massive skeletal structures (thicker corallite wall, thickened axial margins of two first orders of septa). According to modern phylogenetic analyses (Luzon et al., 2007; Fukami et al., 2008; Kitahara et al., 2016), *Galaxea* forms a clade (family Euphyllidae) within the Complexa super-clade that groups *Euphyllia*, *Fimbriaphyllia*, and *Ctenella*. The oldest representatives of *Galaxea* date to the Miocene of the Indo-Pacific region (Wells, 1964; Bromfield, 2013; Santodomingo et al., 2016) but euphylliids have an early Cenozoic fossil record as *Euphyllia* is known from the Paleocene of Costa Rica (Aguilar & Denyer, 2001). Consequently, the Eocene occurrence of the herein proposed euphylliid *Nancygyra* n. gen. is consistent with the Cenozoic diversification of this group. Deciphering of phylogenetic position of euphyllids within Mesozoic groups of scleractinians is difficult due to different taxonomic values ascribed to different characters among the Mesozoic/Cenozoic taxa and/or possible loss in the evolution of euphylliids of some characters of their Mesozoic ancestors. Moreover, a complete recrystallisation of the skeleton of *Nancygyra* n. gen., highlighted by development of successive generations of differently cathodoluminescent mineral deposits, and lack of early ontogeny data of this coral hamper more in-depth skeleton-based phylogenetic

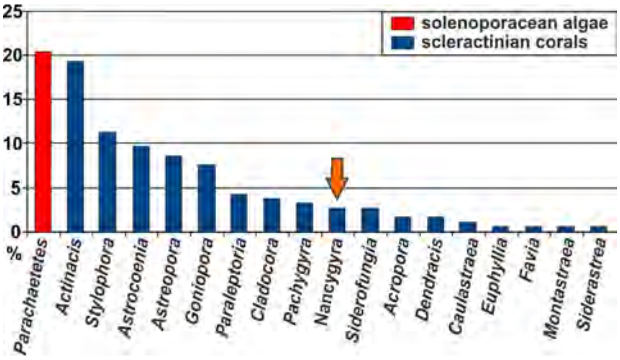

Fig. 5 - (color online) Relative abundance of scleractinian corals and solenoporacean algae genera in the Monte Postale buildups (modified from Vescogni et al., 2016).

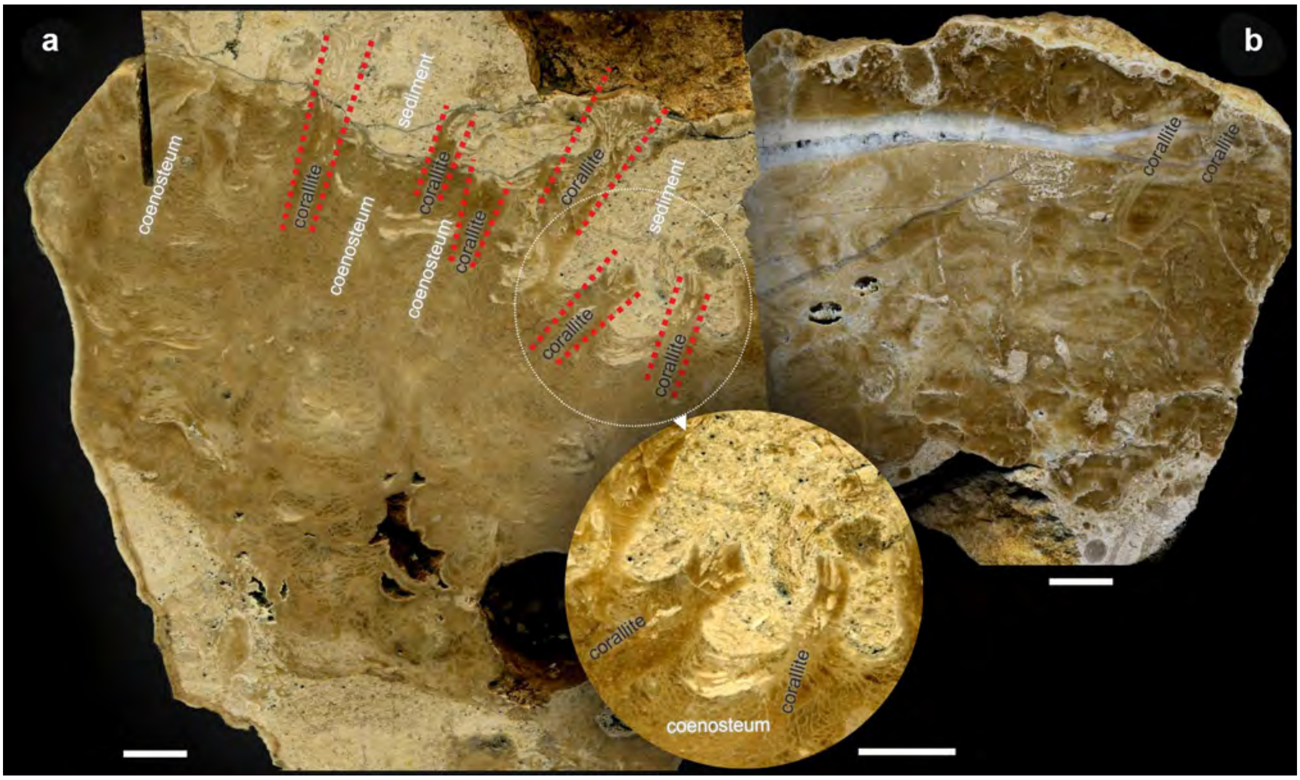

Fig. 6 - (color online) Macroscopic characters. Polished slabs of two colonies (a: holotype IPUM 28983; b: paratype IPUM 28985). Section of the larger specimen (a) shows particularly well the relationship between corallites and vesicular coenosteum, with corallites sticking-out of the natural surface of the colony (covered with sediment); see also slightly enlarged region with enhanced contrast (circle). Scale bars: 1 cm.

analyses. Nonetheless, the similar extent of dissepimental coenosteum development and corallite architecture that exists in *Nancygyra* n. gen. and some rhipidogyrids and amphiastraeids (Kołodziej, 2003) indicates possible further research targets.

The appearance of this new peculiar genus occurred near the end of the hyperthermal event named EECO (Early Eocene Climatic Optimum), when Cenozoic global temperatures reached their maximum under high atmospheric $p\mathrm{CO}_2$ concentrations (Zachos et al., 2001, 2008) and coral reefs underwent a marked decline (Kiessling & Baron-Szabo, 2004; Scheibner & Speijer, 2008; Zamagni et al., 2012). This reef gap, however, did not correspond to a decrease in coral richness. The Eocene of the west Tethyan region has been considered a true hotspot of tropical marine biodiversity (Renema et al., 2008) and an increase in coral richness has been documented from the late Paleocene to the early Eocene (Kiessling & Baron-Szabo, 2004; Weiss & Martindale, 2018). Recent database analysis also underlined that coloniality was favoured during this period of habitat restriction, with heat stress limiting corals to shallow waters because of the shoaling lysocline (Weiss & Martindale, 2018).

Experimental studies show that dissepiments are rapid growing skeletal elements (Brahmi et al., 2012). Formation of light, dissepiment-dominated coralla may therefore be an efficient strategy to compete for space in the warm and shallow-water reef environment represented at Monte Postale. Noteworthy, some modern examples of dissepiment-dominated coralla (e.g., *Symphyllia*) may show buoyancy due to gas trapped interstitially between the dissepiments and may be capable of floating (possible dispersal) after storm events (DeVantier, 1992). Analogous dispersal capability by floating of *Nancygyra* n. gen. seems however unlikely due to the occurrence of this taxon being limited to type locality.

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REFERENCES

Aguilar T. & Denyer P. (2001). Una especie nueva de *Euphyllia* (Scleractinia: Caryophylliidae) en las calizas de Barra Honda (Paleogeno), Costa Rica [A new Euphyllia species (Scleractinia, Caryophylliidae) in the Barra Honda Limestone (Paleogene), Costa Rica]. *Revista de Biologia Tropical,* 49: 195-201.

Barbieri G. & Medizza F. (1969). Contributo alla conoscenza geologica della regione di Bolca (Monti Lessini). *Memorie degli Istituti di Geologia e Mineralogia dell'Università di Padova,* 27: 1-36.

Bassi D., Bianchini G., Mietto P. & Nebelsick J. (2008). Southern Alps in Italy: Venetian Pre-Alps. *In* McCann T. (ed.), The

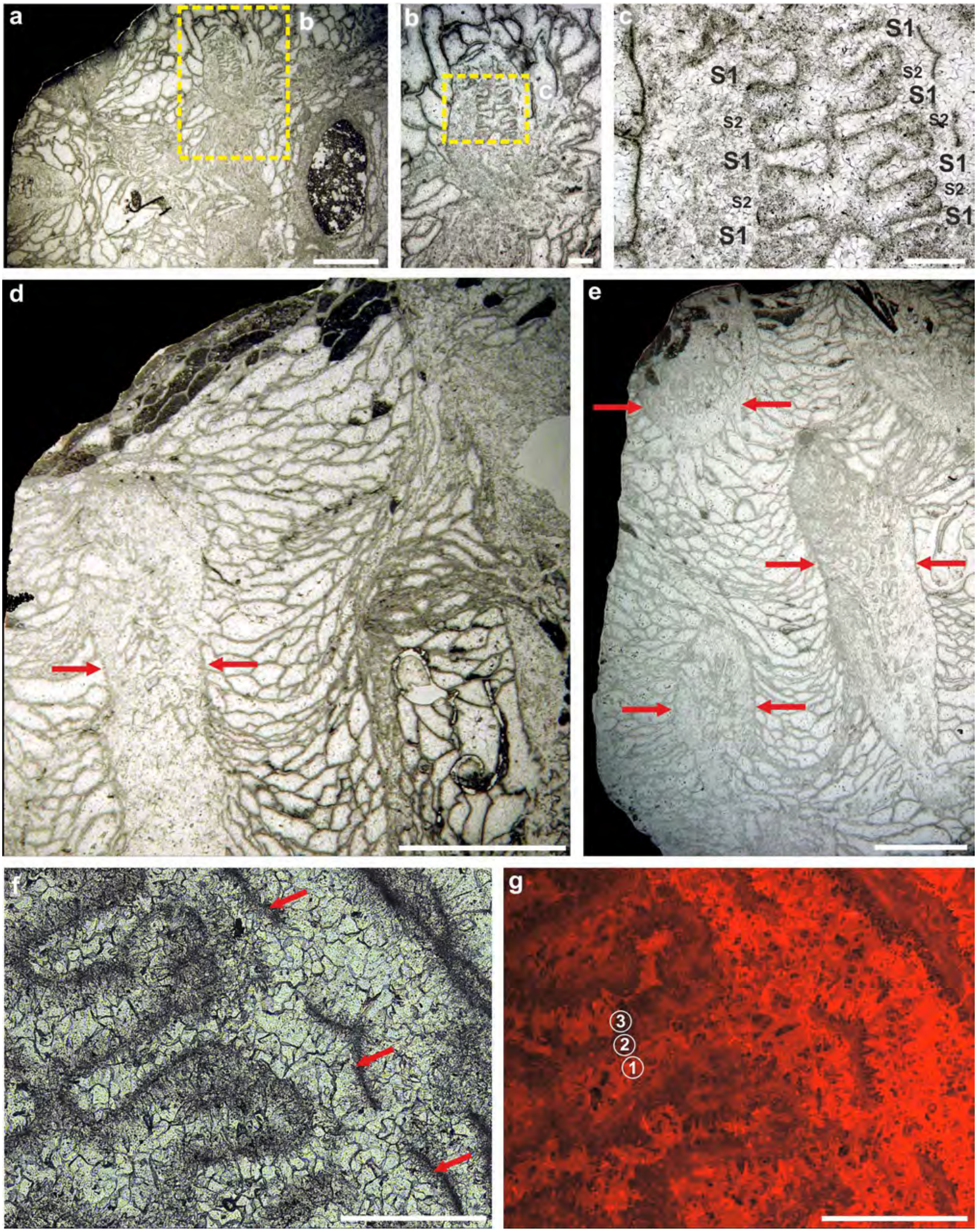

Fig. 7 - (color online) Macro and microstructural characters (paratype IPUM 28984): structural and preservational details. Transverse (approximately) (a-c) and longitudinal (d-e) thin-sections of colony fragments. Corallites sectioned transversely (a-c) show elliptical outline, thick wall and septa of first two cycles with thickened (rhopaloid) inner margins. Longitudinal sections (d-e) show thick-walled corallites embedded in vesicular coenosteum. The skeleton of all coralla is entirely recrystallized (f) with possible traces of original intra-skeletal microstructural boundaries (red arrows). Diagenetic alteration of the skeleton is highlighted by bright-red cathodoluminescence (corresponding g image). The distinct luminescence signals (1-3) correspond to region originally occupied by the coral skeleton (1) and the subsequent generations of secondary deposits (2-3) infilling the calicular space. Scale bars: a, d-e: 5 mm; b: 1 mm; c, f-g: 500 µm.

Geology of Central Europe, v. 2. *Geological Society of London, Special Volume*: 56-62.

Bassi D., Hottinger L. & Nebelsick J. (2007). Larger foraminifera of the Late Oligocene of the Venetian area, north-eastem ltaly. *Palaeontology*, 50: 845-868.

Bassi D. & Nebelsick J. (2010). Components, facies and ramps: redefining Upper Oligocene shallow water carbonates using coralline red algae and larger foraminifera (Venetian area, northeast Italy). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 295: 258-280.

Bosellini A. (1989). Dynamics of Tethyan carbonate platforms. *In* Crevello P.D., Wilson J.L., Sarg J.F. & Read J.F. (eds), Controls on Carbonate Platform and Basin Platform. *S.E.P.M. Special Publication*, 44: 3-13.

Bosellini A., Carraro F., Corsi M., De Vecchi G.P., Gatto G.O., Malaroda R., Sturani C., Ungaro S. & Zanettin B. (1967). Note Illustrative della Carta geologica d'ltalia alla scala 1:100.000, Foglio 49 Verona. 61 pp. Servizio Geologico d'Italia, Nuova Tecnica Grafica, Roma.

Bosellini A., Masetti D. & Sarti M. (1981). A Jurassic "Tongue of Ocean" infilled with oolitic sands: the Belluno Trough, Venetian Alps, Italy. *Marine Geology*, 44: 59-95.

Bosellini F.R. & Trevisani E. (1992). Coral facies and cyclicity in the Castelgomberto Limestone (Early Oligocene, Eastern Lessini Mountains, Northern Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, 98: 339-352.

Bosellini F.R., Vescogni A., Kiessling W., Zoboli A., Di Giuseppe D. & Papazzoni C.A. (2020). Revisiting reef models in the Oligocene of northern Italy (Venetian southern Alps). *Bollettino della Società Paleontologica Italiana*. doi:10.4435/BSPI.2020.11

Brahmi C., Kopp C., Domart-Coulon I., Stolarski J. & Meibom A. (2012). Skeletal growth dynamics linked to trace-element composition in the scleractinian coral. *Geochimica et Cosmochimica Acta,* 99: 146-158.

Bromfield K. (2013). Neogene Corals from the Indo-Pacific: Indonesia, Papua New Guinea, and Fiji. *Bulletins of American Paleontology,* 387: 1-130.

Budd A.F. & Bosellini F.R. (2016). Revision of Oligocene Mediterranean meandroid corals in the scleractinian families Mussidae, Merulinidae, and Lobophylliidae. *Journal of Systematic Palaeontology,* 14: 771-798.

Budd A.F. & Stolarski J. (2011). Corallite wall and septal microstructure in scleractinian reef corals: comparison of molecular clades within the family Faviidae. *Journal of Morphology,* 272: 66-88.

Carraro F., Malaroda R., Piccoli G., Sturani C. & Venzo S. (1969). Note Illustrative della Carta Geologica D'Italia, Scala 1:100.000. Foglio 48, Peschiera del Garda. Poligrafica & Cartevalori Ercolano, Napoli.

Claereboudt M. 1990. *Galaxea paucisepta* nom. nov. (for *G. pauciradiata*), rediscovery and redescription of a poorly known scleractinian species (Oculinidae). *Galaxea, Journal of Coral Reef Studies*, 9: 1-8.

De Zanche V., Sorbini L. & Spagna V. (1977). Geologia del territorio del Comune di Verona. *Memorie del Museo Civico di Storia Naturale di Verona*, 1: 1-52.

DeVantier L.M. (1992). Rafting of tropical marine organisms on buoyant corolla. *Marine Ecology Progress Series,* 86: 301-302.

Esper E.J.C. (1797). Fortsetzungen der Pflanzenthiere in Abbildungennach der Natur mit Farben erleuchtet nebst Beschreibungen. *Erster Theil (Nürnberg)*: 1-230.

Friedman G.M. (1959). Identification of carbonate minerals by staining methods. *Journal of Sedimentary Petrology*, 29: 87-97.

Frost S.H. (1981). Oligocene reef coral biofacies of the Vicentin, northeast Italy. *In* Toomey D.F. (ed.), European fossil reef model. *S.E.P.M. Special Publication*, 30: 483-539.

Fukami H., Chen C.A., Budd A.F., Collins A., Wallace C.C., Chuang Y.Y., Chen C., Dai C.F., Iwao K., Sheppard C. & Knowlton N. (2008). Mitochondrial and nuclear genes suggest that stony corals are monophyletic but most of coral families are not. *PLOS ONE* 3: 3-9.

Kiessling W. & Baron-Szabo R.C. (2004). Extinction and recovery patterns of scleractinian corals at the Cretaceous-Tertiary boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 214: 195-223.

Kitahara M.V., Fukami H., Benzoni F. & Huang D. (2016). The New Systematics of Scleractinia: Integrating Molecular and Morphological Evidence. *In* Goffredo S. & Dubinsky Z. (eds), The Cnidaria, Past, Present and Future. Springer, Cham: 41-59.

Kołodziej B. (2003). Scleractinian corals of suborders Pachythecaliina and Rhipidogyrina: discussion on similarities and description of species from Stramberk-type limestones, Polish Outer Carpathians. *Annales Societatis Geologorum Poloniae,* 73: 193-217.

Linnaeus C. (1767). Systema naturae per regna tria naturae: secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Ed. 12. 1. Regnum Animale. 1 & 2. *Holmiae, Laurentii Salvii*: 533-1327.

Luzon K.S, Lin M., Ablan Lagman M.C.A., Licuanan W.R.Y. & Chen C.A. (2017). Resurrecting a subgenus to genus: molecular phylogeny of *Euphyllia* and *Fimbriaphyllia* (order Scleractinia; family Euphyllidae; clade V). *PeerJ*, 5: e4074.

Marshall D.J. (1988). Cathodoluminescence of Geological Materials. 146 pp. Unwin Hyman, Boston.

Papazzoni C.A., Fornaciari E., Giusberti L., Vescogni A. & Fornaciari B. (2017). Integrating shallow benthic and calcareous nannofossils zones: the lower Eocene of the Monte Postale section (northern Italy). *Palaios*, 32: 1-12.

Renema W., Bellwood D.R., Braga J.C., Bromfiled K., Hall R., Johnson K.G., Lunt P., Meyer C.P., McMonagle L.B., Morley R.J., O'Dea A., Todd J.A., Wessenlingh F.P., Wilson M.E.J. & Pandolfi J.M. (2008). Hopping Hotspots: Global Shifts in Marine Biodiversity. *Science*, 321: 654-657.

Santodomingo N., Renema W. & Johnson K.G. (2016). Understanding the murky history of the Coral Triangle: Miocene corals and reef habitats in East Kalimantan (Indonesia). *Coral Reefs*, 35: 765-781.

Scheibner C. & Speijer R.P. (2008). Late Paleocene-early Eocene Tethyan carbonate platform evolution. A response to long- and short-term paleoclimatic change. *Earth-Science Reviews,* 90: 71-102.

Serra-Kiel J., Hottinger L., Caus E., Drobne K., Ferrandez C., Jauhri A.K., Less G., Pavlovec R., Pignatti J., Samsò J.M., Schaub H., Sirel E., Strougo A., Tambareau Y., Tosquella J. & Zakrevskaya E. (1998). Larger foraminiferal biostratigraphy of the Tethyan Paleocene and Eocene. *Bulletin de la Société Géologique de France,* 169: 281-299.

Trevisani E. (2015). Upper Cretaceous–Lower Eocene succession of the Monte Postale and its relationship with the "Pesciara di Bolca" (Lessini Mountains, northern Italy): deposition of a fossil-fish lagerstätte. *Facies,* 61: 7.

Vescogni A., Bosellini F.R., Papazzoni C.A., Giusberti L., Roghi G., Fornaciari E., Dominici G. & Zorzin R. (2016). Coralgal buildups associated with the Bolca Fossil-Lagerstätten: new evidences from the Ypresian of Monte Postale (NE Italy). *Facies*, 62: 21.

Weiss A.M. & Martindale R.C. (2018). Paleobiological traits determined scleractinian coral survival and proliferation during the Late Paleocene and Early Eocene hyperthermals. *Paleoceanography and Paleoclimatology,* 34: 252-274.

Wells J.W. (1964). Fossil corals from Eniwetok Atoll. *United States Geological Survey Professional Paper,* 260-DD: 1101-1111.

Winterer E.L. & Bosellini A. (1981). Subsidence and sedimentation on Jurassic passive continental margin, Southern Alps, Italy. *Bulletin of the American Association of Petroleum Geologists*, 65: 394-421.

Zachos J.C., Dickens G.R. & Zeebe R.E. (2008). An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature,* 451: 279-283.

Zachos J.C., Pagani M., Sloan L., Thomas E. & Billups K. (2001). Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science,* 292: 686-693.

Zamagni J., Mutti M. & Košir A. (2012). The evolution of mid Paleocene–early Eocene coral communities: how to survive during rapid global warming. *Palaeogeography, Palaeoclimatology, Palaeoecology* 317-318: 48-65.

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A first glimpse on the taphonomy and sedimentary environment of the Eocene siliceous sponges from Chiampo, Lessini Mts, NE Italy

Viviana Frisone*, Nereo Preto, Andrzej Pisera, Claudia Agnini, Luca Giusberti,
Cesare Andrea Papazzoni, Antonio De Angeli, Claudio Beschin, Paolo Mietto,
Ermanno Quaggiotto, Paolo Monaco, Stefano Dominici, Wolfgang Kiessling,
Valeria Luciani, Michel Roux & Francesca R. Bosellini

V. Frisone, Museo di Archeologia e Scienze Naturali "G. Zannato", Piazza Marconi 17, I-36075 Montecchio Maggiore (Vicenza), Italy; museo.scienze@comune.montecchio-maggiore.vi.it **corresponding author*
N. Preto, Dipartimento di Geoscienze, Università degli Studi di Padova, Via Gradenigo 6, I-35131 Padova, Italy; nereo.preto@unipd.it
A. Pisera, Institute of Paleobiology, Polish Academy of Sciences, Twarda 51/55, P-00818 Warszawa, Poland; apis@twarda.pan.pl
C. Agnini, Dipartimento di Geoscienze, Università degli Studi di Padova, Via Gradenigo 6, I-35131 Padova, Italy; claudia.agnini@unipd.it
L. Giusberti, Dipartimento di Geoscienze, Università degli Studi di Padova, Via Gradenigo 6, I-35131 Padova, Italy; luca.giusberti@unipd.it
C.A. Papazzoni, Dipartimento di Scienze Chimiche e Geologiche, Università degli Studi di Modena e Reggio Emilia, Via Campi 103, I-41125 Modena, Italy; papazzoni@unimore.it
A. De Angeli, Museo di Archeologia e Scienze Naturali "G. Zannato", Piazza Marconi 17, I-36075 Montecchio Maggiore (Vicenza), Italy; antonio.deangeli@alice.it
C. Beschin, Museo di Archeologia e Scienze Naturali "G. Zannato", Piazza Marconi 17, I-36075 Montecchio Maggiore (Vicenza), Italy; beschin.cl@libero.it
P. Mietto, Dipartimento di Geoscienze, Università degli Studi di Padova, Via Gradenigo 6, I-35131 Padova, Italy; paolo.mietto@unipd.it
E. Quaggiotto, Museo di Archeologia e Scienze Naturali "G. Zannato", Piazza Marconi 17, I-36075 Montecchio Maggiore (Vicenza), Italy; ermanno.quaggiotto@libero.it
P. Monaco, Dipartimento di Fisica e Geologia, Università degli Studi di Perugia, Via Pascoli, I-06123 Perugia, Italy; paolo.monaco@unipg.it
S. Dominici, Museo di Storia Naturale-Sistema Museale d'Ateneo, Università degli Studi di Firenze, Via La Pira 4, I-50121 Firenze, Italy; stefano.dominici@unifi.it
W. Kiessling, GeoZentrum Nordbayern, Friedrich-Alexander Universität Erlangen, Loewenichstraße 28, D-91054 Erlangen, Germany; wolfgang.kiessling@fau.de
V. Luciani, Dipartimento di Fisica e Scienze della Terra, Università degli Studi di Ferrara, Via Saragat 1, I-44122 Ferrara, Italy; valeria.luciani@unife.it
M. Roux, Muséum national d'Histoire naturelle, UMR7205 ISYEB MNHN-CNRS-UPMC-EPHE, Département Systématique et Évolution, CP 51, 57 rue Cuvier, F-75231 Paris Cedex 05, France; mich.roux51@gmail.com
F.R. Bosellini, Dipartimento di Scienze Chimiche e Geologiche, Università degli Studi di Modena e Reggio Emilia, Via Campi 103, I-41125 Modena, Italy; francesca.bosellini@unimore.it

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ABSTRACT - A diverse assemblage of bodily preserved sponges has been recovered from a lower Lutetian tuffite horizon in the Chiampo Valley, Lessini Mountains, Italy. The sponge assemblage is dominated by hexactinellids and lithistids. Using uniformitarian criteria, the composition of the assemblage suggests a water depth greater than 200 m. Sponges are often preserved in growth position including sponge clusters. Taphonomic processes facilitating sponge preservation include rapid burial of a living sponge community and early diagenetic calcification. Different modes of attachment suggest heterogeneous substrate conditions. The associated fauna, such as abundant pteropods in the matrix and in-situ preserved crinoids, confirms a rather deep-water environment. However, there are also common benthic elements of shallow-water origin. Although some of these elements show signs of transport, others, such as decapod crustaceans, do not. Moreover, trace fossils indicate high-energy environments. To reconcile these observations, we propose rapid, tectonically triggered sea-level changes.

INTRODUCTION

Due to the low preservation potential of many taxa, especially those with organic skeleton, the fossil record of sponges is rather incomplete. Only sponges with a rigid skeleton, e.g., lithistids (demosponges with desmas), Hexactinosida and Lychniscosida (Class Hexactinellida) and sponges with a massive calcareous skeleton (polyphyletic demosponges and Calcarea), have a more or less continuous fossil record (Pisera, 2006). Moreover, the geological history of sponges is difficult to generalize, because of biases in the fossil record and uncertainties over identifying causal relationships (e.g., with regard to climatic changes; Muir et al., 2017).

The present study deals with a middle Eocene siliceous sponge assemblage from the Chiampo Valley, Lessini Mountains, north-eastern Italy. The poriferan assemblage consists of 33 species: 15 hexactinellids and 18 demosponges (Frisone et al., 2016; Frisone & De Angeli, 2017). The sponges are three-dimensionally preserved but their originally siliceous spicules are replaced by calcite. Whereas the taxonomy of this sponge assemblage is now well understood, little is known about the environment in which these sponges lived. Sponge taxonomy, however, provides already some interesting hints; most relevant is that the most common extant relatives of the sponge taxa from the Lutetian of Chiampo inhabit rather deep waters today. Furthermore, the presence of different modes of attachment in the investigated specimens suggests heterogeneous substrate conditions. Small, possibly young sponges are present in the assemblage, as well as sponge clusters (Frisone et al., 2016).

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Field sampling revealed hexactinellids to be strongly dominant over lithistids, thus suggesting a deep-water setting below 200 m water depth (Frisone et al., 2018). This interpretation is at odds with the traditional interpretation of a shallow-water environment in Chiampo (e.g., Fabiani, 1915; De Zanche, 1965), and hence with the notion that the "sponge assemblages developed in a shallow-water paleoenvironments" (Matteucci & Russo, 2011, p. 34).

In this study, we investigate the preservation, associated fauna and sedimentary context of the Chiampo sponges, in order to provide a better clue on their habitat. We also aim at a clarification of the taphonomic and diagenetic processes that led to the preservation of this unique sponge assemblage. Our hypothesis is that the sponges were fossilised in situ, in a deep-water setting, and buried alive.

GEOLOGICAL SETTING

The studied area is located in the eastern Lessini Mountains, a portion of the Prealps of north-eastern Italy, on the western side of the Chiampo Valley (Fig. 1). The Lessini Mountains are a triangular-shaped tableland, which occupies some 800 km^2 in the western Venetian Region, at the transition between the Prealps and the Po Plain. They belong to the Cenozoic Lessini Shelf, a carbonate platform with scattered reefs, lagoons, islands and volcanoes circumscribed northwards by lands and surrounded by deeper water to the south and the east (e.g., Bosellini, 1989; Bosellini & Papazzoni, 2003; Bassi et al., 2008).

The studied material comes from two adjacent quarries, both located in the municipality of Chiampo (Vicenza): Cengio dell'Orbo, 45° 32' 25.56" N, 11° 15' 44.47" E (called "Boschetto di Chiampo" in Beschin et al., 1991; Beccaro et al., 2001 and other references) and Lovara, 45° 32' 11.87" N, 11° 15' 58.92" E (part of which is named "Zanconato" in e.g., Ancona, 1966; Visentin, 1994). A single small outcropping section (less than 3 m thick) that yielded a few fossil sponges was logged and sampled in Via Motti, 45° 32' 28.9" N, 11° 15' 34.2" E, near the Cengio dell'Orbo quarry. The outcrop lies near the tip of the lens-shaped sponge-bearing tuffite horizon (Fig. 2). The studied sites are located within a NNW-trending extensional structure known as the Alpone-Agno or Alpone-Chiampo graben (Barbieri et al., 1982, 1991,

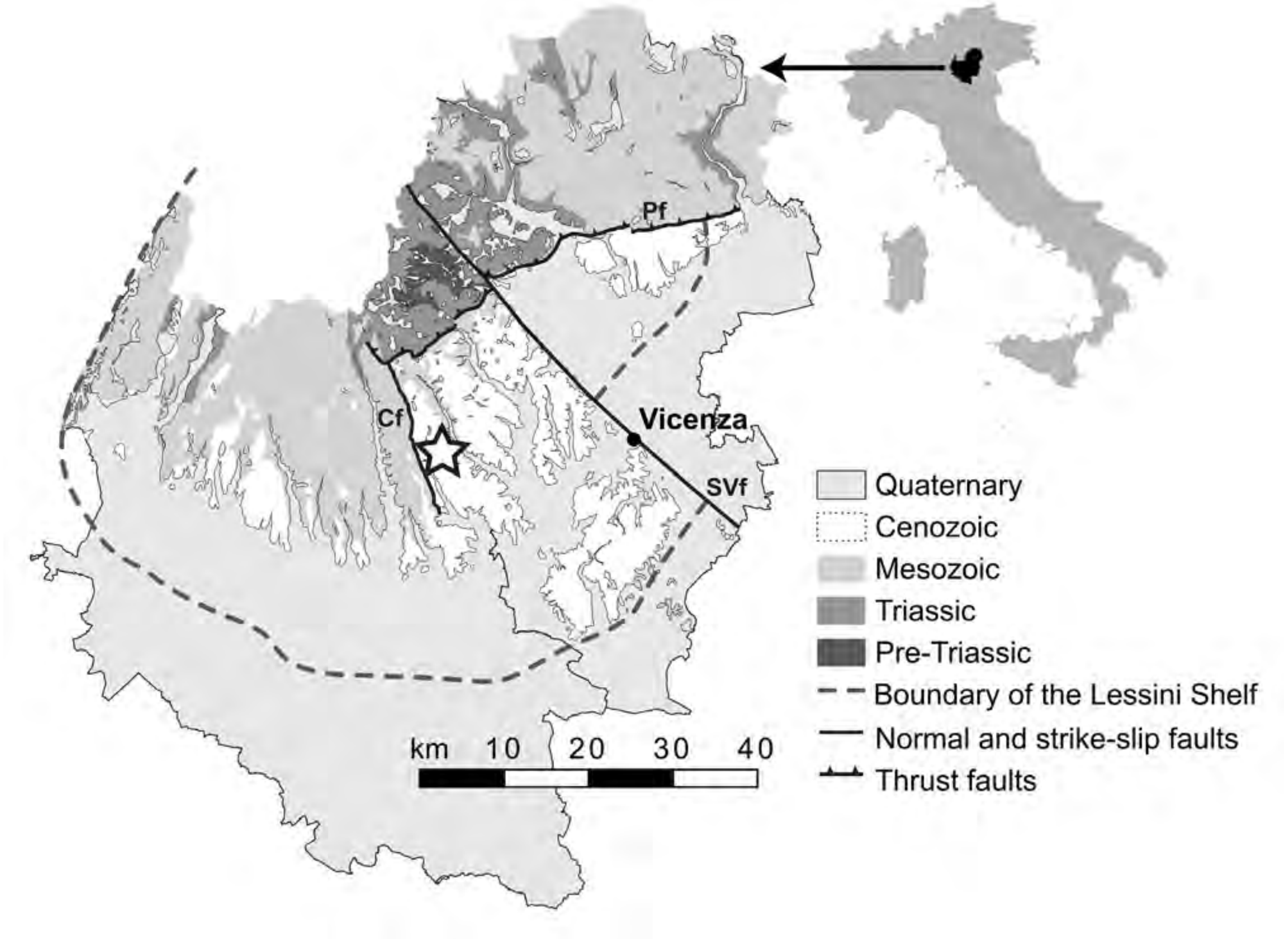

Fig. 1 - Simplified geological map of the study area (Verona and Vicenza provinces, Northern Italy), modified from Frisone et al. (2018). Regione Veneto, Sezione Geologia e Georisorse, released under the Italian Open Data License 2.0 (https://www.dati.gov.it/content/italian-open-data-license-v20). Outline of the Lessini Shelf during the Eocene modified from Bosellini (1989). The sponge-bearing outcrop near Chiampo is indicated by the white star. Cf: Castelvero fault; SVf: Schio-Vicenza fault; Pf: Pedemontana thrust fault.

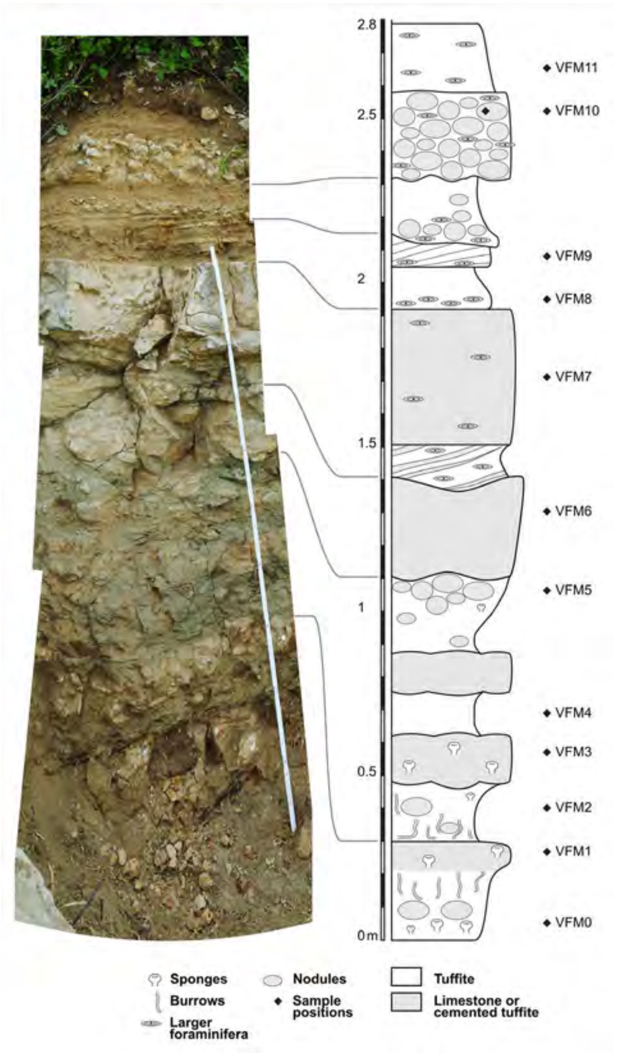

Fig. 2 - (color online) Field photomosaic and stratigraphic log of the Via Motti section. The wooden meter is 2 m long. The picture and log scales do not coincide perfectly because of perspective distortions of the photomosaic.

among others), bounded to the west by the Castelvero normal fault. Zampieri (1995) proposed that the Alpone-Agno graben developed in the South Alpine foreland as an extensional response to the active convergence between the European and Adriatic plates. It was about 20 km wide and at least 35 km long. The area belongs to the Veneto Volcanic Province, identified by principally mafic and ultramafic rocks erupted during the Paleocene-Oligocene. Large volumes of mainly subaqueous volcanics and their contemporaneous reworking products (hyaloclastites and tuffites) accumulated in the graben. The eruptive centers in the eastern Lessini Mts were aligned with the Castelvero fault (e.g., Piccoli, 1966). This fault was active during the Eocene, controlling the accumulation of volcanics, their reworked products and the interlayered carbonates (Barbieri & Zampieri, 1992). As a consequence, the accumulation of volcanic and volcaniclastic products was maximal on the eastern, lowered block of the fault. Interlayered carbonates are also thicker on the eastern side of the block, which was subsiding faster. Several magmatic pulses were separated by periods of magmatic inactivity during which marine sedimentation took place (De Vecchi & Sedea, 1995, and references therein). The sedimentary intercalations are locally called “Chiampo limestone”. This unit was quarried until the 1990s for extracting building stone. It belongs to a lower to middle Eocene informal unit named “Nummulitic limestone”, which is widespread in the western part of the Veneto region (e.g., Fabiani, 1915). This lithostratigraphic unit is poorly constrained and still in need of revision. It includes limestones with nummulitids of different ages and depositional settings (Bassi et al., 2013; Papazzoni et al., 2014). Beccaro et al. (2001) interpreted the “Nummulitic limestone” of the studied sites as belonging to a distal carbonate ramp, and the debris as transported by debris flows and turbidites. Several volcaniclastic horizons are intercalated within the “Nummulitic limestone”. Some of these horizons are rich in very well-preserved fossils, including three-dimensionally preserved crustaceans complete with appendages and ventral parts (e.g., De Angeli & Garassino, 2006; Beschin et al., 2016). Beccaro et al. (2001) interpreted these tuffitic horizons as belonging to different stratigraphic levels with limited lateral extension. Other authors consider the fossil-bearing volcaniclastics horizons as one continuous unit, also known as “*Lophoranina* tuff” (sensu Beschin et al., 1991; see also Matteucci & Russo, 2005). The name derives from *Lophoranina marestiana* (König, 1825), a decapod crustacean that is common in this horizon.

Volcaniclastic sediments often have a lens shape and channelised morphology (Márton et al., 2011) and sedimentary structures, such as high-angle cross bedding, are sometimes visible in the field. Pelagic fossils (e.g., pteropods) are common and locally (Lovara quarry) there are accumulations of planktic and nektonic fossils (e.g., planktic foraminifera, shark teeth; Beccaro et al., 2001). In Cengio dell’Orbo and Lovara quarries, in a single horizon of volcaniclastics enclosed in the “Nummulitic limestone”, sponges represent the most common macrofaunal element (Matteucci & Russo, 2005). Outside of the Chiampo Valley, bodily preserved sponges are absent in the Eocene of the Southern Alps (Frisone et al., 2016). Isolated spicules of Demospongiae were reported (Frisone et al., 2014b) from the Bartonian of Monte Duello, Montecchia di Crosara, Lessini Mts (Verona, Italy).

The sponge assemblage investigated here originates from a 50-200 cm thick horizon of tuffites and hyaloclastites in the Lovara and Cengio dell’Orbo quarries (Menin, 1972; Visentin, 1994; Matteucci & Russo, 2005; Frisone et al., 2016). The rock is a tuffite, composed of rounded volcanic fragments, calcareous bioclasts and calcitic cement. The volcanic clasts are strongly altered, with palagonitised glass in vesicles. The associated fauna is mainly composed of smaller benthic, planktic and larger foraminifera. There are also crustaceans (decapods and ostracods), echinoderms, bryozoans, mollusks (especially pteropods, and other gastropods, and rare cephalopods and bivalves), red algae and rare corals (this study and Fabiani, 1915; Schaub, 1962; De Zanche, 1965; Ancona, 1966; Beschin et al., 1991, 2016; Fornasiero & Vicariotto, 1997; De Angeli & Beschin, 2010; Pacaud & Quaggiotto, 2011; Frisone et al., 2016). The bioclasts, especially the larger benthic foraminifera, are often fragmented. This feature was also observed by Beschin et al. (1991) at

Lovara quarry. The age of the sponge horizon is Lutetian (Beccaro et al., 2001; Matteucci & Russo, 2005; Frisone et al., 2016).

MATERIALS AND METHODS

The sponge material consists of more than 900 specimens, housed in six Italian public museums: Museo di Storia Naturale di Venezia (MSNV); Museo di Archeologia e Scienze Naturali "G. Zannato", Montecchio Maggiore (MCZ-PAL); Museo Civico "D. Dal Lago", Valdagno (MCV); Museo "Padre Aurelio Menin", Chiampo (MMC); Museo di Geologia e Paleontologia dell'Università degli Studi di Padova (MGP-PD and IG-PD) and Museo Naturalistico Archeologico, Vicenza (IG-VI). The study material was mainly collected by amateur paleontologists between the 1960s and 1990s.

Our study focuses on sponge assemblage and associated fossils and sediments from the Lovara and Cengio dell'Orbo quarries. As these quarries are abandoned and the sponge-bearing horizons are inaccessible, we have had to rely mainly on specimens that were collected with different approaches, by different people, at different times (e.g., Frisone et al. 2014a; Frisone & Favaretto, 2017). Although in Lovara and Cengio dell'Orbo quarries there are various volcaniclastic horizons, only one horizon yielded sponges (see geological setting and Matteucci & Russo, 2005). In Museum collections only seldom the horizon is defined in the specimens' labels. For the purpose of the study, we selected collections that were clearly identified in the label as coming from the sponge horizon only. Thin sections, washings and smear slides from samples of Via Motti outcrop were prepared at the Università degli Studi di Padova. Eleven thin sections were analysed also with fluorescent light microscopy. Selected specimens of sponges were chosen for preparing 52 thin sections. The thin sections were studied with petrographic microscopes, under transmitted optical (Leica DM EP T and Zeiss Axiophot) and fluorescent (Leica 5000B) light, all at the Università degli Studi di Padova. At the end of 2013, clearing work resulted in the accumulation of debris from the Lovara and Cengio dell'Orbo quarries. Fossil sponges were visible on the surface of the debris heap, which was selected for a quantitative bulk surface sampling (Frisone et al., 2018). From 2014 to 2017 specimens appearing on the surface were randomly picked for one hour per sampling event. This prolonged sampling campaign allowed us to collect 365 additional sponge specimens that were studied by Frisone et al. (2018).

Associated macro- and micropaleontological content

Specimens from three Museum collections were used for the study of the associated fauna, named after their collectors: Berti (Museo di Storia Naturale di Venezia, Venice), Lovato (Museo di Archeologia e Scienze Naturali "G. Zannato", Montecchio Maggiore) and Rossi (Museo di Geologia e Paleontologia dell'Università degli Studi di Padova). All the studied specimens from these museum collections come from the sponge-bearing level at Cengio dell'Orbo quarry. Moreover, samples from Via Motti section, near Cengio dell'Orbo quarry (section acronym VFM) were collected to prepare ten washing residues and eleven smear slides.

Calcareous nannofossil biostratigraphy [C. Agnini]

For calcareous nannofossil analysis, raw sediments were processed to prepare standard smear slides (Bown & Young, 1998). A total of 12 samples from the Via Motti section were examined under a Zeiss light microscope at 1250× magnification. Calcareous nannofossils were determined using the taxonomy proposed by Aubry (1984, 1988, 1989, 1990, 1999) and Perch-Nielsen (1985). We adopted the zonal scheme of Agnini et al. (2014) for regional to global correlations.

Calcareous nannofossils are generally rare in the investigated samples and we thus decided to perform counts on a standardised area of 9 mm^2 (three traverses; modified after Backman & Shackleton, 1983) in order to check the presence of marker species.

Planktic foraminifera [V. Luciani]

Planktic foraminifera were analysed in washed residue (> 63 and < 500 µm fraction). A total of 11 samples from Via Motti section (VFM0 to VFM9 and VFM11) were observed under a stereoscopic microscope for planktic foraminiferal content. Planktic foraminifera were determined using the taxonomic criteria of Pearson et al. (2006). For the biostratigraphic attribution, we adopted the zonal scheme by Wade et al. (2011) with the modification proposed by Luciani & Giusberti (2014).

Crinoids [M. Roux & L. Giusberti]

Crinoids were picked up under the stereomicroscope from the residues of the > 500 µm fraction obtained from the tuffite horizon of Cengio dell'Orbo quarry (Lovato collection). Most of the specimens (more than one hundred ossicles) were obtained from the residues provisionally labelled as MCZ 1, 6 and 7. Preliminary observations were carried out under the stereomicroscope and SEM.

RESULTS

Sponge preservation

Sponge skeletons and spicules are replaced with calcite. The space between spicules is often partially filled by clotted peloidal micrite. A veil of micrite and peloidal micrite forms coatings around spicules (Fig. 3a). At least two cement generations grew on the spicular skeleton and on clotted peloidal micrite: a cloudy early cement is followed by a second generation of clear mosaic spar (Fig. 3b). Spicules and cement spar are not fluorescent, while the axial canals of spicules (when present) are slightly fluorescent. Clotted peloidal micrite is brightly fluorescent. Sometimes, a fluorescent thin veil was observed around spicules (Fig. 3d). Small (2-10 µm) pyrite crystals and framboids of pyrite are common and associated with clotted peloidal micrite of lithistid sponges (Fig. 3e). Generally, volcaniclastic grains are not observed in sponge spicules meshes and internal canals (that can be up to 1 mm) but only in the spongocoel, when present. This feature is observed both in hexactinellid (e.g., *Camerospongia visentinae* Frisone et al., 2016, *C.*

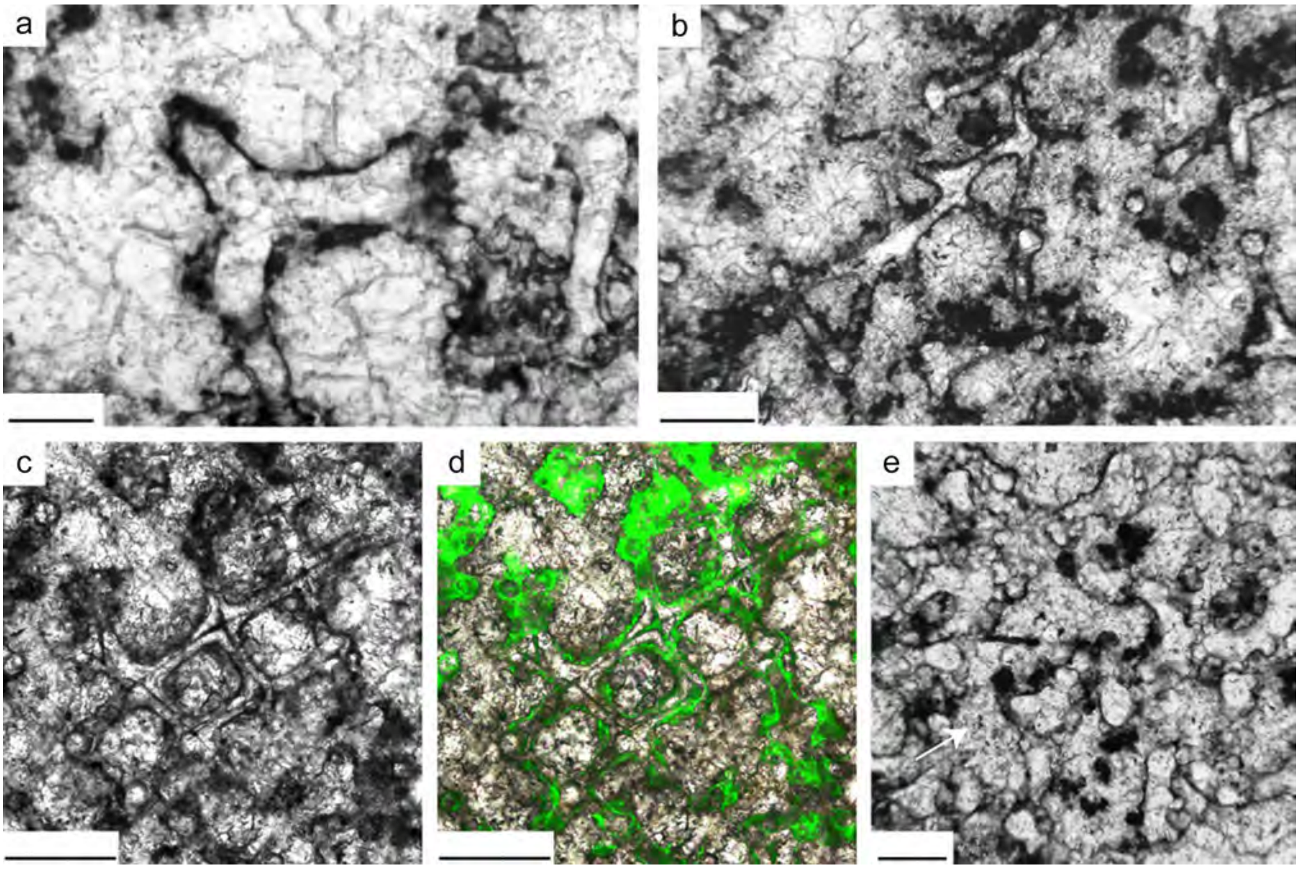

Fig. 3 - (color online) Thin sections of lithistid and hexactinellid sponges. a) Lithistid, with the space between spicules (desmas) partially filled by clotted peloidal micrite. A veil of micrite and peloidal micrite forms coatings around spicules (scale bar = 100 μm). b) Hexactinellid. Two cement generations grow on the spicular skeleton and on clotted peloidal micrite: a cloudy early cement and then a second generation of clear mosaic spar (scale bar = 200 μm). c-d) Hexactinellid sponge under optical (c) and fluorescent (d) light; in (d) spicules and cement sparite are not fluorescent while the infilling of axial canals of spicules is slightly fluorescent, and clotted peloidal micrite is bright fluorescent. There is also a fluorescent thin veil around spicules (scale bar = 200 μm). e) Lithistid sponges with small (2-10 μm) pyrite crystals and framboids (arrow) in association with clotted peloidal micrite (scale bar = 100 μm).

tuberculata Frisone et al., 2016, *Hexactinella clampensis* Frisone et al., 2016 and *Anomochone* sp.) and lithistid demosponges (e.g., ?*Rhoptrum* sp. and *Corallistes multiosculata* Frisone et al., 2016) (Fig. 4).

Associated macro- and micropaleontological content of the embedding sediment

The embedding sediment is a sandy tuffite composed of rounded volcanic fragments, skeletal grains and calcitic cement (Fig. 5). The volcanic clasts are strongly altered, with palagonitised glass in vesicles (Fig. 5a). Pteropods are common in the sediment and clearly associated with the sponges. The association of sponges with other faunal elements is less clear. In the Via Motti section, the sponge-bearing sediment is bioturbated and includes distinct ichnofossils.

Ichnofossils [P. Monaco]

The ichnofossils are cylindrical and have average diameter of ca. 4 mm (Fig. 6). They cross both the sponge body and the embedding sediment. They belong to *Ophiomorpha nodosa* Lundgren, 1891, a trace of burrowing crustaceans (mainly callianassids). This ichnospecies is very common in coastal sediments; it has a branched form and externally a peloidal structure, produced by the mucus of crustaceans to consolidate the tunnels. Peloids are concentrated only on the outer part of the trace, whereas the inside is smooth. *Ophiomorpha nodosa* develops in three dimensions, but often shows branched tunnels arranged horizontally or vertically, depending on the current regime and the amount of sands reaching in the coastal sea. *Ophiomorpha nodosa* prefers a high hydrodynamic regime and moderate sedimentation rates (e.g., Soria et al., 2014).

Crustaceans [A. De Angeli & C. Beschin]

Ten species of decapod crustaceans have been described so far from the sponge-bearing horizon in the Cengio dell'Orbo quarry (Beschin et al., 1988, 2016; De Angeli & Beschin, 2007): *Albunea cuisiana* Beschin & De Angeli, 1984, *Lessinipagurus boschettensis* Beschin et al., 2016 (Anomura), *Dromiopsis vicetinus* Beschin et al., 2016 (Dromioidea), *Antonioranina globosa* (Beschin et al., 1988), *Italianira punctulata* (Beschin et al., 1988), *Raniliformis ornata* De Angeli & Beschin, 2007, *Lophoranina marestiana*, *Notopoides exiguus* Beschin et al., 1988 (Raninoidea), *Liocarcinus priscus* Beschin et al., 2016 (Portunoidea), and *Palaeograpsus inflatus* Bittner, 1875 (Xanthoidea).

The decapods are generally three-dimensionally

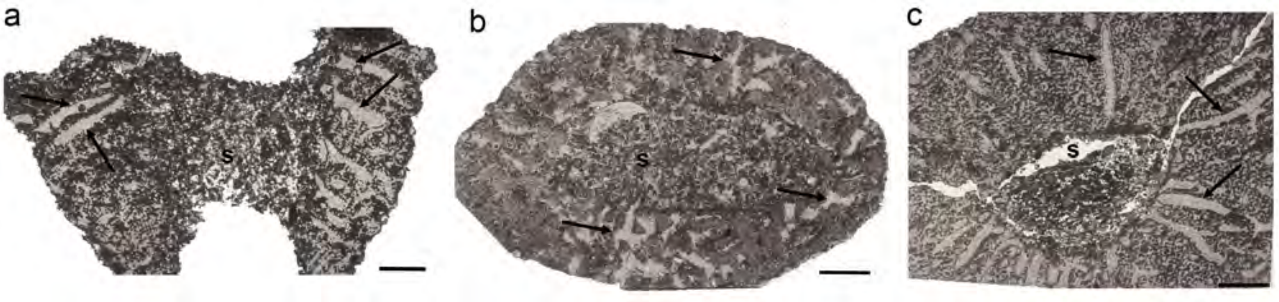

Fig. 4 - (color online) Thin sections showing specimens with large internal canals (arrows) devoid of sediment which is only observed in the spongocoel (s). a) Longitudinal thin section of *Camerospongia visentinae* MCZ-PAL 3712 with large radial canals. b) *Anomochone* sp. MCZ-PAL 3708 transverse thin section of a branch, with deep labyrinthine canals. c) ?*Rhoptrum* sp. MCZ-PAL 3742 transverse thin section showing large radial canals. Scale bars = 5 mm.

preserved and complete with appendages and ventral parts. They probably lived in the sediment like the extant Raninoidea (Bellwood, 2002). Other species, such as *Lessinipagurus boschettensis*, are hermit crabs of which only the claws have been found. None of the species described so far are compatible with the burrows of *Ophiomorpha nodosa* described above.

The crustacean *Lophoranina marestiana* that commonly occurs in the sponge horizon is related to the extant *Ranina ranina* (Linnaeus, 1758). This large "frog crab" lives in the subtidal zones of coasts of India, Indonesia, Vietnam, the Philippines, Hawaii and eastern Australia, hiding under the sediments (Baylon & Tito, 2012; Franţescu, 2013).

Pteropods [P. Mietto & E. Quaggiotto]

The sponge-bearing horizon in the Cengio dell'Orbo quarry is rich in pteropods (Fig. 7). In fact, the sedimentary matrix qualifies as a pteropod ooze. Pteropod shells are densely packed and found together with nautiloid larval shells, and yet unidentified micromollusks, resembling forms that currently live in circalittoral environments. From the micromollusks identified in the sponge matrix, the discovery of an undescribed species of *Thecopsella* Cossmann, 1888 (cf. Janssen, 2005) is noteworthy (MGP-PD 32335).

Whereas some pteropods could be identified at species level, other morphotypes are unknown from Paleogene sediments and largely represent new species.

Overall, there are at least 26 species-rank taxa, 13 of which belong to the Cavolinoidea and the remaining to the Limacinoidea (Tab. 1). Among the former there are nine new species, whereas among the latter five new species have been recognised so far. The Cengio dell'Orbo quarry pteropod assemblage has been recorded in other localities near Vicenza and consistently lies in the basal Lutetian (within the calcareous nannofossil Zone NP15; Beccaro, 2003). Although data are preliminary and poorly comparable with available literature, because of the presence of very little documented Praecuvierinidae and *Tibiella* Meyer, 1884 in Europe it seems that this assemblage shows greater affinity with those from North America than those from Central and Northern Europe.

Before the discovery of the Chiampo pteropods, the oldest known fossil pteropods from Italy were of Oligo-Miocene age (Bernasconi & Robba, 1982). In addition to the single Bayan (1870a) report, the discovery of pteropods in Eocene deposits in the Vicenza area (Beccaro et al., 2001; Beccaro, 2003), and, in particular, in the Alpone-Agno graben is of particular significance. There, pteropods occur in lower Eocene to lower Oligocene volcano-arenitic, volcanopelitic, tuffitic and marly-clayey sediments. They are very frequent locally in the Ypresian-Lutetian interval, sporadic in the Bartonian, completely absent in the Priabonian and rare in the Rupelian.

Other mollusks [S. Dominici]

The benthic mollusk assemblage coming from the sponge-bearing horizon of Cengio dell'Orbo (called "Boschetto di Chiampo" as in Beschin et al., 1991; Beccaro et al., 2001; Rossi collection, Box C13, MGP-PD) indicates a neritic environment. Gastropods other than pteropods include *Pterynotus tripteroides* (Lamarck, 1822), *Eoconus* sp., *Volutilithes* cf. *frederici* (Bayan, 1870b), *Siphonalia* sp. and Buccinoidea indet., all of which are carnivores, implying a complex base level trophic web. Co-occurring bivalves are *Astarte* sp. and *Barbatia* sp. *Volutilithes frederici* has been recorded from the Lutetian (Cossmann & Pissarro, 1910-1913) and the Priabonian (Piccoli & Savazzi, 1983), whereas *Pterynotus tripteroides* is typical of the Lutetian. A Lutetian age is consistent with the chronostratigraphic distribution of the other taxa.

Calcareous nannofossils [C. Agnini]

Samples are virtually barren of nannofossils, except for VFM2, VFM3 and VFM4, where calcareous nannofossils are sporadically occurring. Marker species defining biohorizons used in the standard zonations of Martini (1971) and Okada & Bukry (1980) are not present in the study samples. Nevertheless, the presence of two specimens of *Nannotetrina cristata* (Martini, 1958) Perch-Nielsen, 1971 and the absence of specimens ascribable to *Sphenolithus furcatolithoides* Locker, 1967 indicate that the investigated interval belongs to Zones CNE8-CNE9 of Agnini et al. (2014). This datum is likely correlative with the upper part of NP14-lower part of NP15 (Martini, 1971) and CP12b-lower part of CP13 (Okada & Bukry, 1980) and thus the study samples are of early Lutetian age. This result is consistent with that reported by Beccaro et al. (2001) and Matteucci & Russo (2005) for the sponge horizon.

Planktic foraminifera [V. Luciani]

Some of the samples analysed are barren of planktic foraminifera or contain extremely rare specimens (VFM2,

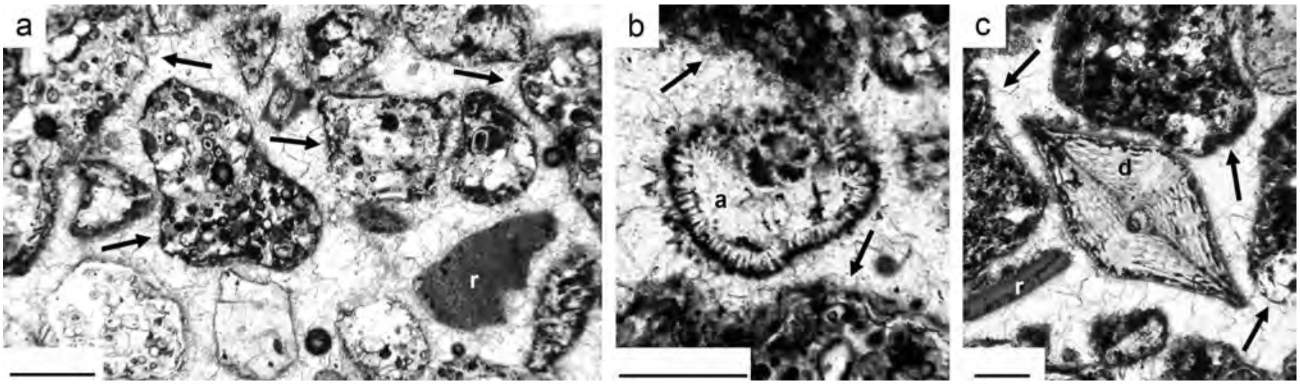

Fig. 5 - Thin sections of the tuffite surrounding the sponges. a) Rounded volcanic fragments (arrows), a red alga (r), and calcitic cement. The volcanic clasts are strongly altered, with palagonitised glass in vesicles. b) Volcanic clasts (arrows) and the planktic foraminifer *Acarinina* sp. (a). c) The larger foraminifer *Discocyclina* sp. (d), red algae fragment (r) and volcanic clasts (arrows). Scale bar = 200 µm.

VFM6, VFM7). Other samples (VFM0, VFM1, VFM3, VFM4, VFM5, VFM8, VFM9, VFM11) comprise similar assemblages that include: *Acarinina bullbrooki* (Bolli, 1957), *A. cuneicamerata* (Blow, 1979), *A. mcgowrani* Wade & Pearson, 2006, *A. pentacamerata* (Subbotina, 1947), *A. primitiva* (Finlay, 1947), *A. punctocarinata* Fleisher, 1974, *Morozovella aragonensis* (Nuttall, 1930), *Morozovelloides bandyi* (Fleisher, 1974), *M. coronatus* (Blow, 1979), *M. crassatus* (Cushman, 1925), *Parasubbotina inaequispira* (Subbotina, 1953), *Subbotina hagni* (Gohrbandt, 1967), *S. linaperta* (Finlay, 1939), *S. roesnaesensis* Olsson & Berggren, 2006, *S. senni* (Beckmann, 1953), and *Turborotalia frontosa* (Subbotina, 1953).

The occurrence of *Turborotalia frontosa* allows us to refer the samples analysed to the Zone E7b (Wade et al., 2011). The top of this zone was defined by Wade et al. (2011) based on the first appearance of *Guembelitroides nuttalli* (Hamilton, 1953). The latter species, however, proved to appear significantly earlier (Zone E5), albeit with rare specimens (rare occurrence) (Luciani & Giusberti, 2014), thus these authors proposed the common occurrence of *G. nuttalli* to identify the Lutetian Zone E8. The absence of this species in the study samples supports the attribution to Zone E7b. The base of *T. frontosa* is estimated to be ~ 550 kyr older than the primary event to identify the Ypresian/Lutetian boundary, that is the first appearance of calcareous nannofossil *Blackites inflatus* (Payros et al., 2009). Samples from Chiampo can be referred to the lower part of Lutetian Zone E7b, according to the calcareous nannofossil results.

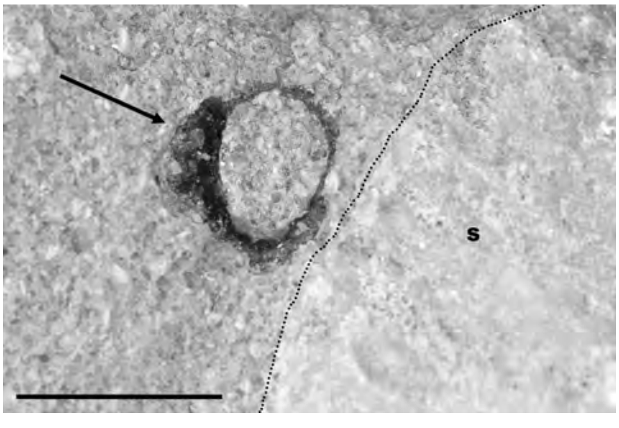

Fig. 6 - *Ophiomorpha nodosa* ichnofossils (arrow) crossing the embedding sediment near a hexactinellid sponge (s). Note the peloids concentrated at the margin of the burrow. Photo M. Bellanda. Scale bar = 1 cm.

Larger foraminifera [C.A. Papazzoni]

Abundant larger foraminifera were collected both in the Cengio dell'Orbo and the Lovara quarries. The material contains several isolated tests and some of them are naturally split, showing diagnostic equatorial sections. The preservation of the material is variable, sometimes excellent, with empty tests, sometimes with strongly recrystallised tests infilled by calcite. Moreover, even material from the same level is preserved with a variety of colors including reddish, greenish, and whitish gray. Some of the tests are badly broken or worn, suggesting transport and possibly in part reworking. The mixing of foraminifera coming from the shallow-water environment with pelagic elements such as pteropods and planktic foraminifera reinforces the case for resedimentation of this material. A preliminary survey of the larger foraminifera permitted to identify some index species, assigning both localities to the same biozones.

In the Via Motti outcrop, a sample from the base of the section (VFM 0) contains among others *Nummulites burdigalensis cantabricus* Schaub, 1981, *Assilina parva* (Douvillé, 1930), *Discocyclina pulcra pulcra* (Checchia-Rispoli, 1909), *Nemkovella strophiolata strophiolata* (Gümbel, 1870), and *Asterocyclina stellata adourensis* Less, 1987. This assemblage indicates the zones SB13 (higher part) to SB14 (Serra-Kiel et al., 1998), or the lower-middle Lutetian. The presence of *Nummulites burdigalensis cantabricus* should indicate the SB11 Zone, but the poor preservation of the material suggests reworking.

In the Lovara quarry the larger foraminiferal assemblage includes *Nummulites kugleri* Schaub, 1981, *N. maior* de la Harpe, 1883, *Assilina parva*, *Discocyclina pulcra pulcra*, *Nemkovella strophiolata strophiolata*, and *Orbitoclypeus varians angoumensis* Less, 1987. This assemblage also indicates zones SB13-SB14 (Serra-Kiel et al., 1998).

Corals [F.R. Bosellini]

Only two fragments of colonial scleractinian corals were observed in the studied collections, one ascribed

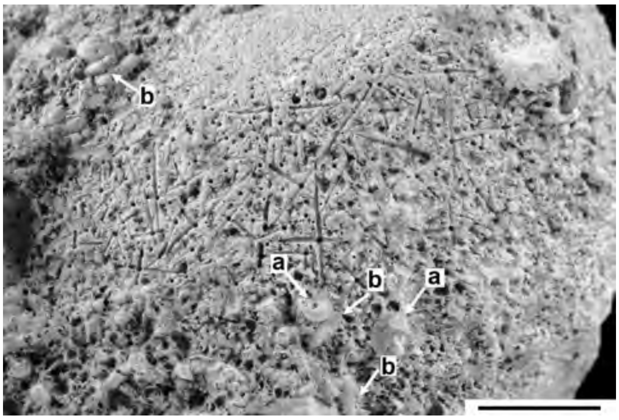

Fig. 7 - Detail of the external surface of the sponge *Stauractinella eocenica* Frisone et al., 2016 (IG-PD 366220) with imprints of pentactines spicules (dermalia). The sponge is associated with pteropods belonging to the Limacinidae (a) and Cuvierinidae (b). Photo S. Castelli. Scale bar = 1 cm.

to *Astrocoenia* sp. (Berti collection, Venice) and one to *Stylophora* sp. (MCZ-PAL 3739). These corals are inferred to have harbored photosymbionts, thus indicating a shallow water origin and transportation. The occurrence of the solitary coral *Heterocyathus* is also recorded from the Lovara quarry (Rossi collection, MGP-PD).

Crinoids [M. Roux & L. Giusberti]

The crinoid fauna from the Cengio dell'Orbo quarry (Lovato microfossil collection-MCZ-PAL) includes isocrinids, cyrtocrinids and rhizocrinids forming an exceptionally diverse fossil assemblage. Isocrinid stalk fragments consist of isolated thick columnals of small size displaying a diplocrinin-like articulation such as in ?*Isocrinus archiaci* (Pasotti, 1929). Cyrtocrinids are represented by several calyces and numerous brachials of *Holopus spileccense* (Schlüter, 1878) and one calyx of *Cyathidium* sp. Abundant small aboral cups with globulous basals and flared radials belong to yet undescribed cyrtocrinid taxa. Several small encrusting disks might be attributed to these taxa, which presumably had a short thin stalk. Rhizocrinid columnals and aboral cups of two species of *Conocrinus*, of which one has long interradial projections and is close to *C. veronensis* (Jaekel, 1891), and one species of *Paraconocrinus* are frequent.

Conocrinus and *Paraconocrinus* are well-known in the Eocene foreland basins of the Pyrenees and Alps (Roux et al., 2019), as well as isolated columnals of ?*Isocrinus archiaci* (Pasotti, 1929; Roux & Plaziat, 1978). *Holopus spileccense* is the single fossil species of the genus based on rare calyx described from the Spilecco Hill, near Bolca (Manni, 2005). In the reddish crinoidal facies of the Spilecco hills, rhizocrinid ossicles strongly predominate. The Cengio dell'Orbo site differs from other Eocene crinoidal assemblages in yielding three cyrtocrinid taxa represented by numerous ossicles, which are sometimes more frequent than rhizocrinid ones. Moreover, the assemblages include ossicles from different skeletal parts (attachment disks, columnals, calyces and brachials), frequently well-preserved despite some of them are fragile (*Holopus* brachials, interradial projections of *Conocrinus* radials). This suggests a rapid in situ burial without hydrodynamic selection of the different kinds of ossicles.

DISCUSSION

Sedimentary environment

The fossil content of the sponge-bearing tuffite horizon at Chiampo clearly represents a mixture of shallow and deep marine fauna. Some benthic elements (e.g., larger foraminifera and the rare fragments of colonial corals) are of shallow-water origin and have been likely transported into the deeper water environment where sponges were thriving. Some other benthic elements (e.g., decapod crustaceans, larger gastropods) are also of shallow water origin but do not show obvious evidence of transport. As an example, the crustacean *Lophoranina marestiana* is generally three-dimensionally preserved and complete with delicate appendages and ventral parts. Its association with the sponges is unclear.

The diverse crinoidal fauna suggests a heterogeneous seafloor. Rhizocrinids usually have branching roots penetrating soft sediment, whereas cyrtocrinids are attached on hard bottom by a distal stalk encrusting disk, or directly by the calyx base. Isocrinids frequently inhabit environments with irregular bottom including coarse sediment, pebbles and boulders (Tunnicliffe et al., 2016). Using the associated macrofauna and microfauna, Roux et al. (2006) evidenced that Eocene and extant stalked crinoids had about the same bathymetric distribution at depths greater than 100 m and similar ecophenotypic adaptive characters. In present seas, the shallowest known sites are 216 m for *Holopus* and 171 m for *Cyathidium* (Améziane et al., 1999). Dense *Holopus* populations were observed on vertical and overhanging walls at depths between 430 and 640 m in the Caribbean Sea (Syverson et al., 2015). A paleoenvironmental reconstruction based on a uniformitarian approach of the crinoid assemblage at Cengio dell'Orbo thus suggests a paleodepth greater than 170 m and likely more than 210 m.

Diversity analysis of random field sampling collections (Frisone et al., 2018) revealed that the sponge assemblage is dominated by hexactinellids. Using uniformitarian criteria, this suggests a water depth of more than 200 m. This interpretation is consistent with the paleodepth suggested by the crinoidal assemblage. The most common extant sponge taxa at Chiampo, e.g., *Laocoetis* (24.9% in bulk field sampling; Frisone et al., 2018) and *Hexactinella* Carter, 1885 (9.6%), inhabit rather deep water today. *Laocoetis perion* Lévi, 1986 is known from 250-750 m water depth in the Southern Indian Ocean (Lévi, 1986; Tabachnick & Lévi, 1997; Pisera & Tabachnick, 2014), whereas *Hexactinella* has a depth range of approximately 200-1200 m (Tabachnick, 1990; Reiswig et al., 2008; Reiswig & Kelly, 2011). The lyssacinosid *Stauractinella* is also expected to occur in this depth range. With a few exceptions, Recent lyssacinosids live in the bathyal or and even abyssal zone (e.g., Janussen et al., 2004; Van Soest et al., 2007; Janussen & Reiswig, 2009) and this environment is generally confirmed in the fossil record (among others e.g., Pisera & Busquets, 2002; Świerczewska-Gładysz & Jurkowska, 2013). Consistently, the abundant pteropods and planktic foraminifera in the sponge-bearing

Superfamilies	Families	Genera and species	Repository MGP-PD
Cavolinoidea	Creseidae	*Euchiloteca elegans* Harris, 1894	32336
		Creseis simplex (Meyer, 1886)	32337
		Creseis Rang, 1828 sp. indet.	28455
	Praecuvierinidae	*Texacuvierina gutta* Hodgkinson in Hodgkinson et al., 1992	32338
		Praecuvierina aff. *lura* Hodgkinson in Hodgkinson et al., 1992	32339
	Cuvierinidae	*Bucanoides* Hodgkinson in Hodgkinson et al., 1992 n. sp.	28456
		Ireneia Janssen, 1995 sp. indet.	28454
		Cuvierina Boas, 1886 (2 sp. indet.)	28458-28459
		Tibiella Meyer, 1884 (4 sp. indet.)	28460 to 28463
Limacinoidea	Limacinidae	*Altaspiratella multispira* (Curry, 1982)	32340
		Altaspiratella bearnensis (Curry, 1982)	32341
		Altaspiratella gracilens Hodgkinson in Hodgkinson et al., 1992	32342
		Currylimacina cossmanni (Curry, 1982)	32343
		Limacina angustana (Gardner, 1951)	32344
		Limacina davidi Hodgkinson in Hodgkinson et al., 1992	32345
		Limacina aff. *gormani* (Curry, 1982)	32346
		Limacina cf. *pygmaea* (Lamarck, 1805)	32347
		Limacina Bosc, 1817 (5 sp. indet.)	32348 to 32352

Tab. 1 - Preliminary composition of the pteropod fauna of Cengio dell'Orbo quarry, with reference to the systematics by Janssen (2012).

sediment indicate rather deep-water sedimentation. Our interpretation is at odds with the traditional interpretation of a shallow-water environment of Chiampo (e.g., Fabiani, 1915; De Zanche, 1965), and hence with the notion that the "sponge assemblages developed in a shallow-water paleoenvironments" (Matteucci & Russo, 2011, p. 34).

The material available for this study did not allow a sedimentological interpretation of the sedimentary environments: this work is mostly based on materials from previous collections, and the only available outcrop (Via Motti section) is too limited for a robust facies analysis. Nevertheless, previous works may be challenged in the light of the new data that have become available with the present study. The studied sites have been interpreted to represent an outer carbonate ramp (Beccaro et al., 2001) rather than a platform-reef-slope system, on the base of the faunal association dominated by foraminifera, and lacking reef-building organisms, except for the sponges. This interpretation accounts for the biotic association of both the "Nummulitic limestone" and the volcaniclastic horizons, which also both show evidence of reworking in debris and turbidity flows (Márton et al., 2011). The biotic association described here confirms this interpretation. The skeletal association of the "Nummulitic limestone" and of the tuffite horizons include abundant typical elements of Eocene Mediterranean, oligophotic middle ramps (e.g., Nebelsick et al., 2005), such as *Nummulites*, other larger foraminifera, and rhodoliths (Beccaro et al., 2001).

The occurrence of mass-transport deposits on a carbonate ramp depositional environment is not easy to explain. Such deposits should in fact not be easy to form on the gentle inclinations of a carbonate ramp. In such depositional systems, the mixing of shallow-water and deeper-water elements may be expected offshore of the middle ramp, especially for ramps that are distally steepened. There, the ramp may achieve a sufficient inclination to trigger mass-transport processes (e.g., Mateu-Vicens et al., 2008). Furthermore, it cannot be excluded that reworked shallow-water sediment (i.e., sediment bearing abraded corals, red algae and larger foraminifera) may have originated outside of the Alpone-Agno graben, west of the Castelvero fault or at the footwall of other similar normal faults, and its deposition was triggered at the scarp of these active faults.

We thus propose the following paleoenvironmental setting for the sponge assemblage: 1) the setting was the distal, oligophotic to aphotic part of a distally steepened carbonate ramp (see also Beccaro et al., 2001; Márton et al., 2011); 2) the shallow-water fauna observed in the sponge-bearing horizon has been transported from the inner and middle ramp, or from outside the area of the Alpone-Agno graben, and redeposited in an outer ramp environment at substantially greater depths. Overall, heterogeneous substrate conditions are suggested both by sponges and crinoids. The occurrence of the trace fossil *Ophiomorpha nodosa* at Via Motti, usually interpreted as diagnostic for a high-energy, shallow waters, requires further investigation. Rapid sea-level changes, due to regional tectonics, may explain the close association of deep-water and shallow water tracers.

Taphonomy of Chiampo sponge fauna

There is evidence that the fossilisation process of the sponges of Chiampo involved bacterial activity. During early diagenesis, the precipitation of pyrite and peloidal micrite within the body of sponges could have been induced by the activity of sulfate reducing bacteria. The clotted peloidal carbonates are strongly fluorescent under UV light, and as UV fluorescence is induced mostly by unsaturated organic compounds, the fluorescence implies that organic matter has been incorporated during the precipitation of carbonate, possibly within a biofilm, and it is thus a microbial carbonate. The idea

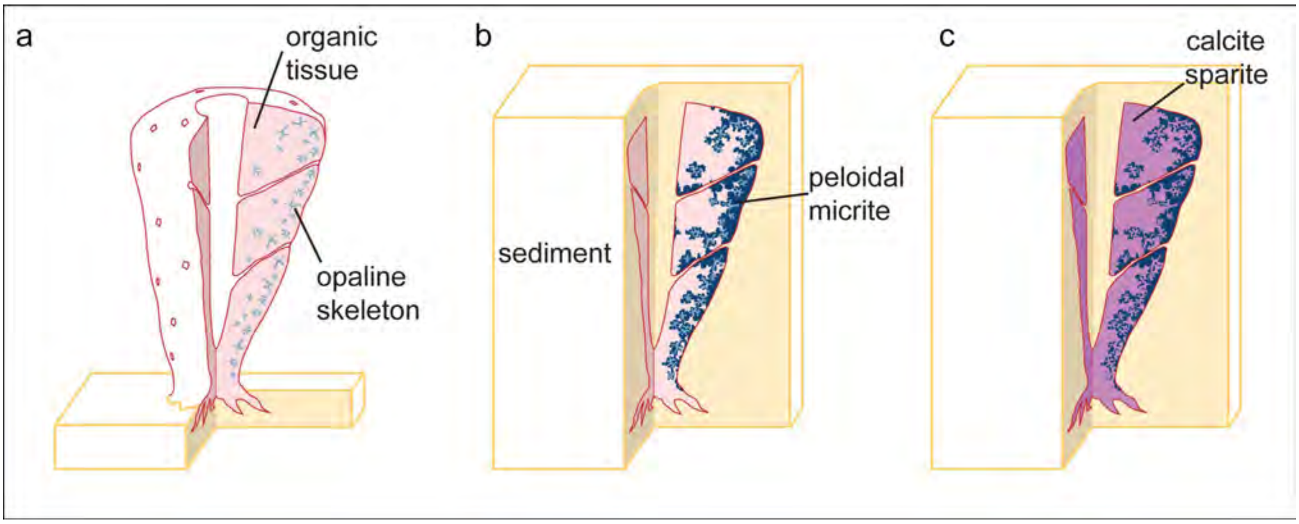

Fig. 8 - (color online) Schematic representation of taphonomic and diagenetic events (sponge anatomy is simplified). a) The living demosponge had an opaline skeleton and organic tissue. b) The sponge was buried very quickly by volcaniclastic sediments. Partial calcification of decaying tissue by sulfate-reducing bacteria produced clotted peloidal micrite. c) Complete solution of opaline skeleton and filling of interspicular and spicular voids by sparry calcite.

that micrite formation in sponges may be induced by microbial communities is widespread in the literature (e.g., Narbonne & Dixon, 1984; Brachert et al., 1987; Reitner, 1993; Warkne, 1995; Buckeridge et al., 2013). Calcification occurs within those portions of the sponge that are buried in the sediment and it is an in-vivo to early post-mortem process (Brachert, 1991; Neuweiler et al., 2007). Gaillard (1983) provided a scheme of this diagenetic process with different preservational stages. In the Upper Jurassic epicontinental limestones of central Europe sponges are preserved as calcareous "mummies", where the entire specimens were preserved by very early precipitation of micrite by bacteria associated with decaying sponges (e.g., Brachert, 1991; Keupp et al., 1993; Pisera, 1997; Leinfelder, 2001). The Chiampo sponges seem to differ from calcareous "mummies" mainly because in the Chiampo sponge bodies the voids among spicules are mostly filled by sparite instead of micrite. Clotted peloidal micrite is present in the Chiampo sponges but not as abundantly as in Jurassic sponges. However, the microbial metabolisation of soft tissues of sponges seems to have been important for preservation in the studied case: spicules are only recognisable in thin section because they are coated by a thin veil of fluorescent micrite. This micrite is locally in continuity with patches of fluorescent clotted peloidal micrite and is thus most probably the product of microbial anaerobic metabolisation of the sponge soft tissue.

Preservation like that of the Chiampo sponges has been often reported, for example from the Eocene of Spain (Astibia et al., 2014) and New Zealand (Buckeridge et al., 2013). Other examples are from the Upper Cretaceous: hexactinellids from Ukraine (Świerczewska-Gładysz & Olszewska-Nejbert, 2013) and demosponges from Denmark (Madsen & Stemmerik, 2009). Bacteria could have also contributed to volcanic glass alteration. Palagonite is the first stable product of aquatic mafic glass alteration. Stroncik & Schminke (2002) reported that microbial activity enhances the rate of dissolution of volcanic glass by creating a local microenvironment as a result of the fluids of their metabolic products.

The fact than generally no sediment was found inside the sponge canals suggests that the sponges were buried alive, with their organic tissue still covering them. The presence of organisms testifying to different water depths in the embedding sediment (e.g., planktic and larger foraminifera together) is an evidence of resedimentation and confirms the facies analysis of Beccaro et al. (2001): the volcaniclastics of Lovara and Cengio dell'Orbo quarries were probably resedimented within the outer part of a carbonate ramp.

Based on the above observations, the following model of the taphonomic and diagenetic sequence can be proposed (Fig. 8):

1. The sponges are largely preserved in growth position (evidence documented in Frisone et al., 2016: delicate encrusting base, various ontogenetic stages, sponge clusters).

2. The sponges were rapidly buried alive, possibly by a gentle subaqueous volcaniclastic sediment flow (evidence: volcanic glass, no sediment in the sponges interspicular space and canals, mixed associated macro-micropaleontological content, siliceous membrane preserved in some specimens; this study and Frisone et al., 2016).

Partial calcification of decaying tissue by sulfate-reducing bacteria (evidences: clotted peloidal micrite, pyrite) occurred immediately after burial.

3. Complete dissolution of opaline skeletons, filling of interspicular and spicular voids by calcite sparite during burial.

CONCLUSIONS

Our work confirms the hypothesis that the Chiampo sponge assemblage was buried alive, at a water depth greater than 200 m and fossilised in situ. The fossilisation of the sponges involved bacterial activity during early diagenesis calcification. We provide evidence that the associated fossils of the embedding sediment represent a mixture of shallow and deep marine fauna. Some benthic elements (corals, larger foraminifera) are of shallow-water origin and have been resedimented into the deeper water habitat of sponges and crinoids. Some other benthic elements (e.g., the decapod crustacean *Lophoranina marestiana*) are also of shallow water origin but do not show evidence of transport. Their association with the sponges is unclear. Pteropods and planktic foraminifera in background sediment indicate deep-water hemipelagic sedimentation whereas trace fossils suggest high-energy environments. Although further studies are needed to explain these controversial observations, we propose that rapid sea-level changes, due to regional tectonics, best explain all our findings.

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REFERENCES

Agnini C., Fornaciari E., Raffi I., Catanzariti R., Pälike H., Backman J. & Rio D. (2014). Biozonation and biochronology of Paleogene calcareous nannofossils from low and middle latitudes. *Newsletters on Stratigraphy*, 47: 131-181.

Améziane N., Bourseau J.P., Heinzeller T. & Roux M. (1999). Les genres *Cyathidium* et *Holopus* au sein des Cyrtocrinida (Crinoidea; Echinodermata). *Journal of Natural History*, 33: 439-470.

Ancona L. (1966). Esemplari di *Ranina* (Decapodi, Brachiuri) eccezionalmente ben conservati nell’Eocene medio della Valle del Chiampo (Vicenza). *Memorie del Museo Civico di Storia Naturale di Verona*, 14: 401-408.

Astibia H., Elorza J., Pisera A., Álvarez-Pérez G., Payros A. & Ortiz S. (2014). Sponges and corals from the Middle Eocene (Bartonian) marly formations of the Pamplona Basin (Navarre, western Pyrenees): taphonomy, taxonomy, and paleoenvironments. *Facies*, 60: 91-110.

Aubry M.P. (1984). Handbook of Cenozoic Calcareous Nannoplankton, Book 1, Ortholithae (Discoaster). 263 pp. American Museum of Natural History, Micropaleontology Press, New York.

Aubry M.P. (1988). Handbook of Cenozoic Calcareous Nannoplankton, Book 2, Ortholithae (Holococcoliths, Ceratoliths, Ortholiths and Other). 279 pp. American Museum of Natural History, Micropaleontology Press, New York.

Aubry M.P. (1989). Handbook of Cenozoic Calcareous Nannoplankton, Book 3, Ortholithae (Pentaliths and Other), Heliolithae (Fasciculiths, Sphenoliths and Others). 279 pp. American Museum of Natural History, Micropaleontology Press, New York.

Aubry M.P. (1990). Handbook of Cenozoic Calcareous Nannoplankton, Book 4, Heliolithae (Helicoliths, Cribriliths, Lopadoliths and Other). 381 pp. American Museum of Natural History, Micropaleontology Press, New York.

Aubry M.P. (1999). Handbook of Cenozoic Calcareous Nannoplankton, Book 5, Heliolithae (Zygoliths and Rhabdoliths). 368 pp. American Museum of Natural History, Micropaleontology Press, New York.

Backman J. &. Shackleton N.J. (1983). Quantitative biochronology of Pliocene and early Pleistocene calcareous nannoplankton from the Atlantic, Indian and Pacific Oceans. *Marine Micropaleontology*, 8: 141-170.

Barbieri G., De Zanche V., Medizza F. & Sedea R. (1982). Considerazioni sul vulcanismo terziario del Veneto occidentale e del Trentino meridionale. *Rendiconti della Società Geologica Italiana*, 4: 267-270.

Barbieri G., De Zanche V. & Sedea R. (1991). Vulcanesimo paleogenico ed evoluzione del semigraben Alpone-Agno (Monti Lessini). *Rendiconti della Società Geologica Italiana,* 14: 5-12.

Barbieri G. & Zampieri D. (1992). Deformazioni sinsedimentarie eoceniche con stile a domino e relativo campo di paleostress (Monti Lessini). *Atti Ticinensi di Scienze della Terra*, 35: 25-31.

Bassi D., Bianchini G., Mietto P. & Nebelsick J.H. (2008). Southern Alps in Italy: Venetian Pre-Alps. *In* McCann T. (ed.), The Geology of Central Europe. Volume 2, Mesozoic and Cenozoic. The Geological Society, London: 1087-1092.

Bassi D., Nebelsick J.H., Puga-Bernabéu Á. & Luciani V. (2013). Middle Eocene *Nummulites* and their offshore re-deposition: A case study from the Middle Eocene of the Venetian area, northeastern Italy. *Sedimentary Geology*, 297: 1-15.

Bayan F. (1870a). Sur les terrains tertiaires de la Vénétie. *Bulletin de la Société géologique de France*, (2), 27: 444-500.

Bayan F. (1870b). Études faites la collection de l’École des Mines sur des fossiles nouveaux ou mal connus. *Fascicule I. Mollusques Tertiaires*. 81 pp. F. Savy, Paris.

Baylon J.C. & Tito O.D. (2012). Natural diet and feeding habits of the red frog crab (*Ranina ranina*) from southwestern Mindanao, Philippines. *Philippine Agricultural Scientist*, 95: 391-398.

Beccaro L. (2003). Revisioni stratigrafiche nel Paleogene del Veneto. Unpublished Ph.D. Thesis, A.A. 2002-2003. 200 pp. Università degli Studi di Padova.

Beccaro L., Fornaciari E., Mietto P. & Preto N. (2001). Analisi di facies e ricostruzione paleoambientale dei ‘Calcari nummulitici’ (Eocene; Monti Lessini orientali–Vicenza): dati preliminari. *Studi Tridentini di Scienze Naturali–Acta Geologica,* 76 (1999): 3-16.

Beckmann J.P. (1953). Die Foraminiferen der Oceanic Formation (Eocaen-Oligocaen) von Barbados, Kl. Antillen. *Eclogae geologicae Helvetiae*, 46: 301-412.

Bellwood O. (2002). The occurrence, mechanics and significance of burying behaviour in crabs (Crustacea; Brachyura). *Journal of Natural History*, 36: 1223-1238.

Bernasconi M.P. & Robba E. (1982). The Thecosomatous Pteropods: a contribution toward the Cenozoic Tethyan paleobiogeography. *Bollettino della Società Paleontologica Italiana*, 21: 211-222.

Beschin C., Busulini A., De Angeli A. & Tessier G. (1988). Raninidae del Terziario berico-lessineo (Italia settentrionale). *Lavori Società Veneziana di Scienze Naturali*, 13: 155-215.

Beschin C., Busulini A., De Angeli A., Tessier G. & Ungaro S. (1991). Due nuovi generi di Raninidae dell'Eocene del Veneto (Italia). *Lavori Società Veneziana di Scienze Naturali*, 16: 187-212.

Beschin C. & De Angeli A. (1984). Nuove forme di Anomura Hippidea: *Albunea cuisiana* sp. n. e *Albunea lutetiana* sp. n. *Lavori Società Veneziana di Scienze Naturali*, 9: 93-105.

Beschin C., De Angeli A., Checchi A. & Zarantonello G. (2016). Crostacei decapodi del "tufo a *Lophoranina*" (Luteziano inferiore) della Valle del Chiampo (Vicenza - Italia settentrionale). 92 pp. Museo di Archeologia e Scienze Naturali "G. Zannato", Montecchio Maggiore (Vicenza).

Bittner A. (1875). Die Brachyuren des Vicentinischen Tertiärgebirges. *Denkschriften der kaiserlichen Akademie der Wissenschaften in Wien*, 34: 63-106.

Blow W.H. (1979). The Cainozoic Globigerinida. 3 vols. 1413 pp. E.J. Brill, Leiden.

Boas J.E.V. (1886). Spolia Atlantica. Bidtrag til Pteropodernes. Morfology og Systematik samt til Kundskaben om deres geografiske Udbredelse. *Kongelige Danske Videnskabernes-Selskabs Skrifter, Naturvidenskabelig og Mathematisk Afdeling*, 4/1: 1-231.

Bolli H.M. (1957). The genera *Globigerina* and *Globorotalia* in the Paleocene-Lower Eocene Lizard Springs Formation of Trinidad, B.W.I. *United States National Museum Bulletin*, 215: 61-81.

Bosc L.A.H. (1817). Limacine. Limacina. *Nouveau dictionaire d'histoire naturelle appliquée aux arts, à l'agriculture, à l'economie rurale et domestique, à la médicine, etc.*, 18: 42-43.

Bosellini A. (1989). Dynamics of Tethyan carbonate platforms. *In* Crevello P.D., Wilson J.L., Sarg J.F. & Read J.F. (eds), Controls on Carbonate Platform and Basin Development. *SEPM Special Publication*, 44: 3-13.

Bosellini F.R. & Papazzoni C.A. (2003). Palaeoecological significance of coral-encrusting foraminiferan associations: A case-study from the Upper Eocene of northern Italy. *Acta Palaeontologica Polonica*, 48: 279-292.

Bown P.R. & Young J.R. (1998). Techniques. *In* Bown P.R. (ed.), Calcareous Nannofossil Biostratigraphy. Chapman & Hall, London: 16-28.

Brachert T.C. (1991). Environmental control on fossilization of siliceous sponge assemblage: A proposal. *In* Reitner J. & Keupp H. (eds), Fossil and Recent Sponges. Springer-Verlag: 543-553.

Brachert T.C., Dullo W.C. & Stoffers P. (1987). Diagenesis of siliceous sponge limestones from the Pleistocene of the Tyrrhenian Sea (Mediterranean Sea). *Facies*, 17: 41-49.

Buckeridge J.S., Kelly M., Janussen D. & Reiswig H.M. (2013). New Palaeogene sponges from the Red Bluff Tuff, Chatham Island, New Zealand. *New Zealand Journal of Geology and Geophysics*, 56: 171-185.

Checchia-Rispoli G. (1909). La serie nummulitica dei dintorni di Termini Imerese. II. La regione Cacasacco. *Giornale di Scienze Naturali ed Economiche*, 27: 177-207.

Cossmann A. (1888). Catalogue illustré des coquilles fossiles de l'Eocène des environs de Paris. *Annales de la Societé Royale de Malacologie de Belgique*, 23: 3-328.

Cossmann M. & Pissarro G. (1910-1913). Iconographie complète des coquilles fossiles de l'Eocène des environs de Paris. Tome 2e, Scaphopodes, Gastropodes, Brachiopodes et Supplement. Hermann, Paris.

Curry D. (1982). Ptéropodes éocènes de la tuilerie de Gan (Pyrénées-Atlantiques) et de quelques autres localiteés du SW de la France. *Cahiers de Micropaléontologie*, 4 (1981): 35-44.

Cushman J.A. (1925). Some new foraminifera from the Velasco Shale of Mexico. *Contributions from the Cushman Laboratory for Foraminiferal Research*, 1: 18-23.

De Angeli A. & Beschin C. (2007). I crostacei Notopodinae (Brachyura, Raninidae) del Terziario del Vicentino. *Studi e Ricerche, Associazione Amici del Museo, Museo Civico "G. Zannato", Montecchio Maggiore (Vicenza)*, 14: 25-42.

De Angeli A. & Beschin C. (2010). *Lovaracarcinus granulatus* gen. nov., sp. nov., nuovo brachiuro eocenico della Valle del Chiampo (Vicenza – Italia settentrionale). *Studi e Ricerche, Associazione Amici del Museo, Museo Civico* "G. Zannato"*, Montecchio Maggiore (Vicenza)*, 17: 29-34.

De Angeli A. & Garassino A. (2006). Catalog and bibliography of the fossil Stomatopoda and Decapoda from Italy. *Memorie Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, 35: 1-95.

De Vecchi G.P. & Sedea R. (1995). The Paleogene basalts of the Veneto Region (NE Italy). *Memorie di Scienze Geologiche*, 47: 253-274.

De Zanche V. (1965). Le microfacies eoceniche nella Valle del Chiampo tra Arzignano e Mussolino (Lessini orientali). *Rivista Italiana di Paleontologia e Stratigrafia*, 71: 925-948.

Douvillé H. (1930). L'Éocène du Béarn; Appendice I – Description de la faune de Biron. *Bulletin de la Société géologique de France,* (4), 29: 351-383.

Fabiani R. (1915). Il Paleogene del Veneto. *Memorie dell'Istituto di Geologia della Regia Università di Padova*, 3: 1-336.

Feuda R., Dohrmann M., Pett W., Hervé P., Rota-Stabelli O., Lartillot, N., Wörheide G. & Pisani D. (2017). Improved modeling of compositional heterogeneity supports sponges as sister to all other animals. *Current Biology,* 27: 3864-3870.

Finlay H.J. (1939). New Zealand foraminifera: key species in stratigraphy. No 2. *Transactions of the Royal Proceedings Society of New Zealand,* 69: 89-128.

Finlay H.J. (1947). New Zealand foraminifera: key species in stratigraphy. *New Zealand Journal of Science and Technology*, 5, section B, 28: 259-292.

Fleisher R.L. (1974). Cenozoic planktonic foraminifera and biostratigraphy. Arabian Sea, Deep Sea Drilling Project, Leg 23A. *In* R.B. Whitmarsh et al. (eds), *Initial Report DSDP*, 23: 1001-1072.

Fornasiero M. & Vicariotto M. (1997). A new species of *Spirulirostra* (Cephalopoda, Coleoidea) from the Venetian Middle Eocene (Italy). *Memorie di Scienze Geologiche*, 49: 65-72.

Franțescu A.L. (2013). Comparative study of the Eocene fossil decapod crustaceans of the north American Atlantic Coast and European Tethyan provinces. 668 pp. Ph.D. Thesis, Kent State University, Kent, Ohio.

Frisone V. & De Angeli A. (2017). New record of the lithistid demosponge *Moretispongia pyriformis* (Pomel, 1872) from the Middle Eocene of north-eastern Italy (Chiampo, Vicenza, Lessini Mountains). *Studi e Ricerche, Associazione Amici del Museo, Museo Civico "G. Zannato"*, 24: 18-22.

Frisone V. & Favaretto B. (2017). Le collezioni di spugne fossili della Valle del Chiampo (Vicenza) conservate presso il Museo di Storia Naturale di Venezia. *Bollettino del Museo di Storia Naturale di Venezia*, 67: 125-136.

Frisone V., Fornasiero M., Mietto P. & Preto N. (2014a). "Sponge connection": studio di un'enigmatica fauna a spugne fossili. *Museologia Scientifica Memorie*, 11: 197-200.

Frisone V., Pisera A., Hajdu E., Preto N., Zorzi F. & Zorzin R. (2014b). Isolated spicules of Demospongiae from Mt. Duello (Eocene, Lessini Mts., northern Italy): preservation, taxonomy, and depositional environment. *Facies*, 60: 883-904.

Frisone V., Pisera A. & Preto N. (2016). A highly diverse siliceous sponge fauna (Porifera: Hexactinellida, Demospongiae) from the Eocene of northeastern Italy: systematics and palaeoecology. *Journal of Systematic Palaeontology*, 14: 949-1002.

Frisone V., Pisera A., Preto N. & Kiessling W. (2018). Biodiversity of museum and bulk field samples compared: The Eocene Chiampo sponge fauna, Lessini Mountains, Italy. *Acta Palaeontologica Polonica*, 63: 795-805.

Gaillard C. (1983). Les biohermes à spongiaires et leur environment dans l'Oxfordien du Jura Méridional. *Documents des Laboratoires de Géologie de Lyon,* 90: 1-515.

Gardner J. (1951). Two new guide fossils from the Tallahatta formation of the Southeastern States. *Journal of the Washington Academy of Sciences,* 41: 8-12.

Gohrbandt K.H.A. (1967). Some new planktonic foraminiferal species from the Austrian Eocene. *Micropaleontology*, 13: 319-326.

Gümbel C.W. (1870). Beiträge zur Foraminiferenfauna der nordalpinen, älteren Eocängebilde oder der Kressenberger Nummulitenschichten. *Abhandlungen der königlich bayerischen Akademie der Wissenschaften, Mathematisch-Physikalische Classe*, 10: 581-730.

Harpe P. de la (1883). Étude des Nummulites de la Suisse et révision des espèces éocènes des genres *Nummulites* et *Assilina*. Troisième et dernière partie (posthume). *Mémoires de la Société Paléontologique Suisse*, 10: 141-180.

Harris G.F. (1894). On the discovery of a pteropod in British Eocene strata, with a description of a new species. *Proceedings of the Malacological Society of London*, 1: 60-61.

Hodgkinson K.A., Garvie C.L. & Bé A.W.H. (1992). Eocene euthecosomatous Pteropoda (Gastropoda) of the Gulf and Eastern Coasts of North America. *Bulletins of American Paleontology*, 103: 1-62.

Jaekel O. (1891). Ueber Holopocriniden mit besonderer Berücksichtigung der Stramberger Formen. *Zeitschrift der Deutschen geologischen Gesellschaft*, 43: 557-670.

Janssen A.W. (1995). Systematic revision of holoplanktonic Mollusca in the collections of the "Dipartimento di Scienze della Terra" of Torino, Italy. *Museo Regionale di Scienze Naturali, Torino, Monografie*, 17: 1-233.

Janssen A.W. (2005). Development of Cuvierinidae (Mollusca, Euthecosomata, Cavolinioidea) during the Cainozoic: a non-cladistic approach with a re-interpretation of Recent taxa. *Basteria*, 69: 25-72.

Janssen A.W. (2012). Late Quaternary to Recent holoplanktonic Mollusca (Gastropoda) from bottom samples of the eastern Mediterranean Sea: systematics, morphology. *Bollettino Malacologico*, 68: 1-105.

Janussen D. & Reiswig H.M. (2009). Hexactinellida (Porifera) from the ANDEEP III Expedition to the Weddell Sea, Antarctica. *Zootaxa*, 2136: 1-20.

Janussen D., Tabachnick K.R. & Tendal O.S. (2004). Deep-sea Hexactinellida (Porifera) of the Weddell Sea. *Deep Sea Research Part II: Topical Studies in Oceanography*, 51: 1857-1882.

Keupp H., Jenisch A., Herrmann R., Neuweiler F. & Reitner J. (1993). Microbial carbonate crusts–a key to the environmental analysis of fossil spongiolites? *Facies*, 29: 41-54.

König C. (1825). Icones Fossilium Sectiles; Centuria Prima. 4 pp. G.B. Sowerby, London.

Lamarck J.-B.P.A. de (1804-1806). Mémoires sur les fossiles des environs de Paris, comprenant la détermination des espèces qui appartiennent aux animaux marins sans vertèbres, et dont la plupart sont figurées dans la collection des vélins du Muséum. *Annales du Muséum national de Histoire Naturelle*, 5: 28-36, 91-98, 179-188, 237-245, 349-357.

Lamarck J.-B.P.A. de (1822). Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent; précédée d'une introduction offrant la détermination des caractères essentiels de l'animal, sa distinction du végétal et des autres corps naturels; enfin, l'exposition des principes fondamentaux de la zoologie, 7. 711 pp. Guiraudet, Paris.

Leinfelder R.R. (2001). Jurassic reef ecosystems. *In* Stanley G.D. Jr (ed.), The History and Sedimentology of Ancient Reef Systems. Kluwer Academic/Plenum Publishers: 251-309.

Less G. (1987). Paleontology and stratigraphy of the European Orthophragminae. *Geologica Hungarica,* (*series Palaeontologica*), 51: 1-373.

Lévi C. (1986). *Laocoetis perion* nov. sp., Spongiaire Hexactinellide Craticulariidae de l'océan Indien. *Bulletin du Muséum National d'Histoire Naturelle de Paris*, *Section* A, *Zoologie, biologie et écologie animales,* 8: 437-442.

Linnaeus C. (1758). Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. 824 pp. Laurentii Salvii, Holmiae (Stockholm).

Locker S. (1967). Neue Coccolithophoriden (Flagellata) aus dem Alttertiär Norddeutschlands. *Geologie*, 6: 361-365.

Luciani V. & Giusberti L. (2014). Reassessment of the early–middle Eocene planktic foraminiferal biomagnetochronology: New evidence from the Tethyan Possagno section (NE Italy) and Western North Atlantic Ocean ODP site 1051. *Journal of Foraminiferal Research*, 44: 187-201.

Lundgren B. (1891). Studier öfver fossilförande lösa block. *Geologiska Föreningen i Stockholm Förhandlingar*, 13: 111-121.

Madsen H.B. & Stemmerik L. (2009). Early diagenetic celestite replacement of demosponges in Upper Cretaceous (Campanian–Maastrichtian) chalk, Stevns, Denmark. *Geology,* 37: 355-358.

Manni R. (2005). The non-isocrinid crinoids of the Michelotti Collection. *Bollettino della Società Paleontologica Italiana*, 44: 211-218.

Martini E. (1958). Discoasteriden und verwandte Formen im NW-deutschen Eozän (Coccolithophorida). 1. Taxonomische Untersuchungen. *Senckenbergiana Lethaea*, 39: 353-388.

Martini E. (1971). Standard Tertiary and Quaternary calcareous nannoplankton zonation. *In* Farinacci A. (ed.), Proceedings of the 2nd Planktonic Conference. Tecnoscienza, Roma, 2: 739-785.

Márton E., Zampieri D., Kázmér M., Dunkl I. & Frisch W. (2011). New Paleocene–Eocene paleomagnetic results from the foreland of the Southern Alps confirm decoupling of stable Adria from the African plate. *Tectonophysics*, 50: 89-99.

Mateu-Vicens G., Hallock P. & Brandano M. (2008). A depositional model and paleoecological reconstruction of the lower Tortonian distally steepened ramp of Menorca (Balearic Islands, Spain). *Palaios*, 23: 465-481.

Matteucci R. & Russo A. (2005). The Middle Eocene siliceous sponges from Val di Chiampo (Lessini Mountains, northern Italy). Annali dell'Università di Ferrara, *Sezione Museologia Scientifica e Naturalistica, Volume speciale*: 51-62.

Matteucci R. & Russo A. (2011). The Italian Cenozoic siliceous sponges: a review, with a revision of the Catullo (1856) collection. *Journal of Mediterranean Earth Sciences*, 3: 33-43.

Menin A. (1972). Silicosponge dell'Eocene medio della Valle del Chiampo (M. Lessini, Vicenza). *Annali dell'Università di Ferrara (nuova serie), Scienze Geologiche e Paleontologiche*, 5: 63-69.

Meyer O. (1884). Notes on Tertiary shells. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 36: 104-112.

Meyer O. (1886). Contributions to the Eocene Paleontology of Alabama and Mississippi. *Geological Survey of Alabama Bulletin*, 1: 61-85.

Muir L.A., Botting J.P. & Beresi M.S. (2017). Lessons from the past: Sponges and the geological record. *In* Carballo J.L. & Bell J.J. (eds), Climate Change, Ocean Acidification and Sponges. Springer International Publishing: 13-47.

Narbonne G.M. & Dixon O.A. (1984). Upper Silurian lithistid sponge reefs on Somerset Island, Arctic Canada. *Sedimentology*, 31: 25-50.

Nebelsick J.H., Rasser M. & Bassi D. (2005). Facies dynamics in Eocene to Oligocene circumalpine carbonates. *Facies*, 51: 197-216.

Neuweiler F., Daoust I., Bourque P.A. & Burdige D.J. (2007). Degradative calcification of a modern siliceous sponge from the Great Bahama Bank, the Bahamas: A guide for interpretation of ancient sponge-bearing limestones. *Journal of Sedimentary Research*, 77: 552-563.

Nuttall W.L.F. (1930). Eocene Foraminifera from Mexico. *Journal of Paleontology*, 4: 271-293.

Okada H. & Bukry D. (1980). Supplementary modification and introduction of code numbers to the low-latitude coccolith biostratigraphic zonation (Bukry, 1973; 1975). *Marine Micropaleontology*, 5: 321-325.

Olsson R.K. & Berggren W.A. (2006). Taxonomy, biostratigraphy, and phylogeny of Eocene *Globigerina*, *Globoturborotalita*, *Subbotina*, and *Turborotalita*. *In* Pearson P.N., Olsson R.K., Huber B., Hemleben C. & Berggren W.A. (eds), Atlas of Eocene Planktonic Foraminifera. *Cushman Foundation Special Publication*, 41: 111-168.

Pacaud J.M. & Quaggiotto E. (2011). Nouvelles espèces de Gastéropodes (Mollusca, Gastropoda) de l'Éocène d'Italie. Partie 1: Neritimorpha. *Studi e Ricerche – Associazione Amici del Museo - Museo Civico "G. Zannato", Montecchio Maggiore (Vicenza),* 18: 21-29.

Papazzoni C.A., Bassi D., Fornaciari E., Giusberti L., Luciani V., Mietto P., Roghi G. & Trevisani E. (2014). Geological and stratigraphical setting of the Bolca area. *In* Papazzoni C.A., Giusberti L., Carnevale G., Roghi G., Bassi D. & Zorzin R. (eds), The Bolca Fossil-Lagerstätten: A window into the Eocene World. *Rendiconti della Società Paleontologica Italiana*, 4: 19-28.

Pasotti P. (1929). Di alcuni Crinoidi paleogenici con particolare riguardo a quelli di Gassino. *Bollettino della Società Geologica Italiana*, 48: 71-89.

Payros A., Orue-Etxebarria X., Bernaola G., Apellaniz E., Dinarès-Turell J., Tosquella J. & Caballero F. (2009). Characterization and astronomically calibrated age of the first occurrence of *Turborotalia frontosa* in the Gorrondatxe section, a prospective Lutetian GSSP: implications for the Eocene time scale. *Lethaia*, 42: 255-264.

Pearson P.N., Olsson R.K., Huber B.T., Hemleben C. & Berggren W.A. (2006). Atlas of Eocene Planktonic Foraminifera. *Cushman Foundation for Foraminiferal Research, Special Publication*, 41: 1-514.

Perch-Nielsen K. (1971). Durchsicht Tertiärer Coccolithen. *In* Farinacci A. (ed.), Proceedings of the 2nd Planktonic Conference, 1970. Tecnoscienza, Roma, 2: 939-981.

Perch-Nielsen K. (1985). Cenozoic calcareous nannofossils. *In* Bolli H.M., Saunders J.B. & Perch-Nielsen K. (eds), Plankton Stratigraphy. Cambridge University Press, New York: 427-554.

Piccoli G. (1966). Studio geologico del vulcanismo paleogenico veneto. *Memorie dell'Istituto di Geologia e Mineralogia dell'Università di Padova*, 26: 1-100.

Piccoli G. & Savazzi E. (1983). Five shallow benthic mollusc faunas from the Upper Eocene (Baron, Priabona, Garoowe, Nanggulan, Takashima). *Bollettino della Società Paleontologica Italiana*, 22: 31-47.

Pisera A. (1997). Upper Jurassic siliceous sponges from the Swabian Alb: taxonomy and paleoecology. *Palaeontologia Polonica*, 57: 1-216.

Pisera A. (2006). Palaeontology of sponges - a review. *Canadian Journal of Zoology*, 84: 242-261.

Pisera A. & Busquets P. (2002). Eocene siliceous sponges from the Ebro Basin (Catalonia, Spain). *Geobios*, 35: 321-346.

Pisera A. & Tabachnick K. (2014). The sponge genus *Laocoetis* Pomel, 1972 (Hexactinosida, Craticulariidae): a living fossil? *In* Rubinstein C.V., Marsicano C.A. & Waisfeld B.G. (eds), The History of Life: A View from the Southern Hemisphere, Abstract Volume, 4th International Paleontological Congress, Mendoza, Sept. 28-Oct. 3, 2014. CONICET, Mendoza: 782.

Rang P.C. (1828). Notice sur quelques Mollusques nouveaux appartenant au genre Cléodore, et établissement et monographie du sous-genre Créseis. *Annales des Sciences naturelles*, 13: 302-319.

Reiswig H.M., Dohrmann M., Pomponi S. & Wörheide G. (2008). Two new tretodictyids (Hexactinellida: Hexactinosida: Tretodictyidae) from the coast of North America. *Zootaxa*, 1721: 53-64.

Reiswig H.M. & Kelly M. (2011). The Marine Fauna of New Zealand: Hexasterophoran Glass Sponges of New Zealand (Porifera: Hexactinellida: Hexasterophora): Orders Hexactinosida, Aulocalycoida and Lychniscosida. 124 pp. National Institute of Water and Atmospheric Research, Wellington.

Reitner J. (1993). Modern cryptic microbialite/metazoan facies from Lizard Island (Great Barrier Reef, Australia) formation and concepts. *Facies*, 29: 3-39.

Roux M., Cahuzac B. & Sztrákos K. (2006). Les paléoenvironnements éocènes à Crinoïdes pédonculés des marnes de Miretrain (Angoumé, SW de la France): interprétations paléobathymétriques. *Comptes Rendus Géoscience*, 338: 262-271.

Roux M., Eléaume M. & Améziane N. (2019). A revision of the genus *Conocrinus* d'Orbigny (Echinodermata, Crinoidea, Rhizocrinidae) and its place among extant and fossil crinoids with a xenomorphic stalk. *Zootaxa*, 4560: 51-84.

Roux M. & Plaziat J.C. (1978). Inventaire des Crinoïdes et interprétation paléobathymétrique de gisements du Paléogène pyrénéen franco-espagnol. *Bulletin de la Société géologique de France*, (7), 10: 299-308.

Schaub H. (1962). Contribution à la stratigraphie du Nummulitique du Véronais et du Vicentin. *Memorie della Società Geologica Italiana*, 3: 59-66.

Schaub H. (1981). Nummulites et Assilines de la Téthys Paléogène. Taxinomie, phylogenèse et biostratigraphie. *Schweizerische Paläontologische Abhandlungen*, 104-106: 1-236.

Schlüter C. (1878). Ueber einige astylide Crinoiden. *Zeitschrift der Deutschen geologischen Gesellschaft*, 30: 28-66.

Serra-Kiel J., Hottinger L., Caus E., Drobne K., Ferràndez C., Jauhri A.K., Less G., Pavlovec R., Pignatti J., Samsó J.M., Schaub H., Sirel E., Strougo A., Tambareau Y., Tosquella J. & Zakrevskaya E. (1998). Larger foraminiferal biostratigraphy of the Tethyan Paleocene and Eocene. *Bulletin de la Société géologique de France,* 169: 281-299.

Soria J.M., Giannetti A., Monaco P., Corbí H., García-Ramos D., Viseras C. (2014). Cyclically-arranged, storm-controlled, prograding lithosomes in Messinian terrigenous shelves (Bajo Segura Basin, western Mediterranean). *Sedimentary Geology*, 310: 1-15.

Stroncik N.A. & Schminke H.U. (2002). Palagonite, a review. *International Journal of Earth Sciences*, 91: 680-697.

Subbotina N.N. (1947). Foraminifera of the Danian and Paleogene deposits of the northern Caucasus. *In* Microfauna of the Caucasus Emba region and central Asia. *Trudy VNIGRI*: 39-160. [in Russian]

Subbotina N.N. (1953). Fossil foraminifers of the USSR: *Globigerinidae, Hantkeninidae* and *Globorotaliidae. Trudy VNIGRI* (new series), 76: 1-296. (in Russian). Translated in English by Lees E. (1971). Fossil foraminifera of the URSS: Globigerinidae, Hantkeninidae and Globorotaliidae. 321 pp. Collet's Ltd, London.

Świerczewska-Gładysz E. & Jurkowska A. (2013). Occurrence and paleoecological significance of lyssacinosid sponges in the Upper Cretaceous deposits of southern Poland. *Facies*, 59: 763-777.

Świerczewska-Gładysz E. & Olszewska-Nejbert D. (2013). New Cenomanian (Late Cretaceous) hexactinellid sponge species from the western Ukraine. *Journal of Paleontology*, 87: 696-709.

Syverson V.J., Messing C.G., Stanley K. & Baumiller T.K. (2015). Growth, injury, and population dynamics in the extant cyrtocrinid *Holopus mikihe* (Crinoidea, Echinodermata) near Roatán, Honduras. *Bulletin of Marine Science*, 91: 47-61.

Tabachnick K.R. (1990). Hexactinellid sponges from south-east Atlantic Ocean. *Transactions of the Institute of Oceanology, Academy of Sciences of the USSR*, 126: 67-73.

Tabachnick K.R. & Lévi C. (1997). Les Craticulariidae sont des spongiaires Hexactinellida Scopularia. *Zoosystema*, 19: 7-14.

Tunnicliffe V., Roux M., Eléaume M. & Schornagel D. (2016). The stalked crinoid fauna (Echinodermata) of the Molucca and Celebes Seas, Indonesia: taxonomic diversity and observations from remotely operated vehicle imagery. *Marine Biodiversity*, 46: 365-388.

Van Soest R.W.M., Van Duyl, F.C., Maier C., Lavaleye M.S.S., Beglinger E. & Tabachnick K.R. (2007). Mass occurrence of the hexactinellid *Rossella nodastrella* Topsent in bathyal coral reefs of Rockall Bank, W of Ireland (Lyssacinosida, Hexactinellida). *In* Custódio M.R., Lôbo-Hajdu G., Hajdu E. & Muricy G. (eds), Porifera research: biodiversity, innovation and sustainability. Museu Nacional, Rio de Janeiro: 6-13.

Visentin M. (1994). Segnalazione di una spongiofauna eocenica nella Valle del Chiampo (Lessini orientali, Vicenza). *Lavori Società Veneziana di Scienze Naturali*, 19: 229-230.

Wade B.S. & Pearson P.N. (2006). Taxonomy, biostratigraphy, and phylogeny of Eocene *Acarinina*. *In* Pearson P.N., Olsson R.K., Huber B., Hemleben C., Berggren W.A. (eds), Atlas of Eocene Planktonic Foraminifera. *Cushman Foundation Special Publication*, 41: 257-326.

Wade B.S., Pearson P.N., Berggren W.A. & Pälike H. (2011). Review and revision of Cenozoic tropical planktic foraminiferal biostratigraphy and calibration to the geomagnetic polarity and astronomical time scale. *Earth-Science Review*, 104: 111-142.

Warkne K. (1995). Calcification processes of siliceous sponges in Viséan limestones (Counties Sligo and Leitrim, Northwestern Ireland). *Facies*, 33: 215-228.

Zampieri D. (1995). Tertiary extension in the southern Trento Platform, southern Alps, Italy. *Tectonics*, 14: 645-657.

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Short Note

A solitary coral-larger benthic foraminifera association from the late Eocene of Jamaica

Thomas Albert Stemann* & Natalie Robinson

T.A. Stemann, Department of Geography and Geology, The University of the West Indies, Mona Campus, Kingston 7, Jamaica; thomas.stemann@uwimona.edu.jm **corresponding author*

N. Robinson, Department of Geography and Geology, The University of the West Indies, Mona Campus, Kingston 7, Jamaica; natalie.robinson02@mymona.uwi.edu

KEY WORDS - Scleractinia, Lepidocyclina*, settling behaviour, Paleogene, Caribbean.*

There are many records of solitary discoid or patellate corals attached at their base to large benthic foraminifera from the Cretaceous through the Paleogene throughout the Tethyan region. Russo et al. (1996) gave a detailed overview of this coral/foraminiferal association and its links to automobility in some small solitary corals. This association involves preservation of a particular settling behaviour seen in some small discoid scleractinians, in which their base is centered on a large disc or lens-shaped foraminifer, often *Nummulites* sp. or *Discocyclina* sp. Russo et al. (1996) documented that some 19 different species of corals have been shown to possess this settling behaviour. These include species from the genera *Cyclolites*, *Cyclolitopsis*, *Cycloseris*, *Funginellastraea* and others. In the Eocene, especially, there are numerous examples from throughout the Mediterranean and Indo-Pacific (e.g., Duncan, 1880; Oppenheim, 1900; Russo et al., 1996).

To date, there are no reports of this coral/foraminiferal association from the Caribbean. This may be due to the fact that there are very few records of small discoidal scleractinians from the Caribbean. Wells (1934) described one discoid solitary coral, *Cyclolites jamaicaensis* Wells, 1934, from the Upper Cretaceous of Jamaica. While this coral has been found in abundance in Jamaica, there are no records of it settling on foraminifera. One other record from Jamaica (Wells, 1935) is of a single discoid coral from an unknown locality. This material is probably Cretaceous in age based on the similarity of its preservation to other Jamaican material of that age. No solitary discoid scleractinians are recorded from large faunas described from the Caribbean Paleogene (Budd et al., 1992; Stemann, 2004) or the Neogene (Budd et al., 1994).

MATERIAL

This study presents the first record of a discoid coral settling on foraminifera from the Caribbean. Our material comes from the Paleogene portion of the White Limestone Group near the community of Philadelphia in the parish of St. Ann, Jamaica (Lat. 18° 23’ 36.622” N; Long. 77° 19’ 55.952” W). The White Limestone Group includes a series of formations composed of pure carbonate deposited in platform and basinal settings (Mitchell, 2013). These units range in age from middle Eocene to early Miocene and contain a rich fauna of reefal scleractinians (Stemann, 2004). At the studied locality, the area is complexly faulted and the material collected is apparently from a block faulted into the upper Eocene Somerset Formation. The rocks here exposed are pure carbonate comprised of grainstones and packstones deposited in a mostly outer

Fig. 1 - (color online) Specimen showing solitary coral centred on a large benthic foraminiferal test, *Lepidocyclina pustulosa* (UWIGM 2020.01.0001). Scale bar = 1cm.

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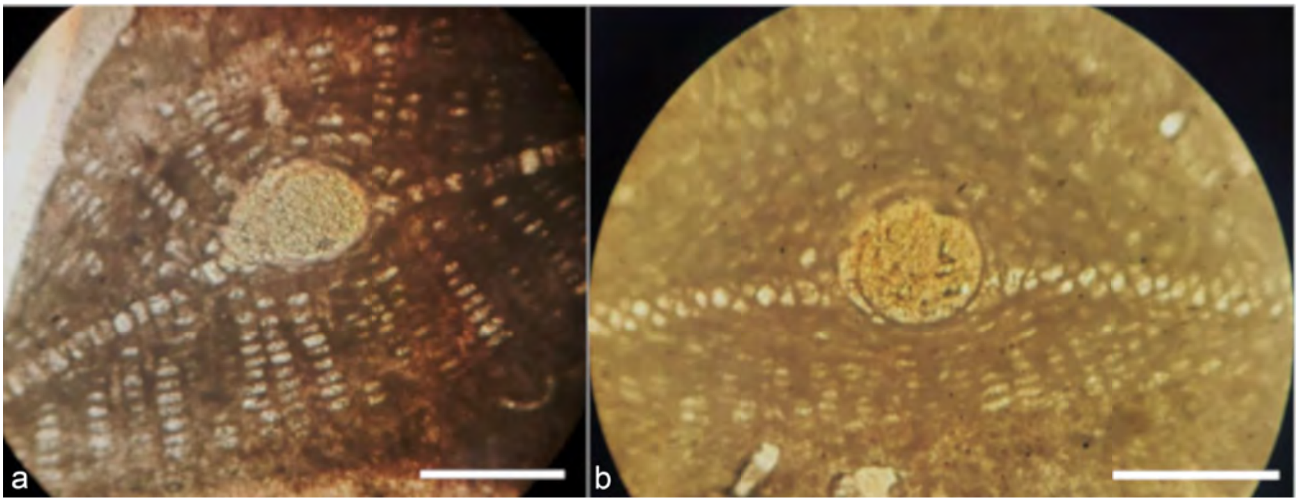

Fig. 2 - (color online) Thin section images of Lepidocyclinid foraminifera identified in this sample, showing protoconch and equatorial chambers. a) *Lepidocyclina pustulosa trinitatis* (UWIGM 2020.01.0002); b) *Lepidocyclina pustulosa* s.s. (UWIGM 2020.01.0003). Scale bars = 0.5 mm.

platform environment based on the benthic foraminifer fauna. The studied unit yields a small fauna of mouldic examples of chiefly thin-branched colonial corals and some solitary species. The studied locality is unusual for this part of the White Limestone Group in that it includes some corals preserved as casts. It also contains a flood of the lens-shaped foraminifer, *Lepidocyclina* spp., many of which attain diameters of greater than 1.5 cm.

The material is stored in The University of the West Indies Mona Campus Geology Museum (UWIGM).

CORAL/FORAMINIFERAL ASSOCIATION

The coral figured here (Fig. 1) is a solitary discoid form, 1.3 cm in diameter, that is centered on a specimen of *Lepidocyclina pustulosa* (Douvillé, 1917) with a diameter of 0.7 cm. The mouldic preservation of the coral and the fact that the foraminifer covers much of the coral's axial structure precludes identification of the specimen to the genus or species level. Its discoid form, lack of epitheca and abundant septa that are porous axially suggests that it belongs to the Family Cyclolitidae. This is the first reliable record of this group from the Paleogene of the Caribbean.

The large lenticular foraminifera found at this site are identified as *Lepidocyclina pustulosa*. Here, *L. pustulosa* is characterised by the protoconch being ~0.5 mm, the few pillars, the height of the lateral chambers being low and with a high thickness for the chamber roofs and floor. Two morphs of *L. pustulosa* were identified, *L. pustulosa trinitatis* (Vaughan, 1928) and *L. pustulosa* s.s. (Fig. 2). These are normally found in the upper Eocene of the White Limestone Group, in outer platform to platform margin facies (Robinson & Mitchell, 1999). The largest foraminifera in the sample including the specimen associated with the coral in Fig. 1 are microspheric forms. Unfortunately, these forms generally do not yield the taxonomic characteristics needed to identify them to the species level. For this reason, the foraminifer attached to the coral cannot be identified to the subspecies level.

DISCUSSION

This report represents the first record of a discoid "cyclolitid" coral in the Paleogene of Jamaica. This indicates an extension of the range of these discoid corals into the Caribbean in the Paleogene and an extension of their particular settling behaviour as well. It is interesting to note that this coral/foraminiferal association involves the genus *Lepidocyclina,* a genus that has never been recorded as part of these associations from the Mediterranean or Indo-Pacific. This may suggest that in these associations the particular foraminiferal taxon selected by the coral as a settling site is less important than its the size, shape and availability.

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REFERENCES

Budd A.F., Stemann T.A. & Johnson K.G. (1994). Stratigraphic distributions of genera and species of Neogene to Recent Caribbean reef corals. *Journal of Paleontology*, 68: 951-977.

Budd A.F., Stemann T.A. & Stewart R.H. (1992). Eocene Caribbean reef corals; a unique fauna from the Gatuncillo Formation of Panama. *Journal of Paleontology*, 66: 570-594.

Douvillé H. (1917). Les Orbitoides Developement et Phase Embryonnaire, Leur Evolution Pendant le Cretaceous. Paris Academy of Science, 161: 1-844.

Duncan P.M. (1880). Sind fossil Corals and Alcyonaria. *Memoirs of the Geological Survey of India, Palaeontographica India*, VII & XIV, 1: 1-110.

Mitchell S.F. (2013). Stratigraphy of the White Limestone. *Bulletin de la Société Géologique de France*, 184: 111-118.

Oppenheim P. (1901). Priabonaschichten und ihre Fauna. *Palaeontographica*, 47: 1-348.

Robinson E. & Mitchell S.F. (1999). Middle Eocene to Oligocene stratigraphy and palaeogeography in Jamaica: a window on the Nicaragua Rise. Prepared for the Fourth Annual Meeting of IGCP 393, 12-18 July 1999. Contributions to Geology UWI Mona, 4: 1-47.

Russo A., Cherchi A. & Schroeder R. (1996). An example of auto-mobility and host substrate relationship in "*Cycloseris*" *escosurae* Mallada, 1887, scleractinian coral from the Lower Aptian of Spain. *Bollettino della Società Paleontologica Italiana*, Special Volume 3: 191-203.

Stemann T.A. (2004). Reef corals of the White Limestone Group of Jamaica. *Cainozoic Research*, 3: 83-107.

Vaughan T.W. (1928). Species of Large Arenaceous and Orbitoidal Foraminifera from the Tertiary Deposits of Jamaica. *Journal of Paleontology*, 1: 277-298.

Wells J.W. (1934). Some fossil corals from the West Indies. *Proceedings of the United States National Museum*, 83: 71-110.

Wells J.W. (1935). Corals from the Cretaceous and Eocene of Jamaica. *Annals and Magazine of Natural History*, 10: 183-194.

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Scleractinian corals (Anthozoa) from the lower Oligocene (Rupelian) of the Eastern Alps, Austria

Rosemarie Christine Baron-Szabo* & Diethard Sanders

R.C. Baron-Szabo, Department of Invertebrate Zoology, Smithsonian Institution, NMNH, W-205, MRC 163, P.O. Box 37012, Washington DC, 20013-7012 USA; Forschungsinstitut Senckenberg, Senckenberganlage 25, D-60325 Frankfurt/Main, Germany; rbsz2020@yahoo.com; Rosemarie.Baron-Szabo@senckenberg.de *corresponding author

D. Sanders, Institut für Geologie, Universität of Innsbruck, Innrain 52, A-6020 Innsbruck, Austria; diethard.g.sanders@uibk.ac.at

KEY WORDS - Scleractinia, taxonomy, paleoecology, paleobiogeography.

ABSTRACT - In the Werlberg Member (Rupelian pro parte) of the Paisslberg Formation (Eastern Alps), an assemblage of colonial corals of eleven species pertaining to eleven genera and eleven families was identified: Stylocoenia carryensis, Acropora lavandulina, *?*Colpophyllia *sp.,* Dendrogyra intermedia, Caulastraea pseudoflabellum, Hydnophyllia costata, Pindosmilia *cf.* brunni, Actinacis rollei, Pavona profunda, Agathiphyllia gregaria, *and* Faksephyllia faxoensis. *This is the first Oligocene coral assemblage reported from the Paisslberg Formation (Werlberg Member) of the Eastern Alps, consisting exclusively of colonial forms. The assemblage represents the northernmost fauna of reefal corals reported to date for Rupelian time.*

The Werlberg Member accumulated during marine transgression onto a truncated succession of older carbonate rocks. The corals grew as isolated colonies and in carpets in a protected shoreface setting punctuated by high-energy events. Coral growth forms comprise massive to sublamellar forms, and branched (dendroid, ramose) forms. The coral fauna is dominated by forms with medium- to large size corallites 4 to >10 mm in diameter. The assemblage consists of stress-resistant genera widespread in the Eocene to Miocene of central and southern Europe, Central America, and the Caribbean Islands. On the species level, closest correspondence is with faunas of southern Europe, especially with those of northern Italy (Lessini Shelf). On the genus-level, greatest affinities are with the lower Oligocene faunas of northern Italy (Lessini Shelf). Regarding similarities to other lower Oligocene faunas, seven genera have also been reported from Jamaica, Germany (Reit im Winkel), and Slovenia, and five genera were found in Greece. Ten (91%) of the described Austrian coral taxa from the Paisslberg Formation were found elsewhere in (sub)tropical reefal and peri-reefal settings. The caryophylliine coral Faksephyllia faxoensis*, however, stands out as the only taxon which, in addition, has been reported from deep-water environments.*

INTRODUCTION

In the Eastern Alps, Oligocene shallow neritic deposits are very rarely preserved. During the Rupelian, the northern molasse foredeep was connected with the Mediterranean by seaways along both the western and eastern end of the emergent Alpine-Carpathian arc (Popov et al., 2004). Along the southern slope of the Alps and their foreland, Rupelian coral locations are much more common, and range from Slovenia in the East (Nebelsick et al., 2000; Silvestri et al., 2011) via the Lessini Shelf in the center (e.g., Geister & Ungaro, 1977; Frost, 1981; Bosellini & Trevisani, 1992; Bosellini & Stemann, 1996) to Piedmont, Liguria and southern France in the West (e.g., Pfister, 1985; Quaranta et al., 2009; Vannucci et al., 2010).

Scleractinian corals from the lower Oligocene (Rupelian) have been reported from various localities worldwide, most notably from reef structures in the Caribbean/Central America (Duncan, 1863, 1868; Vaughan, 1900, 1919; Frost & Langenheim, 1974; Frost et al., 1983; Stemann, 2004) and from localities throughout the Mediterranean Tethys (northern Italy: Catullo, 1856; d'Achiardi, 1866, 1868; Barta-Calmus, 1973; Reuss, 1868, 1869; Angelis d'Ossat, 1894; Prever, 1922; Pfister, 1980a, b; Frost, 1981; Bosellini, 1988; Bosellini & Trevisani, 1992; Fravega et al., 1994; Budd & Bosellini, 2016; Spain: Álvarez et al., 1993; Libya: Hladil et al., 1992; Slovenia: Reuss, 1864; Silvestri et al., 2008; southern France: Chevalier, 1956, 1962; Hungary: Hegedüs, 1962; Greece: Marcopoulou-Diacantoni et al., 1996; Schuster, 2002c; Kołodziej & Marcopoulou-Diacantoni, 2003; Turkey: Islamoglu, 2008; southern Germany: Reis, 1889).

In addition, lower Oligocene scleractinian coral occurrences that are characterised by either reefal or non-reefal associations have been described from various localities in central, eastern, and western Europe (Germany [excluding southern areas]: Kühn, 1954; Glibert, 1974; Bulgaria: Bontscheff, 1897; Ukraine: Sokolow, 1894; England: Duncan, 1866); Asia (Indonesia: Santodomingo, 2014; Iran: Reuter et al., 2009; Myanmar: Vredenburg, 1921; United Arab Emirates: Gameil & Aly, 2001); the Americas (USA: Vaughan, 1900; Durham, 1942, 1943; Weisbord, 1973; Dockery, 1982; Peru: Wells, 1941); and the Pacific (Marshall Islands: Wells, 1964; New Zealand: Squires, 1958, 1962); Antarctica (Stolarski & Taviani, 2001).

With respect to lower Oligocene scleractinians, no reports were known from the Paisslberg Formation, Eastern Alps. A first documentation of Rupelian corals (Sanders & Baron-Szabo, 2007) was followed by a description of *Faksephyllia faxoensis* (Beck in Lyell, 1837) identified in that assemblage (Baron-Szabo, 2016). The present paper, in turn, provides the first taxonomic description of the entire Rupelian coral fauna collected from the Tyrolian outcrops Wimpissinger and Entfelden.

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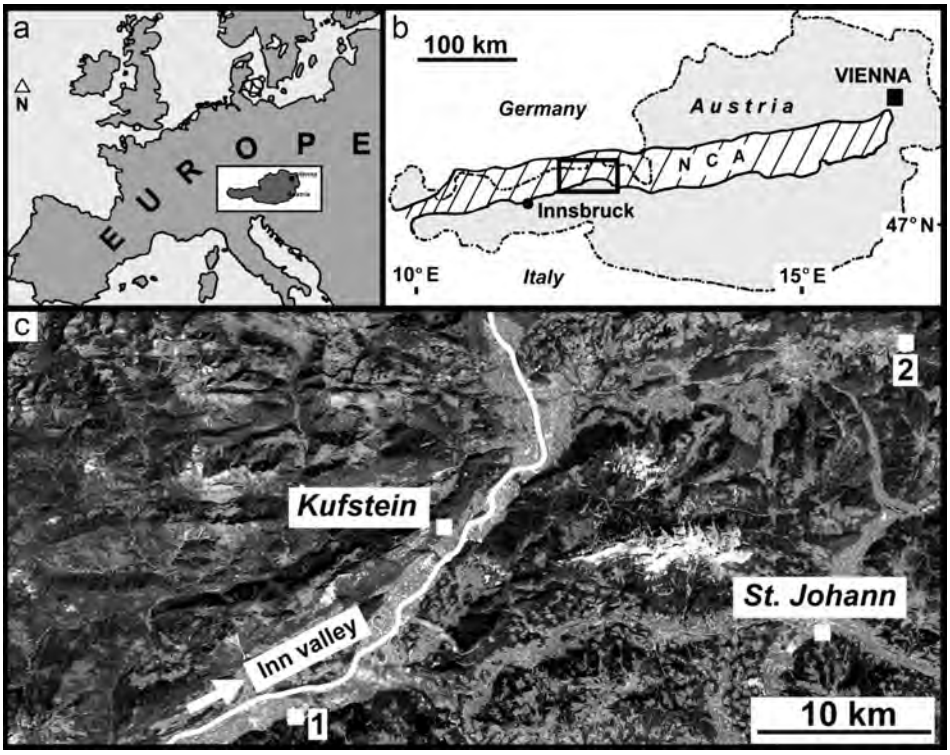

Fig. 1 - a) Location of study area. b) Close-up of Fig. 1a. The two quarries from which the material was collected are in the box. Coordinates of quarry Wimpissinger: 47.467235/12.014900; coordinates of quarry Entfelden: 47.674201/12.492871; coordinates in WGS 1984 decimal notation. NCA = Northern Calcareous Alps. c) Aerial view of study area outlined by box in Fig. 1b (Location 1: Wimpissinger; Location 2: Entfelden).

MATERIAL, METHODS AND ABBREVIATIONS

The Oligocene succession had been mapped in the field on a scale of 1:10,000 by staff of the Institute of Geology of the University of Innsbruck (Gruber, 1995; Ortner & Stingl, 2001). One of us (DS), in turn, had logged and sampled sections at selected locations (Fig. 1). A total of 80 polished slabs and 61 large thin sections provided documentation of lithologies. For determination of corals, in a total of 34 specimens, structures identified on the upper surface of hand specimens as well as features seen in 19 thin sections were used.

The material used in this work is housed at the Department of Geology, University of Innsbruck, Austria (Institut für Geologie, Universität Innsbruck, Österreich), acronym ICPUIBK.

Symbols used in the synonymies and descriptions are: * = first description of taxon to which the assignment of specimen refers; v = material was studied by author (RBS).

SETTING

The coral-bearing succession is located in the Northern Calcareous Alps (NCA, part of Eastern Alps), a belt of thrust nappes dominated by Triassic shallow-water carbonate rocks (e.g., Brandner, 1984; Mandl, 1999) (Fig. 1). During the early Oligocene, orogenesis led to surface uplift of the Alpine-Carpathian arc as a peninsula (e.g., Popov et al., 2004; Handy et al., 2015). During the Rupelian, the study area was located on the northern shelf of that peninsula, at ~43°N latitude (Popov et al., 2004). In the study area, marine transgression over subaerially exposed carbonate-rocky terrain resulted in a mixed carbonate-lithic/biogenic nearshore setting inhabited by the corals described herein. The thickness of the corresponding sedimentary succession, the Werlberg Member of the Paisslberg Formation (cf. Ortner & Stingl, 2001), ranges from less than a meter to typically a few meters. A Rupelian age of the Werlberg Member of the Paisslberg Formation is indicated by the co-presence of *Nummulites* ex gr. *vascus* Joly & Leymerie, 1848, *N. fichteli* Michelotti, 1841 and *Amphistegina* (Nebelsick et al., 2001). Above the Werlberg Member, the neritic marls of the Paisslberg Formation are dated into the Rupelian by nannofossils and by benthic foraminifera (e.g., Löffler, 1999; Ortner & Stingl, 2001; Scherbacher et al., 2001). Up-section, the Paisslberg Formation is overlain by the Unterangerberg Formation that was age-dated to the Chattian. Today, the coral-bearing Oligocene deposits are preserved in numerous erosional relicts each a few hundreds of meters to a few kilometers in lateral extent. The transgressive surface along the base of the Werlberg Member is deeply and densely macrobored and colonised by encrusters (e.g., serpulids), to a degree that renders it difficult even in thin section to identify the boundary between Triassic rocks and the overlying Oligocene limestones. In addition, lithoclasts up to boulder-size within the transgressive succession are similarly deeply bored and may show complex encrustations. Branched corals, in turn, typically are coarsely fragmented and toppled. The corals grew as isolated colonies and in open carpets. Coral growth forms comprise massive-hemispherical to sublamellar-encrusting forms, and branched (dendroid, phaceloid, fasciculate, ?subreproid, ramose) forms (Tab. 1). No coral fabric was observed that would suggest a biohermal development. Together, the evidence suggests that the corals thrived in a rocky to pebbly shoreface environment of overall low energy, and devoid of siliciclastic input, but that was punctuated by episodic high-energy events (Baron-Szabo & Sanders, 2018).

CORAL FAUNA

Diversity

The Werlberg coral fauna consists of 11 species belonging to 11 genera living in a rocky to pebbly shoreface environment of overall low energy that was subjected to episodic high-energy events. Similar environments have been described from various time periods. In the present Florida Bay, depending on location, coral assemblages consist of up to five colonial taxa (*Porites*, *Siderastrea*, *Cladocora*, *Solenastrea*), and the mobile form *Manicina areolata* (Linnaeus, 1758) (Ginsburg, 1972), each of a high resilience to ecostress (cf. Sanders & Baron-Szabo, 2005). In tidal channels between the Florida Bay and the shelf, coral assemblages consist of eight species pertaining to four genera (Abbott, 1975). In Puerto Rico, in Oligocene shelf reefs (thickets, small patch reefs) considered as "sediment-stressed" by Frost et al. (1983, p. 13-15), seven species belonging to five colonial coral genera are present. In the Rupelian of the Lessini Shelf, "pioneer" coral assemblages in areas of substantial terrigenous input consist of nine to eleven genera (two of 11 genera are of questionable affiliation; no species determined) (Frost, 1981). Similarly, within the Castelgomberto Formation

Austrian species	Polyp integration, polypar size*	Colony shape	Austrian occurrences		Stratigraphic ranges	Geographic distribution in the lower Oligocene	Distribution outside the lower Oligocene
			WIM	EN			
***Acropora lavandulina* (Michelin, 1842)**	plocoid, small	columnar, ramose	X	X	Eocene-middle Miocene	Austria, Bulgaria, France, Indonesia	Eocene of Italy, middle Eocene of France, lower Miocene of Egypt, France, and Portugal, lower-middle Miocene of Italy
***Actinacis rollei* Reuss, 1864**	plocoid, small	multicolumnar, submassive, lamellar	X	X	upper Eocene-upper Oligocene	Austria, Germany, Italy, Slovenia	upper Eocene of Hungary and Italy, upper Oligocene of Iran and Libya
***Agathiphyllia gregaria* (Catullo, 1852)**	plocoid, medium to large	massive, small hemispherical		X	upper Eocene-lower Miocene	Austria, Bulgaria, Germany, Greece, Hungary, Italy, Libya, Slovenia	upper Eocene and lower Miocene of Italy
***Caulastraea pseudoflabellum* (Catullo, 1852)**	phaceloid-subflabellate, medium to large	branching	X		Eocene- lower Oligocene	Austria, Germany, Bulgaria, Hungary, Italy	Eocene of Italy and Spain, middle Eocene of Slovenia, upper Eocene of Germany and Hungary
?*Colpophyllia* sp.	meandroid, medium to large	massive	X		lower Oligocene	Austria	-------
***Dendrogyra intermedia* Michelotti, in Sismonda, 1871**	meandroid, small to medium	massive	X		lower Oligocene	Austria, Italy	-------
***Faksephyllia faxoensis* (Beck in Lyell, 1837)**	phaceloid, subdendroid, fasciculate, small to medium	arborescent, bushy	X		Paleocene-Oligocene	Austria, Germany, ?Hungary, Italy	Paleocene of Austria, Azerbaijan, Denmark, and Sweden, ?Eocene of Bosnia-Herzegovina
***Hydnophyllia costata* (Catullo, 1856)**	meandroid-subthamnasterioid, medium to large	massive		X	Oligocene	Austria, Italy	upper Oligocene of Italy
***Pindosmilia* cf. *brunni* Chevalier in Brunn et al., 1955**	subdendroid (-?subreproid), large	branching		X	Oligocene	Austria, Greece	possibly upper Oligocene of Greece
***Pavona profunda* Reuss, 1868**	thamnasterioid-submeandroid, large	submassive		X	Oligocene	Austria, Italy	upper Oligocene of France
***Stylocoenia carryensis* Chevalier, 1962**	cerioid, small	massive, encrusting		X	lower Oligocene-lower Miocene	Austria	lower Miocene of France

Tab. 1 - Coral species identified in quarries Wimpissinger (WIM) and Entfelden (EN), characteristics of their skeletal elements, and their stratigraphic and geographic ranges; *(corallite size: small = 2 mm or less; medium = >2 to 10 mm; large = >10 mm).

(Rupelian) of the Lessini Shelf, Bosellini & Trevisani (1992) determined a total of 11 genera (species not determined for each genus) of colonial corals. Thus, in view of the shoreface environment inhabited (Sanders & Baron-Szabo, 2018), which represents a comparable high-stress ecosystem to scleractinian corals, the 11/11 genera/species composition of the Werlberg coral fauna ranges near the documented high-diversity end of nearshore assemblages.

Morphology

The fauna consists of exclusively colonial forms of three general categories of polyp integration, none of which is dominant: cerioid to plocoid forms (four species), meandroid to thamnasterioid forms (four species), and branching forms (three species) (Tab. 1). With regard to polypar size, the fauna is distinctly dominated by forms with medium to large corallites (4 to >10 mm in diameter), including the meandroid-thamnasterioid and the branching groups as well as the plocoid *Agathiphyllia gregaria* (Catullo, 1852) (73%). In contrast, only corals of the plocoid-cerioid group (with the exception of *Agathiphyllia gregaria*), are characterised by small corallites (~2 mm in diameter) (27%). Coral growth forms are comprised of massive to sublamellar morphotypes, and branched (dendroid, ramose) forms (Tab. 1). With regard to the latter growth forms, comparisons of coral assemblages before and after heavy, prolonged stress from saltation and turbidity indicates that the assemblage became dominated by both massive meandroid forms (Dodge & Vaisnys, 1977) and by ramose-branched forms *Madracis* and *Oculina* (Dryer & Logan, 1978). In environments of intermittently rapid sedimentation mobile meandroid corals (*Manicina, Trachiphyllia*) are also common (Gill & Coates, 1977). Recent *Acropora* shows vertical growth rates of up to about 10 cm/yr, thus preventing choking by sediment, and is able to disperse by fragmentation. The (sub)meandroid corals with polypars of medium to large size (*Pavona*, *Dendrogyra*, *Colpophyllia*) probably were similar to the extant *Diploria* which is an efficient sediment rejecter able to thrive very shallow subtidal habitats. The branched types with small to medium (*Faksephyllia*) and medium to large polypars (*Caulastraea*), respectively, closely correspond to recent *Cladocora* and similar forms (Baron-Szabo, 2016, tab. 2), i.e., rapidly-growing pioneer corals colonising new substrata (Barnes & Hughes, 1988). The subdendroid *Pindosmilia* with closely adjacent, medium to large polypars corresponds to recent genera such as *Astroides*, *Balanopsammia*, and *Dichopsammia*, which typically thrive in waters less than 30 m in depth (Cairns, 2001; Baron-Szabo & Cairns, 2019). Finally, with its very "plastic" skeleton and high tolerance to sediment input, the extinct *Actinacis* was among the most ecoresilient corals ever (cf. Sanders & Baron-Szabo, 2005). From that it can be concluded that the determined coral genera were forms resilient to ecostress.

Stratigraphic and paleobiogeographic distribution

The colonial coral assemblage described herein is the first one from the Paisslberg Formation, which belongs to the northern shelf of the emerging Alpine-Carpathian arc. The assemblage represents the northernmost coral fauna reported to date for Rupelian time (cf. Perrin & Bosellini, 2012, fig. 7). As mentioned, the location corresponds to a paleolatitude of ~43°N. Today, the northernmost assemblage of colonial corals thrives at 34°N (Tateyama, Japan) (Veron, 1992); this non-reefal assemblage, as well as coral reefs growing to > 30°N, are sustained by northward flow of warm oceanic surface waters in the Kuroshio western boundary current (Veron & Michin, 1992; Ikeda et al., 2006). This indicates that, although the Rupelian is characterised by global cooling relative to the late Eocene, colonial corals still could range to distinctly higher northern latitudes than today.

All of the Austrian species had their first appearance in the Paleogene (Tab. 1). Five of the 11 taxa (= 45%) had their first appearance before the Oligocene (Paleocene or Eocene); six taxa (= 55%) are new in the lower Oligocene (Tab. 1). The majority of the species (eight taxa = 73%) did not cross the Paleogene-Neogene boundary. Only three species (27%) had their last occurrence in the Miocene, two of which first appeared during pre-Oligocene time periods (the plocoid species *Acropora lavandulina* [Michelin, 1842] and *Agathiphyllia gregaria*), and the third, the cerioid taxon *Stylocoenia carryensis* Chevalier, 1962, which had its first appearance in the lower Oligocene. None of the Austrian species are known from strata younger than the Miocene.

With respect to their geographic distribution in the Oligocene, the Austrian taxa belong to species that are subcosmopolitan (*Acropora lavandulina*), geographically restricted to the Mediterranean Tethys (eight species = 73%), or endemic and restricted to the Austrian localities described in the current paper (two species = 18%), (= the meandroid ?*Colpophyllia* sp., reported from quarry Wimpissinger, and the single one cerioid taxon *Stylocoenia carryensis*, found at quarry Entfelden) (Tab. 1). Closest correspondence is with faunas of southern Europe, especially with the ones of northern Italy (Lessini Shelf; eight species = 73%) (Tab. 1). The species of the Paisslberg Formation with the largest geographic distributions in the Oligocene all belong to plocoid species *Acropora lavandulina, Actinacis rollei* Reuss, 1864, and *Agathiphyllia gregaria* (three species = 27%), followed by the branching *Faksephyllia faxoensis* and *Caulastraea pseudoflabellum* (Catullo, 1852) (two species = 18%). Four species (36%) are known only from one additional lower Oligocene southern European locality: the branching species *Pindosmilia* cf. *brunni* Chevalier in Brunn et al., 1955, and the (sub-)thamnasterioid to meandroid taxa *Dendrogyra intermedia* Michelotti, in Sismonda (1871), *Hyndophyllia costata* (Catullo, 1856), and *Pavona profunda* Reuss, 1868 (Tab. 1).

With regard to their stratigraphic distributions, seven species (= 64%) either occurred only during the Eocene-Oligocene or were restricted to the Oligocene (*Actinacis rollei*, *Caulastraea pseudoflabellum*, ?*Colpophyllia* sp., *Dendrogyra intermedia*, *Hydnophyllia costata*, *Pindosmilia* cf. *brunni*, *Pavona profunda*) (Tab. 1). The branching *Faksephyllia faxoensis* (Paleocene-Oligocene) and the plocoid-ramose *Acropora lavandulina* (Eocene-middle Miocene) have by far the largest stratigraphic distributions as both species have been reported from strata spanning a time range of around 40 My. The meandroid species ?*Colpophyllia* sp. and *Dendrogyra intermedia* have the shortest stratigraphic distribution. Their occurrence is restricted to the lower Oligocene (Tab. 1).

Austrian species	Environmental occurrences	References*
Acropora lavandulina	shallow subtidal, carpet, small coral patch or fringing reefs	Cahuzac & Chaix (1993); Wilson (1995); Schuster (2002b)
Actinacis rollei	reef, buildup, carpet, or bioherm, shallow subtidal, lagoonal	Pfister (1980, 1985); Frost (1981); Bosellini & Russo (1988); Bosellini & Trevisani (1992); Nebelsick et al. (2000)
Agathiphyllia gregaria	reef, buildup, bioherm, carpet, shallow subtidal, lagoonal	Pfister (1980); Frost (1981); Bosellini & Trevisani (1992); Nebelsick et al. (2000); Silvestri et al. (2011)
Caulastraea pseudoflabellum	mainly reef, buildup, or bioherm, carpet, shallow subtidal	Pfister (1980, 1985); Frost (1981); Bosellini & Trevisani (1992)
?*Colpophyllia* sp.	genus occurs mainly in reef, buildup, carpet, or bioherm, shallow subtidal	Pfister (1980); Bosellini & Trevisani (1992); Schuster (2002c); Johnson (2007)
Dendrogyra intermedia	coral carpets, fan delta systems	Pfister (1980); Silvestri et al. (2008)
Faksephyllia faxoensis	shallow (incl. lagoonal)- to deep-water (300 m depth); often in coral thickets, bioherms, carpets	Floris (1972); Frost (1981); Bernecker & Weidlich (1990, 2005); Bosellini & Trevisani (1992); Baron-Szabo (2016)
Hydnohyllia costata	carpet, patch reefs, inner platform	Budd & Bosellini (2016)
Pindosmilia* cf. *brunni	reef, buildup, carpet, bioherm, shallow subtidal	Brunn et al. (1955)
Pavona profunda	reef, buildup, carpet, bioherm, subreefal structure with hermatypic and ahermatypic corals	Frost (1981); Bosellini & Trevisani (1992); Cahuzac & Chaix (1993); Chaix & Cahuzac (2001)
Stylocoenia carryensis	reef, buildup, carpet, shallow subtidal	Chevalier (1962)

Tab. 2 - Environmental occurrences of the Austrian species, *including environmental information concerning the Austrian localities of the current paper (unpublished data; and herein).

With regard to the distributional pattern in the lower Oligocene, on the genus-level, the Austrian corals belong to mainly subcosmopolitan genera (*Acropora*, *Actinacis*, *Agathiphyllia*, *Caulastraea*, *Colpophyllia*, *Pavona*, and *Stylocoenia*; seven genera = 64%), and, to a minor extent, taxa that are very restricted geographically (*Dendrogyra*, *Faksephyllia*, *Hydnophyllia*, and *Pindosmilia*; four genera = 36%) (Tab. 3). Greatest affinities are with the faunas of northern Italy (Lessini Shelf) (ten genera = 91%). Regarding similarities to other lower Oligocene faunas, eight genera (= 73%) were also described from Germany (Reit im Winkel) and Slovenia, seven genera (= 64%) were reported from Jamaica, and five genera (= 46%) were found in Greece (Tab. 3).

	Caribbean/ Central America				**Europe**											**Africa**		**Asia**	
Coral genera	**Antigua & Barbuda**	**Haiti**	**Jamaica**	**Mexico**	**Austria**	**Bulgaria**	**England**	**France**	**Germany**	**Greece**	**Hungary**	**Italy**	**Slovenia**	**Spain**	**Turkey**	**Libya**	**Somalia**	**Indonesia**	**Iran**
Acropora	X	X	X		X	X	X	X	X			X	X		X			X	
Actinacis		X	X		X				X	X		X	X	X*			X*		
Agathiphyllia			X	X	X	X			X	X*		X	X		X	X			
Caulastraea	X		X		X	X			X		X	X	X						X
Colpophyllia			X	X	X					X		X	X						
Dendrogyra					X							X							
Faksephyllia					X				X		?	X							
Hydnophyllia					X				X			X	X						
Pindosmilia					X					X*									
Pavona			X		X				X	X		X	X						
Stylocoenia			X		X			X	X		X	X	X	X	X	X	X		X

Tab. 3 - Distribution in the lower Oligocene of the coral genera found in Austria. *might also include upper Oligocene sediments at this location (data from Paleobiology Database: https://paleobiodb.org/#/ current paper; and unpublished data from database RBS).

With respect to phylogenetic ancestry, the fauna consists of a mix of mainly genera that appeared during the Paleogene (*Acropora*, *Agathiphyllia*, *Caulastraea*, *Dendrogyra*, *Faksephyllia*, *Hydnophyllia*, *Pindosmilia*, *Pavona*, and *Stylocoenia*) with a small number of Mesozoic hold-over taxa (*Actinacis* and *Colpophyllia*).

With regard to their environmental occurrences, all of the taxa have been found elsewhere in shallow-water, (sub) tropical reefal and peri-reefal settings. The caryophylliine coral *Faksephyllia faxoensis,* however, stands out as the only taxon which, in addition, has been reported from deep-water environments (Tab. 2).

As mentioned, the Werlberg coral fauna is most similar to faunas of the Lessini Shelf. In view of the paleogeographic distribution of land and seaways, this suggests that the carbonate environments along the southern fringe of the Alpine edifice were the crucial reservoir for coral recruitment to the northern shelf.

SYSTEMATIC PALEONTOLOGY

Taxonomic framework

The taxonomic framework followed here is based on the works by Milne Edwards & Haime (1857), Vaughan & Wells (1943), Beauvais (1981), and Baron-Szabo (2014, 2018; and new herein) for higher-level taxa (family), with updates on individual genera and species by Pfister (1980a), Beauvais (1982), Bosellini (1988, 1998), Cahuzac & Chaix (1993), Wallace (2008), Budd & Bosellini (2016), and Baron-Szabo (2003, 2016).

Order Scleractinia Bourne, 1900
Family Acroporidae Verrill, 1902

Genus *Acropora* Oken, 1815

Type species *Millepora muricata* Linnaeus, 1758, Recent, Moluccas, subsequent designation by Verrill (1901).

Diagnosis - See Wallace (2008).

Acropora lavandulina (Michelin, 1842)
(Pl. 1, figs 1-3)

v *1842 *Madrepora lavandulina*, N. - Michelin, p. 67, Pl. 14, fig. 2a-b [chronotypic material from this location studied].

1927 *Acropora lavandulina* Michelin n. sp. 1842 - Felix, pars 33, p. 464 (cum syn.).

2008 *Acropora lavandulina* (Michelin, 1840) - Wallace, p. 327, Fig. 12.1-3.

2014 *Acropora lavandulina* (Michelin, 1840) - Santodomingo, p. 105-107, Fig. 21A-E (cum syn.).

Dimensions - Diameter (lumen) of radial corallites: up to 0.8 mm; diameter (lumen) of axial corallites: 1-1.8 mm; distance of corallite centers: 1-2.2 mm; septa/corallite: 12-24.

Description - Corallum ramose (corymbose), branches generally circular; plocoid; radial corallites tubular, protuberant, circular in outline, embedded in a porous to reticulate coenosteum; septa arranged in two to three cycles in six systems.

Type locality - Middle Eocene of France.

Distribution - Eocene of Italy, middle Eocene-lower Miocene of France, lower Oligocene of Austria (quarries Entfelden and Wimpissinger; this paper), Bulgaria (Haskovo), and Indonesia, lower Miocene of Egypt and Portugal, lower-middle Miocene of Italy.

Material - ICPUIBK-EN 8-VI; -WIM 1; -WIM 6/6-III; -WIM 6/10-II; -WIM 6/11-III; -WIM 6/12-II; -WIM 6/14-II; -WIM 6/23-II.

Family Astrocoeniidae Tomes, 1883
(= Stylocoeniidae Alloiteau, 1952)

Remarks - In general, authors have credited the authorship of the family Astrocoeniidae to Koby (1889). However, the fact has been largely overlooked that Tomes (1883) already used the genus *Astrocoenia* to create the family-level taxon Astrocoeniinae, giving him priority of authorship of each family-level taxon based on this type genus.

Genus *Stylocoenia* Milne Edwards & Haime, 1848

Type species *Astrea emarciata* Lamarck, 1816, Eocene of France (designation by Milne Edwards & Haime, 1848a).

Diagnosis - See Álvarez Perez (1993).

Synonyms - *Hydnoseriatopora* Reig Oriol, 1990 (type species *Hydnoseriatopora viai* Reig Oriol, 1990; fide Álvarez Perez, 1993); *Stylophoropsis* Reig Oriol, 1988 (type species *Stylophoropsis renzii* Reig Oriol, 1988, Tertiary of northeastern Spain; fide Álvarez Perez, 1993); *Triphyllocoenia* d'Orbigny, 1849 (type species *Triphyllocoenia excavata* d'Orbigny, 1849, Eocene of France, Hautes-Alpes).

Remarks - According to Álvarez Perez (1993), the type material of the type species of the genera *Hydnoseriatopora* Reig Oriol, 1990 (= *Hydnoseriatopora viai* Reig Oriol, 1990) and *Stylophoropsis* Reig Oriol, 1988 (= *Stylophoropsis renzii* Reig Oriol, 1988) closely corresponds to *Stylocoenia taurinensis* (Michelin, 1842).

Stylocoenia carryensis Chevalier, 1962
(Pl. 2, fig. 4)

v *1962 *Stylocoenia carryensis* nov. sp. Chevalier, p. 126-127, Pl. 1, figs 1 and 6 [topotypes studied].

Dimensions - Corallite diameter (max, lumen): 1.2-1.5 mm, in areas of intense budding around 0.6 mm; corallite diameter (min, lumen): 0.8-1.2 mm, in areas of intense budding around 0.4 mm; septa/corallite: 12+s3.

Description - Massive to encrusting colony, cerioid; costosepta developed in two complete cycles in six systems, regularly alternating in length; a small number of S3 present in some corallites.

Type locality - Lower Miocene of France (Chainon de La Nerthe, Bouches-du-Rhône).

Distribution - Lower Oligocene of Austria (quarry Entfelden; this paper), lower Miocene of France.

Material - ICPUIBK-EN 8-V.

Family Faviidae Milne Edwards & Haime, 1857
(= Hemiporitidae Alloiteau, 1952, p.p.)

Remarks - Many authors have credited the authorship of the family Faviidae to Gregory (1900) who used the genus *Favia* at this family-level. It has been largely overlooked that Milne Edwards & Haime (1857) erected the taxon Faviacées (including its Latinised version of Faviaceae), which had been immediately accepted as a lower family-level taxon by subsequent authors (e.g., Étallon, 1859, Faviacées; d'Achiardi, 1866, Faviaceae; Duncan, 1884, Favioida; Solomko, 1888, Favioida). In addition, it was de Fromentel (1861) who first used the family-level Faviidae (in the French version of "Famille - Faviens"), clearly referring to the work by Milne Edwards & Haime (for discussion on the Faviidae and designation of its type genus *Favia*, see Baron-Szabo, 2018).

Genus *Colpophyllia* Milne Edwards & Haime, 1848

Type species *Madrepora gyrosa* Ellis & Solander, 1786 (= *Meandrina gyrosa* Lamarck, 1816), Recent, West Indies (genus designation by Milne Edwards & Haime, 1848b).

Diagnosis - See Budd & Johnson (1999).

?*Colpophyllia* sp.
(Pl. 1, fig. 4)

Dimensions - Diameter of corallite series (wall to wall): 3.5-11 mm; septa/mm: 11-13/5.

Description - Fragment of a massive, meandroid colony; septa developed in four-five size orders.

Material - ICPUIBK-WIM 6/11-II; -WIM 6/13-II; ?-WIM 6/25-I (all from the lower Oligocene of Austria; quarry Wimpissinger).

Remarks - Because the specimens represent colony fragments, the identification is provisional.

Genus *Hydnophyllia* Reis, 1889

Type species *Leptoria eocaenica* Reuss, 1864, Polschitza/ Polšica near Oberburg, Steiermark/Gornji Grad, Slovenia, lower Oligocene (Rupelian).

Diagnosis - See Budd & Bosellini (2016).

Hydnophyllia costata (Catullo, 1856)
(Pl. 2, figs 9-10)

v *1856 *Meandrina costata* Cat. Catullo, p. 70, Pl. 15, fig. 1 [chronotypic material from this location studied].
v 2016 *Hydnophyllia costata* (Catullo, 1856) - Budd & Bosellini, p. 779-781, Fig. 5A-I [chronotypic material from this location studied] (cum syn.).

Dimensions - Diameter of corallite series (wall to wall): 10-14 mm, in areas of intense budding around 6 mm; septa (isolated corallites): 20-24; septa/mm: 11-14/10.

Description - Massive, meandroid colony; corallite centers distinct, connected by up to four lamellar linkages; small number of isolated corallites present; costosepta developed in three size orders, irregularly alternating in length and thickness.

Type locality - Oligocene of Italy (Castelgomberto).

Distribution - Oligocene of Italy (Crosara, Castelgomberto, Monteviale, Montecchio Maggiore, Vicenza: Rupelian; Castro: Chattian).

Material - ICPUIBK-EN 8-I.

Family Meandrinidae Gray, 1847

Genus *Dendrogyra* Ehrenberg, 1834

Type species *Maeandra (Dendrogyra) cylindrus* Ehrenberg, 1834, Antilles, Holocene (originally described as subgenus, raised to genus-level by Milne Edwards & Haime, 1848a).

Diagnosis - Genus is in need of revision. Here, genus characterisation by Milne Edwards & Haime (1857) is followed.

Dendrogyra intermedia Michelotti in Sismonda, 1871
(Pl. 1, figs 5-6)

*1871 *Dendrogyra intermedia* Michttl. Michelotti in Sismonda, p. 73, Pl. 6, fig. 2.
1925 *Dendrogyra intermedia* Sismonda, 1871 - Felix, pars 28, p. 36.

Dimensions - Corallite diameter (arranged in meandroid series): 3-6.5 mm; corallite diameter (isolated corallites): 2-3 mm; septa/mm: 6-8/5.

Description - Massive, meandroid colony with corallites arranged mainly in sinuous series; isolated corallites very rare; costosepta developed in six size orders, arranged highly irregularly.

Type locality - Lower Oligocene of Italy (Sassello).

Distribution - Lower Oligocene of Austria (quarry Wimpissinger; this paper) and Italy.

Material - ICPUIBK-WIM 6/18.

Family Merulinidae Milne Edwards & Haime, 1857

Genus *Caulastraea* Dana, 1846

Type species *Caulastraea furcata* Dana, 1846, Recent, Fiji.

Diagnosis - See Pfister (1980a).

Remarks - Recently, *Caulastraea* was compared with genera that are closely related morphologically (Baron-Szabo, 2016, tab. 2).

Caulastraea pseudoflabellum (Catullo, 1852)
(Pl. 1, fig. 7)

v	*1852	*Lithodendron pseudoflabellum*, nob. Catullo, p. 21-22, Pl. 2, fig. 3a-c [topotypes studied].
v	1852	*Lithodendron fusinieri*, nob. Catullo, p. 22, Pl. 3, fig. 2 [topotypes studied].
	1966	*Calamophyllia pseudoflabellum* Catullo - Kolosváry, p. 194-195, Figs 9-10.
v	1980a	*Caulastraea pseudoflabellum* (Catullo, 1852) - Pfister, p. 65-67, Pl. 5, figs 1-3 (cum syn.).
v	1988	*Caulastrea pseudoflabellum* (Catullo) - Bosellini, p. 132, Pl. 3, fig. 2 [chronotypic material from this location studied] (cum syn.).
non	2002c	*Caulastraea pseudoflabellum* (Catullo, 1852) - Schuster, p. 94, Pl. 4, fig. 3.

Dimensions - Great diameter of corallites: 7-9 mm; small diameter of corallites: 5-6 mm; septa/corallite: 32-48.

Description - Fragments of phaceloid colony; corallites are subcircular to subflabellate in outline; septa slightly wavy to sinuous, developed in three to four size orders, regularly alternating in length and thickness; up to around 15 septa reach corallite center where their axial ends often fuse with columella.

Type locality - Lower Oligocene of Italy (Vicenza).

Distribution - Eocene of Italy, middle Eocene of Slovenia, upper Eocene of Germany (Eisenrichterstein), Hungary, and Italy (Nago Limestone), lower Oligocene of Austria (quarry Wimpissinger; this paper), Bulgaria (Haskovo), Germany, Hungary, and Italy.

Material - ICPUIBK-WIM 6/6-I; -WIM6/10-I; -WIM-6/17-I.

Remarks - In having corallite diameters of up to 17 mm and septa developed in up to five (or ?six) size orders, the material described from the lower Oligocene of Greece (Schuster, 2002c, pl. 4, fig. 3) differs from *C. pseudoflabellum* but closely corresponds to *C. farsis* Schuster, 2002a (pl. 6, figs 1-4) from the upper Oligocene of Iran. Therefore, it is excluded here.

Family Stylophyliidae Frech, 1890

Genus *Pindosmilia* Chevalier in Brunn et al., 1955

Type species *Pindosmilia brunni* Chevalier in Brunn et al., 1955, Oligocene of Greece.

Diagnosis - See Chevalier, in Brunn et al. (1955).

Remarks - According to Chevalier, in Brunn et al. (1955), the genus *Pindosmilia* is characterised by

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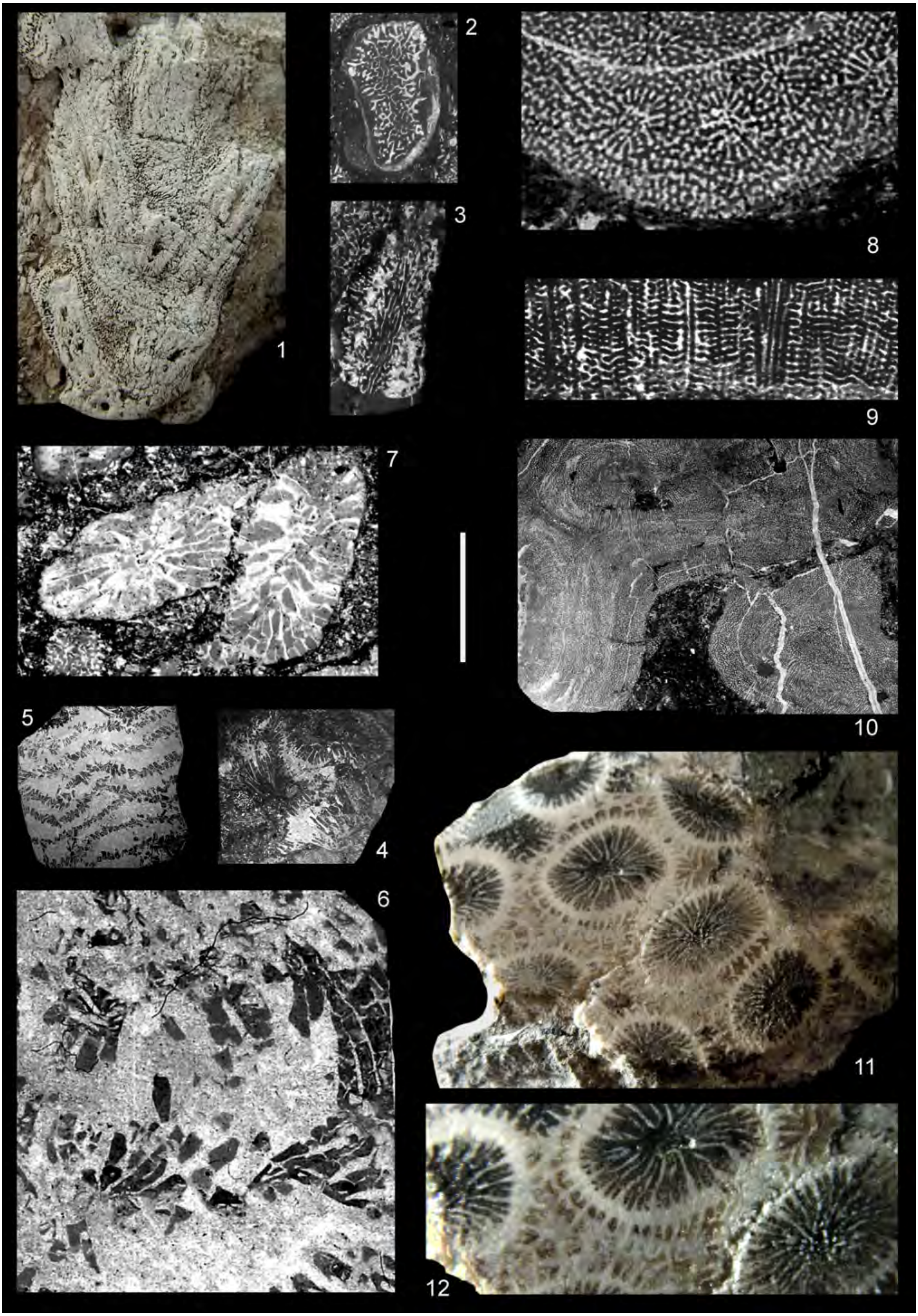
EXPLANATION OF PLATE 1

Lower Oligocene corals from the Paisslberg Formation, Austria (quarries Wimpissinger and Entfelden) (color online).

Figs 1-3 - *Acropora lavandulina* (Michelin, 1842).
  1 - Upper surface of colony, longitudinal view; quarry Entfelden, ICPUIBK-EN 8-VI; scale bar: 5 mm.
  2 - Oblique view of branch, thin section; quarry Wimpissinger, ICPUIBK-WIM-6/6-III; scale bar: 2.5 mm.
  3 - Longitudinal view of branch, thin section; quarry Wimpissinger, ICPUIBK-WIM-6-/1-IV; scale bar: 1.5 mm.
Fig. 4 - ?*Colpophyllia* sp.; cross view of colony, thin section; quarry Wimpissinger, ICPUIBK-WIM-6/13-II; scale bar: 5 mm.
Figs 5-6 - *Dendrogyra intermedia* Michelotti in Sismonda, 1871.
  5 - Cross view of colony, thin section; quarry Wimpissinger, ICPUIBK-WIM-6/18; scale bar: 6 mm.
  6 - Close-up of fig. 5; scale bar: 2.5 mm.
Fig. 7 - *Caulastraea pseudoflabellum* (Catullo, 1852); calicular view of colony fragment, slightly oblique, thin section; quarry Wimpissinger, ICPUIBK-WIM-6/17-I; scale bar: 3 mm.
Figs 8-10 - *Actinacis rollei* Reuss, 1864.
  8 - Calicular view of colony, thin section, close-up of fig. 10; scale bar: 1.5 mm.
  9 - Longitudinal view of colony, thin section; quarry Wimpissinger, ICPUIBK-WIM-6/6-II; scale bar: 2.5 mm.
  10 - View of ramose to incrusting colony, thin section; quarry Wimpissinger, ICPUIBK-WIM-6/20; scale bar: 6.5 mm.
Figs 11-12 - *Agathiphyllia gregaria* (Catullo, 1852).
  11 - Calicular view of colony, partially polished; quarry Entfelden, ICPUIBK-RIW; scale bar: 7 mm.
  12 - Close-up of fig. 11; scale bar: 3 mm.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extracalicular budding and plocoid polyp integration. However, based on the original illustrations of the type specimen (Brunn et al., 1955, pl. 9, figs 1-3), both lamellar linkages and remains of a common wall formerly enclosing at least two corallites are present typical of corallites that formed by intracalicular budding (see Brunn et al., 1955, pl. 9, fig. 1). In addition, the longitudinal view of the type material (Brunn et al., 1955, pl. 9, fig. 2) clearly shows some corallites in branching (subdendroid and ?reptoid) arrangement.

Pindosmilia cf. *brunni* Chevalier in Brunn et al., 1955
(Pl. 2, figs 5-7)

*1955 *Pindosmilia brunni* nov. sp. Chevalier in Brunn et al., p. 200-201, Pl. 9, figs 1-3.
non 2002c *Pindosmilia brunni* nov. sp. Chevalier, 1955 - Schuster, p. 93-94, Pl. 4, figs 1-2.

Dimensions - Great diameter of corallite: 11-15 mm; small diameter of corallite (min): 8-11 mm; distance of corallite centers: 15 mm; septa/corallite: 48 to around 60.

Description - Fragment of subdendroid (-?subreptoid) colony, produced by extracalicular budding; septa arranged in four complete cycles in six systems; S5 present to absent; up to 12 septa reach corallite center; corallites stand off of each other at angles of up to 90°.

Type locality - Oligocene of Greece (Pentalofon).

Distribution - Oligocene of Greece, lower Oligocene of Austria (quarry Entfelden; this paper).

Material - ICPUIBK-EN 8-III.

Remarks - In the original description of the type material by Chevalier in Brunn et al. (1955), the corallite diameter is given as 20-30 mm. However, as can be seen in the original illustrations of the type specimen (Brunn et al., 1955, pl. 9, figs 1-3), the range given by Chevalier does not include (?juvenile) corallites of around 10-15 mm. Because the Austrian material is a colony fragment, the total dimensions of its skeletal elements cannot be determined. Its range of corallite diameters corresponds to the small (?juvenile) corallites seen in the type material of *Pindosmilia brunni.*

In forming a solitary corallum that has a septotheca, the material described from the upper Oligocene of Greece (Doutsiko) in Schuster (2002c) rather corresponds to the genus *Syzygophyllia* Reuss and is, therefore, excluded here. The reasons for the author to assume that it could be a part of a colonial form remain unclear. Nevertheless, the presence of a septothecal wall in the material from Doutsiko excludes it from *Pindosmilia* which is characterised by a wall that is mainly parathecal.

Family ACTINACIDIDAE Vaughan & Wells, 1943

Genus *Actinacis* d'Orbigny, 1849

Type species *Actinacis martiniana* d'Orbigny, 1849, upper Santonian of France (Figuères).

Diagnosis - See Beauvais (1982) and Baron-Szabo (2003).

Actinacis rollei Reuss, 1864
(Pl. 1, figs 8-10)

v *1864 *Actinacis Rollei* Reuss, p. 27-28, Pl. 8, fig. 6a-b [topotypes studied].
non 1874 *Porites polystyla* nov. sp. - Reuss, p. 40-41, Pl. 56, figs 1-3.
non 1914 *Actinacis Rollei* Reuss - Oppenheim, p. 164-170, Pl. 3, fig. 4.
non 1937 *Actinacis* n. sp. cfr. *delicata* Rss - Zuffardi-Comerci, p. 289-290, Pl. 26, fig. 6.
v 1967 *Actinacis rollei* Reuss - Kolosváry, p. 211, Fig. 7 [chronotypic material from this location studied].
non 1992 *Actinacis rollei* Reuss, 1864 - Darga, p. 76, Pl. 7, fig. 5; Pl. 15, fig. 4.
1992 *Actinacis* cf. *rollei* Reuss, 1864 - Hladil, Otava & Galle, p. 1403 and p. 1407, Pl. 1, figs 1-2.
v 1995 *Actinacis rollei* Reuss, 1864 - Bosellini & Russo, p. 120-123, 125, Pl. 2, figs 1-6; Pl. 3, fig. 1; Text-figs 2-3 [chronotypic material from this location studied] (cum syn.).
non 2001 *Actinacis rollei* Reuss, 1864 - Gameil & Aly, p. 164-167, Fig. 6.1-3.
2002a *Actinacis rollei* Reuss, 1864 - Schuster, p. 18-19.

Dimensions - Diameter of corallite: 1-1.5 mm; distance of corallite centers: 1.2-2 mm; septa/corallite: 14-22.

Description - Knobby, columniform, and encrusting colonies; corallites circular in outline, regularly disposed over the colony; septa equal in thickness, developed in unclear systems.

Type locality - Lower Oligocene of Slovenia (Gornji Grad/Oberburg; Gornji Grad Formation/Oberburg Beds).

Distribution - Upper Eocene of Hungary and Italy (Nago Limestone), lower Oligocene of Austria (quarry Wimpissinger; this paper), Germany (Reit im Winkel), Italy, and Slovenia, upper Oligocene of Iran and Libya.

Material - ICPUIBK-WIM-6/6-II; -WIM 6/10-II; -WIM 6/14-I; - WIM 6/17-II; -WIM 6/20; -WIM 6/26-I.

Remarks - In having cerioid to cerio-plocoid polyp integration and up to 24 septa, the material described from the Oligocene of southern France by Oppenheim (1914, pl. 3, fig. 4) differs from both the genus *Actinacis* (rather resembling a *Goniopora*) and the species *rollei*. In having 24 septa in corallites throughout the colony, the material described from the upper Eocene of Germany in Darga (1992, pl. 7, fig. 5; pl. 15, fig. 4) differs from *A. rollei*. In having corallite diameters of up to 2 mm and up to 24 septa (in contrast to the information given in the description [18-20 septa] but seen in the illustrations) the material described from the lower Oligocene of the United Arab Emirates in Gameil & Aly (2001, fig. 6.1-3) differs from *A. rollei*. The material described as *Porites polystyla*

Reuss from the Oligocene of Italy which was grouped with *A. delicata* (here considered as a junior synonym of *A. rollei*) in Oppenheim (1914) and also was included in the list of synonyms of *A. rollei* by subsequent authors (e.g., Felix, 1925; Bosellini & Russo, 1995), differs from *A. rollei* in having both generally 24 septa and corallites that are 1.5-2 mm in diameter (dimensions as provided in the original description and illustrations in Reuss, 1874). In having 24 septa and corallites that are 1 mm in diameter, the material described as *Actinacis* cf. *delicata* from the Oligocene of Somalia (Zuffardi-Comerci, 1937) (*A. delicata* is here considered as a junior synonym of *A. rollei*) differs from *A. rollei*. Therefore, they are excluded from the synonymy of *A. rollei*.

Family Agariciidae Gray, 1847
(= Lamellofungiidae Alloiteau, 1957)

Genus *Pavona* Lamarck, 1801

Type species *Madrepora cistata* Ellis & Solander, 1786, Red Sea, Holocene
(subsequent designation Vaughan, 1918).

Diagnosis - See Pfister (1980a).

Pavona profunda (Reuss, 1868)
(Pl. 2, figs 3-4)

*1868 *Mycedium profundum* nov. sp. Reuss, p. 179, Pl. 16, fig. 2a-b.
2001 *Pavona (Pavona) profunda* (Reuss, 1868) - Chaix & Cahuzac, p. 22-23, Pl. 4, fig. 1.

Dimensions - Width of corallite series: 7-10 mm; diameter of isolated corallites: 4-7 mm; distance of corallite centers (same series): 6-10 mm, in areas of intense budding the distance is around 3 mm; septa/mm: 10-12/5.

Description - Submassive, thamnasterioid-submeandroid colony with mainly distinct to subdistinct corallites; isolated corallites sparse; septa developed in four to five size orders, alternating in length and thickness; up to around 12 septa reach corallite center; columella small, usually fused with axial ends of septa.

Type locality - Lower Oligocene of Italy (Castelgomberto Formation).

Distribution - Lower Oligocene of Italy (Castelgomberto Formation) and Austria (quarry Entfelden; this paper), upper Oligocene of southern France.

Material - ICPUIBK-EN 8-II.

Family Agathiphylliidae Vaughan & Wells, 1943

Genus *Agathiphyllia* Reuss, 1864

Type species *Agathiphyllia explanata* Reuss, 1864, lower Oligocene of Slovenia (subsequent designation by Vaughan, 1919).

Diagnosis - See Pfister (1980a).

Agathiphyllia gregaria (Catullo, 1852)
(Pl. 1, figs 11-12)

v *1852 *Lobophyllia gregaria*, nob. Catullo, p. 27, Pl. 2, fig. 5a-b [topotypes studied].
v 1871 *Heliastraea apenninica* d'Ach. - Michelotti, in Sismonda, p. 49.
v 1889 *Cyathomorpha Rochettina* Michelin sp. - Reis, p. 147-150, Pl. 3, figs 17-19.
v 1980a *Agathiphyllia gregaria* (Catullo, 1852) - Pfister, p. 80-82, Pl. 13, fig. 1; Pl. 14, fig. 7 (cum syn.).
v 1988 *Agathiphyllia gregaria* (Catullo, 1852) - Bosellini, p. 150-153, Pl. 5, fig. 3a-b [chronotypic material from this location studied].
1992 *Agathiphyllia gregaria* (Catullo, 1852) - Hladil, Otava & Galle, p. 1403 and 1407, Pl. 2, Fig. 2.
non 2001 *Agathiphyllia gregaria* (Catullo, 1852) - Gameil & Aly, p. 175-178, Fig. 9.4-6.
2002c *Agathiphyllia gregaria* (Catullo, 1852) - Schuster, p. 98, Pl. 11, figs 1-2; Pl. 12, figs 1-4.

Dimensions - Great diameter of corallites (lumen): 7.5-14 mm; small diameter of corallites (lumen): 4.5-9 mm; distance of corallite centers: 7.5-20 mm; septa/corallite: 30 to around 60.

Description - Small (around 60 mm in diameter) submassive colony; corallites subcircular to very elongate in outline; septa developed in three to four complete cycles in six systems; some septa of S5 present in corallites having a great diameter (lumen) of around 9 mm or larger.

Type locality - Oligocene of Italy (Montecchio Maggiore).

Distribution - Upper Eocene (Nago Limestone)-lower Miocene of Italy (Montecchio Maggiore, Castelgomberto Limestone, Sassello, Dego, Colli Torino), lower Oligocene of Austria (quarry Entfelden, this paper), Bulgaria (Haskovo), Germany (Reit im Winkel), Hungary, Libya, and Slovenia, Oligocene of Greece (Mesolouri, Doutsiko).

Material - ICPUIBK-RIW.

Remarks - In having corallite diameters of up to 25 mm and a distance of corallite centers of up to 40 mm, the material described from the lower Oligocene of the United Arab Emirates in Gameil & Aly (2001, fig. 9.4-6) differs from *A. gregaria*. In having cerio-plocoid corallites with diameters ranging between 4 and 10 mm, and pennular structures, the material described as *Agathiphyllia rochettina* (here considered as a junior synonym of *A. gregaria*) from the lower Oligocene of the United Arab Emirates in Gameil & Aly (2001) differs from both the genus *Agathiphyllia* and the species *A. gregaria*. Therefore, these specimens are excluded here.

Family Caryophylliidae Dana, 1846 (= Caryophylliinae Milne Edwards & Haime, 1857; = Desmophylliinae Vaughan & Wells, 1943; = Parasmiliinae Vaughan & Wells, 1943; = Parasmiliidae Alloiteau, 1952)

Remarks - The classification system of the caryophylliids has long been discussed. Vaughan & Wells (1943) and Wells (1956) divided the Family Caryophylliidae into the six subfamilies Caryophylliinae, Turbinoliinae, Thecocyathinae, Desmophylliinae, Parasmiliinae, and Eusmiliinae. Chevalier & Beauvais (1987) treated these as distinct families, even adding a seventh family (Dasmiidae; type genus *Dasmia* Milne Edwards & Haime, 1848c, grouped with the Desmophylliinae in Vaughan & Wells, 1943). Cairns (1994; also see discussion in Cairns, 1997) elevated the subfamily Turbinoliinae to the family level but did not recognise the distinction of the other families or subfamilies, respectively. Likewise, Stolarski (1995) elevated the Thecocyathinae to family status. Recent molecular studies (Romano & Cairns, 2000) imply that the Caryophylliidae is an unnatural, or polyphyletic, family. Therefore, the recognition of subfamilies cannot be supported until further research is conducted. Based on the current understanding of this group, the genus *Faksephyllia* would be grouped with the Parasmiliinae (Baron-Szabo, 2016).

Genus *Faksephyllia* Floris, 1972

Type species *Caryophyllia faxoensis* Beck in Lyell, 1837, middle Danian of Denmark (Fakse limestone); neotype designation by Floris (1972).

Diagnosis - See Baron-Szabo (2016).

Remarks - From the Nielsen collection, Floris (1972, pl. 4, fig. 11) chose specimen MMH 2043 as the neotype of the type species *Faksephyllia faxoensis* (Beck in Lyell, 1837). This specimen was originally figured as a sketch in Nielsen (1922, pl. 1, fig. 1). Later, Floris (1972, pl. 4, fig. 11) presented the same specimen as a photograph. Recently, reproductions of both images were presented (Baron-Szabo, 2016, pl. 1, figs 1-2).

Floris (1972) mentioned that considerable effort was made to track down the original Beck/Lyell (Mineralogical Museum of Copenhagen University) material but without success.

Based on the presence of a sparsely developed endotheca; dendroid, fasciculate or phaceloid colony formation; compact costosepta that are smooth or have small (<50 µm) granules laterally; costae that are short or absent; and a corallite wall that can be a very thick septotheca, the genus *Faksephyllia* was grouped with the family Caryophylliidae (Baron-Szabo, 2016).

Faksephyllia faxoensis (Beck in Lyell, 1837)
(Pl. 2, figs 1-2)

*v 1837 *Caryophyllia faxoensis* Beck in Lyell, p. 249, Fig. 4 [topotypes studied].
parsv 1868 *Rhabdophyllia tenuis* nov. sp. Reuss, p. 144, Pl. 2, fig. 4a-b (non figs 3 and 5).
? 1896 *Rhabdophyllia tenuis* Reuss - Oppenheim, p. 262.
? 1912 *Calamophyllia rosicensis* n. sp. - Oppenheim, p. 124, Pl. 16, fig. 7-7c.
v 1972 *Faksephyllia faxoensis* gen. n. & Beck, in Lyell, 1837 sp.- Floris, p. 73-80, Pl. 4, figs 7-11; Pl. 5, figs 1-5 [topotypes studied] (cum syn).
v 2016 *Faksephyllia faxoensis* (Beck, in Lyell, 1837) - Baron-Szabo, p. 529-533, Pl. 1, figs 1-13; Pl. 2, figs 1-15 (cum syn.).

Dimensions - Diameter of corallite (monocentric): 2-6 mm, mainly ranging between 3.5-6 mm, in late budding stages often up to 8 mm, maximum size in a few places 10 mm; septa/corallite 18-52; height of branches: 10 to around 30 mm.

EXPLANATION OF PLATE 2

Lower Oligocene corals from the Paisslberg Formation, Austria (quarries Wimpissinger and Entfelden) (color online).

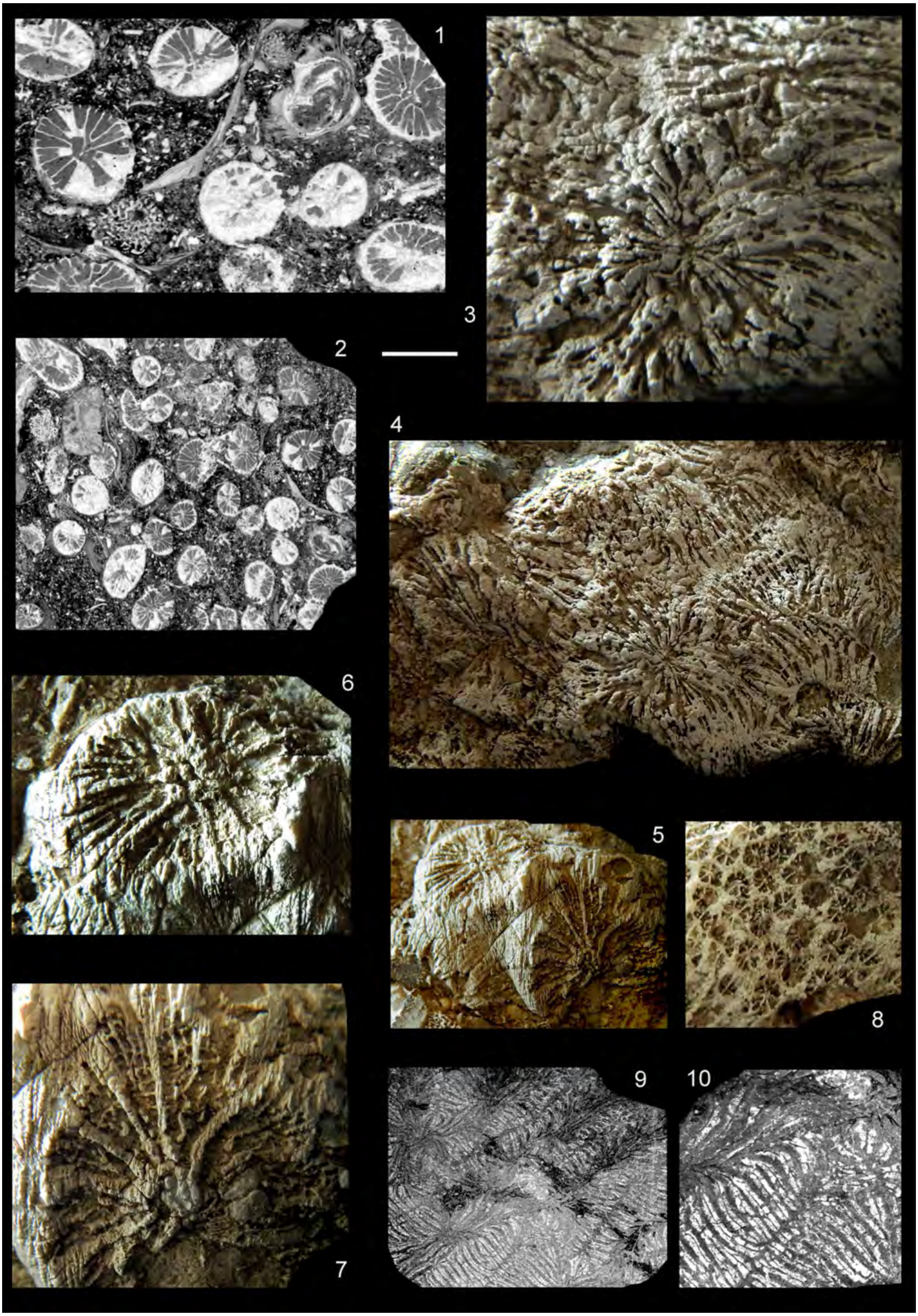
Figs 1-2 - *Faksephyllia faxoensis* (Beck in Lyell, 1837).
1 - Calicular view of colony, thin section, close-up of fig. 2, scale bar: 3.5 mm.
2 - Calicular view of colony; quarry Wimpissinger, ICPUIBK-WIM-6/12-I; scale bar: 8.5 mm.

Figs 3-4 - *Pavona profunda* Reuss, 1868.
3 - Calicular view of colony, close-up of fig. 4; scale bar: 3 mm.
4 - Upper surface of colony, calicular view; quarry Entfelden, ICPUIBK-EN 8-II; scale bar: 5.5 mm.

Figs 5-7 - *Pindosmilia* cf. *brunni* Chevalier in Brunn et al., 1955.
5 - Calicular view, close-up of fig. 7; scale bar: 3.5 mm.
6 - Calicular view, close-up of fig. 7; scale bar: 3.5 mm.
7 - Upper surface of colony, calicular view; quarry Entfelden, ICPUIBK-EN 8-III; scale bar: 6.5 mm.

Fig. 8 - *Stylocoenia carryensis* Chevalier, 1962; upper surface of colony, calicular view; quarry Entfelden, ICPUIBK-EN 8-V-II; scale bar: 3.5 mm.

Figs 9-10 - *Hydnophyllia costata* (Catullo, 1856).
9 - Cross view of colony, thin section; Entfelden, ICPUIBK-EN 8-I; scale bar: 9 mm.
10 - Close-up of fig. 9; scale bar: 5.5 mm.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Description - Phaceloid to subdendroid and fasciculate colony. Corallites circular to irregularly elliptical in outline. In corallites that are not influenced by budding, costosepta developed in two-four cycles in six systems. In corallites of 4 mm in diameter, around 40 septa are present. Septa straight or wavy, oldest of which reach corallite center where they sometimes fuse. Septa are equally thin or, in some corallites, oldest septa significantly increase in thickness towards the corallite wall, becoming up to around ten times as thick as youngest septa. Branching angle often between 30°-45°, can be up to 90°. Columella weakly to well developed, 1-2 mm in length, spongy-papillose or formed by a small number of twisted segments, or absent.

Type locality - Middle Danian of Denmark (Fakse limestone).

Distribution - Paleocene of Austria (Kambühel limestone, Styria), Azerbaijan (Dash-Salakhly), and Denmark (Greenland, Kangilia and Nugssuaq areas), Danian of Denmark (Fakse), Kazakhstan (Mangyshlag), and Sweden (Limhamn), ?Eocene of Bosnia-Herzegovina (Rošići area), lower Oligocene of Italy (Monte Pulgo and Castelgomberto, Vicenza area), Austria (quarry Wimpissinger), Germany (Reit im Winkel, Bavaria, Reiter beds), and ?Hungary.

Material - ICPUIBK-WIM 5; -WIM 6/2-II; -WIM 6/10-I and -IV; -WIM 6/12-I; -WIM 6/13-I; -WIM 6/23-I; -WIM 6/25.

Remarks - In forming phaceloid to subdendroid colonies and having corallite diameters ranging between 3 and 5 mm; number of septa between 20 and 30 that sometimes fuse in a way resembling the dendrophylliid and micrabaciid septal arrangements; trabecular extensions of axial ends of septa that form a pseudo-columella; and sparsely developed endotheca, the material described by Oppenheim (1912, pl. 16, fig. 7-7c) as *Calamophyllia rosicensis* from the Eocene of Bosnia-Herzegovina shows close affinities to *Faksephyllia faxoensis* (Beck). Because information regarding the budding mode is missing, the grouping of this taxon with *Faksephyllia* is only provisional. Oppenheim (1896) assigned material to *Rhabdophyllia tenuis* Reuss from the lower Oligocene of Hungary. Because the Reuss' material represents a mix of specimens that belong to various genera, it remains unclear whether or not the Hungarian material corresponds to *Faksephyllia*.

Based on the current taxonomic model (visit: www.corallosphere.org), *Faksephyllia* represents the earliest colonial caryophylliid (also see Baron-Szabo, 2016, tab. 1).

CONCLUSIONS

The described Austrian coral fauna consists of at least eleven species from eleven genera of eleven families. Considering that approximately 20% of the coral fragments that could not be taxonomically assigned due to poor preservation, seemed to differ from the identified taxa (based on corallite integration and other skeletal elements), it is suggested that the actual taxonomic diversity of this lower Oligocene fauna is higher.

The fauna is represented only by colonial forms of three types of polyp integration, none of which is dominant: cerioid to plocoid; meandroid to thamnasterioid; and branched forms. Most of the species (73%) are characterised by medium- to large-size corallites 4 to >10 mm in diameter, including all of the meandroid-thamnasterioid and the branching groups, as well as the plocoid *Agathiphyllia gregaria*.

The corals grew as isolated colonies and in carpets in a low-energy shoreface seaward of a rocky to pebbly beach that was punctuated by high-energy events. Despite stressors typical of such habitats (e.g., seasonal temperature changes, salinity fluctuations), the fauna is quite diverse compared to both fossil and extant coral faunas reported from similar environments.

All of the described species first appeared in the Paleogene, but the majority (eight taxa = 73%) did not cross the Paleogene-Neogene boundary. None of the species is known from strata younger than the Miocene. On the species level, closest correspondence is with faunas of southern Europe, in particular with those of the Lessini Shelf (seven species = 64%). The species of the Paisslberg Formation with the largest lower Oligocene biogeographic distribution are plocoid (*Acropora lavandulina*, *Actinacis rollei*, and *Agathiphyllia gregaria*) and branching (*Caulastrea*, *Faksephyllia*).

On the genus-level, greatest paleobiogeographic affinity again is with the coral faunas of northern Italy: except for *Pindosmilia,* ten genera (91%) are also known from the Italian Lessini Shelf. Regarding similarities to other lower Oligocene faunas, eight genera (= 73%) were also described from both Germany (Reit im Winkel) and Slovenia, seven genera (= 64%) were reported from Jamaica, and five genera (= 46%) were found in Greece (Tab. 3). In view of the paleogeographic distribution of land and seaways, this suggests that the carbonate environments along the southern fringe of the Alpine edifice were the crucial reservoir for coral recruitment to the northern shelf.

With regard to their environmental occurrences, all of the taxa have been found elsewhere in shallow-water, (sub) tropical reefal and peri-reefal settings. The caryophylliine coral *Faksephyllia faxoensis,* however, stands out as the only taxon which, in addition, has been reported from deep-water environments.

The assemblage represents the northernmost coral fauna found in reefal and peri-reefal settings reported to date for Rupelian time.

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REFERENCES

Abbott B.M. (1975). Implications for the fossil record of modern carbonate bank corals. *Geological Society of America Bulletin*, 86: 203-204.

Achiardi A. d' (1866). Corallarj fossili del terreno nummulitico dell'Alpi venete. *Memorie della Società Italiana di Scienze Naturali*, 2: 1-53.

Achiardi A. d' (1868). Corallarj fossili del terreno nummulitico dell'Alpi venete. Parte Seconda. *Memorie della Società Italiana di Scienze Naturali,* 4: 1-31.

Alloiteau J. (1952). Embranchment des Coelentérés. II. Madréporaires post-paléozoïques. *In* Piveteau J. (ed.), Traité de Paléontologie, 1: 539-684.

Alloiteau J. (1957). Contribution à la systématique des madréporaires fossiles. 462 pp. Centre National Recherche Scientifique, Paris.

Álvarez Perez G. (1993). Cnidaria Fòssils de la Conca d'Igualda. 261 pp. Universitat de Barcelona, Barcelona.

Álvarez Perez G., Busquets P., Vilaplana M. & Ramos-Guerrero E. (1993). Fauna coralina paleógena de las Islas Baleares (Mallorca y Cabrera, España). *Batalleria*, 3 [for 1989]: 61-63.

Angelis d'Ossat G. de (1894). I Corallarj dei terreni terziari dell'Italia settentrionale. Collezione Michelotti. Museo Geologico della R. Università di Roma. *Atti della Reale Accademia dei Lincei,* 5: 164-280.

Barnes R.S.K. & Hughes R.N. (1988). An Introduction to Marine Ecology. 351 pp. Blackwell Scientific, Oxford.

Baron-Szabo R.C. (2003). Taxonomie und ontogenie von scleractinen Korallen der ostalpinen Oberkreide (Hochmoos- und Grabenbachschichten, Gosau-Gruppe, Santon). *Jahrbuch der Geologischen Bundesanstalt,* 143: 107-201.

Baron-Szabo R.C. (2014). Scleractinian Corals from the Cretaceous of the Alps and Northern Dinarides (Helvetic Unit; Austro-Alpine Units; Rhenodanubian Unit; N Dinaric Platform; Inner Dinarides), with remarks on related taxa. *Abhandlungen der Geologischen Bundesanstalt Wien*, 68: 1-297.

Baron-Szabo R.C. (2016). New taxonomic, stratigraphic, and geographic information on the genus *Faksephyllia* Floris, 1972 (Scleractinia; Caryophylliidae); first records from the Oligocene of Austria, Germany, and Italy. *Zootaxa*, 4154: 526-540.

Baron-Szabo R.C. (2018). Nomenclatural notes on the genus *Favia* (Anthozoa: Scleractinia: Faviina: Faviidae). *Proceedings of the Biological Society of Washington*, 131: 197-201.

Baron-Szabo R.C. & Cairns S.D. (2019). Part F, Revised, Volume 2, Chapter 14: Systematic Descriptions of the Scleractinia Family Dendrophylliidae. *Treatise Online*, 119: 1-33.

Baron-Szabo R.C. & Sanders D. (2018). Scleractinian corals from the Lower Oligocene of the Eastern Alps, Austria: taxonomic composition, palaeoecology and palaeobiogeography - preliminary results. PANGEO Austria 2018, Vienna (Austria), 26.09.2018, Abstract: 6.

Barta-Calmus S. (1973). Revision de collections de madréporaires provenants du nummulitique du sudest de la France, de l'Italie et de la Yugoslavie septentrionales. 694 pp. PhD thesis, Université de Paris.

Beauvais L. (1981). Sur le taxinomie des Madréporaires mésozoïques. *Acta Pa1aeontologica Polonica*, 25: 345-360.

Beauvais M. (1982). Révision systématique des Madréporaires des couches de Gosau (Crétacé supérieur, Autriche). *Travaux du Laboratoire de Paléontologie des Invertébrés*, 2: 1-278.

Bernecker M. & Weidlich O. (1990). The Danian (Paleocene) coral limestone of Fakse, Denmark, a model for ancient aphotic, azooxanthellate coral mounds. *Facies*, 22: 103-138.

Bernecker M. & Weidlich O. (2005). Azooxanthellate corals in the Late Maastrichtian-early Paleocene of the Danish basin, bryozoan and coral mounds in a boreal shelf setting. *In* Freiwald A. & Roberts J.M. (eds), Cold-water Corals and Ecosystems, Springer-Verlag, Berlin-Heidelberg: 3-25.

Bontscheff St. (1897). Das Teriärbecken von Haskovo (Bulgarien). *Jahrbuch der Kaiserlich Königlichen Geologischen Reichsanstalt*, 46: 309-384.

Bosellini F.R. (1988). Oligocene corals from Monte Bastia (Vicentin Lessini Mountains, N Italy). *Atti e Memorie della Accademia Nazionale di Scienze Lettere e Arti di Modena*, serie VII, 5: 111-157.

Bosellini F.R. (1998). Diversity, composition and structure of Late Eocene shelf-edge associations (Nago Limestone, northern Italy). *Facies*, 39: 203-226.

Bosellini F.R. & Russo A. (1988). The Oligocene *Actinacis* coral community of the Southern Alps (Italy): Temperature vs. terrigenous control. *In* Choat J.H., Barnes D., Borowitzka M.A., Coll J.C., Davies P.J., Flood P., Hatcher B.G., Hopley D., Hutchings P.A., Kinsey D., Orme G.R., Pichon M., Sale P.F., Sammarco P., Wallace C.C., Wilkinson C., Wolanski E. & Bellwood O. (eds), Contributed Papers. *Proceedings of the 6th International Coral Reef Symposium*, 3: 385-391.

Bosellini F.R. & Russo A. (1995). The scleractinian genus *Actinacis*: systematic revision and stratigraphic record of the Tertiary species with special regard to Italian occurrences. *Rivista Italiana di Paleontologia e Stratigrafia*, 101: 215-230.

Bosellini F.R. & Stemann T. (1996). Autecological significance of growth form in the scleractinian *Actinacis rollei* Reuss (Oligocene, Lessini Mountains, Northern Italy). *In* Cherchi A. (ed.), Autecology of selected fossil organisms: Achievements and problems. *Bollettino della Società Paleontologica Italiana,* Special Volume 3: 31-43.

Bosellini F.R. & Trevisani E. (1992). Coral facies and cyclicity in the Castelgomberto Limestone (Early Oligocene, Eastern Lessini Mountains, Northern Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, 98: 339-352.

Bourne G.C. (1900). Anthozoa. *In* Lankester E.R. (ed.), Treatise on Zoology, Volume 2, Adam & Charles Black, London: 1-84.

Brandner R. (1984). Meeresspiegelschwankungen und Tektonik in der Trias der NW-Tethys. *Jahrbuch der Geologischen Bundesanstalt*, 126: 435-475.

Brunn J.H., Chevalier J.-P. & Marie P. (1955). Quelques formes nouvelles de polypiers et de foraminiféres de l'Oligocène et du Miocène du NW de la Grèce. *Bulletin de la Société Géologique de France, 6e série*, 5: 193-202.

Budd A.F. & Bosellini F.R. (2016). Revision of Oligocene Mediterranean meandroid corals in the scleractinian families Mussidae, Merulinidae and Lobophylliidae. *Journal of Systematic Palaeontology*, 14: 771-798.

Budd A.F. & Johnson K.G. (1999). Neogene paleontology in the northern Dominican Republic 19. The family Faviidae (Anthozoa: Scleractinia). Part II. The genera *Caulastraea, Favia, Diploria, Thysanus, Hadrophyllia, Manicina*, and *Colpophyllia*. *Bulletins of American Paleontology*, 356: 1-83.

Cahuzac B. & Chaix C. (1993). Les faunes de coraux (Anthozoaires Scléractiniaires) de la façade atlantique française au Chattien et au Miocène. *Ciências da Terra*, 12: 57-69.

Cairns S.D. (1994). Scleractinia of the temperate North Pacific. *Smithsonian Contributions to Zoology*, 557: 1-150.

Cairns S.D. (1997). A generic revision and phylogenetic analysis of the Turbinoliidae (Cnidaria, Scleractinia). *Smithsonian Contributions to Zoology*, 591: 1-55.

Cairns S.D. (2001). A generic revision and phylogenetic analysis of the Dendrophylliidae (Cnidaria: Scleractinia). *Smithsonian Contributions to Zoology*, 615: 1-75.

Catullo T.A. (1852). Cenni sopra il terreno di sedimento superiore delle Provincie Venete e descrizione di alcune specie di polipai fossili ch'esso racchiude. *Memorie del Reale Istituto Veneto di Scienze, Lettere ed Arti,* 4: 1-44.

Catullo T.A. (1856). Dei terreni di sedimento superiore della Venezie e dei fossili Bryozoari, Antozoari e Spongiari. Angelo Sicca, Padova: 1-88.

Chaix C. & Cahuzac B. (2001). Une faune inédite de coraux scléractiniaires dans le gisement chattien d'Escornebéou (Landes, SW France); stratigraphie, systématique et paléoécologie. *Annales de Paléontologie*, 87: 3-47.

Chevalier J.-P. (1956). Les polypiers anthozoaires du Stampien de Gaas (Landes). *Bulletin de la Societe d'Histoire Naturelle de Toulouse*, 90: 375-410.

Chevalier J.-P. (1962). Recherches sur les Madréporaires et les Formations Récifales Miocènes de la Méditerranée Occidentale. *Mémoires de la Société Géologique de France*, 40: 1-562.

Chevalier J.-P. & Beauvais L. (1987) Systématique. *In* Grassé P.-P. & Doumenc D. (eds), Ordre des scléractiniaires, XI, Masson, Paris: 679-764.

Dana J.D. (1846). United States Exploring Expedition during the years 1838-1842 under the command of Charles Wilkes, U.S.N. Volume 7: Zoophytes. 740 pp. Sherman, Philadelphia.

Darga R. (1992). Geologie, Paläontologie und Palökologie der südostbayerischen unter-priabonen (Ober-Eozän) Riffkalkvorkommen des Eisenrichtersteins bei Hallthurm (nördliche Kalkalpen) und des Kirchbergs bei Neubeuern (Helvetikum). *Münchner Geowissenschaftliche Abhandlungen Reihe A: Geologie und Paläontologie,* 23: 1-166.

Dockery D.T. (1982). Lower Oligocene Bivalvia of the Vicksburg Group in Mississippi. *Mississippi Department of Natural Resources Bureau of Geology*, 123: 1-261.

Dodge R.E. & Vaisnys J.R. (1977). Coral populations and growth patterns: responses to sedimentation and turbitity associated with dredging. *Journal of Marine Research*, 35: 715-730.

Dryer S. & Logan A. (1978). Holocene reefs and sediments of Castle Harbour, Bermuda. *Journal of Marine Research*, 36: 399-425.

Duncan P.M. (1863). On the fossil corals of the West Indian Islands, Part I. *Quarterly Journal of the Geological Society of London,* 19: 406-458.

Duncan P.M. (1866). A Monograph of the British fossil corals, 2nd Series. VII. Corals from the Tertiary Formations. I. Corals from Brackenhurst and Roydon. *Palaeontographical Society,* Volume for 1865: 40-66.

Duncan P.M. (1868). On the fossil corals (Madreporaria) of the West-Indian Islands, Part IV, Conclusions. *Quarterly Journal of the Geological Society of London,* 24: 9-33.

Duncan P.M. (1884). A revision of the families and genera of the sclerodermic Zoantharia, Ed. and H., or Madreporaria (M. Rugosa excepted). *Journal of the Linnean Society of London, Zoology*, 18: 1-204.

Durham J.W. (1942). Eocene and Oligocene coral faunas of Washington. *Journal of Paleontology,* 16: 84-104.

Durham J.W. (1943). Pacific coast Cretaceous and Tertiary corals. *Journal of Paleontology,* 17: 196-202.

Ehrenberg C.G. (1834). Die Corallenthiere des rothen Meeres physiologisch Untersucht und systematisch Verzeichnet. Beiträge zur physiologischen Kenntniss der Corallenthiere im allegemeinen, und besonders des rothen Meeres, nebst einem Versuche zur physiologischen Systematik derselben. *Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin*, volume for 1832: 225-380.

Ellis J. & Solander D.C. (1786). The Natural History of Many Curious and Uncommon Zoophytes Collected from Various Parts of the Globe. 208 pp. Benjamin White and Son and Peter Elmsly, London.

Étallon A. (1859). Études paléontologiques sur le Haut-Jura. Rayonnés du Corallien. *Mémoires de la Société d'Émulation du Département du Doubs, 3e série*, 6: 53-260.

Felix J.P. (1925). Anthozoa eocaenica et oligocaenica. Fossilium Catalogus I: Animalia, pars 28. 296 pp. Junk, Berlin.

Felix J. (1927). Anthozoa miocaenica. Fossilium Catalogus I: Animalia, pars 33, Junk, Berlin: 297-488.

Floris S. (1972). Scleractinian corals from the Upper Cretaceous and Lower Tertiary of Nugssuaq, West Greenland. *Muséum de Minéralogie et de Géologie de l'Université de Copenhague, Communications paléontologiques*, 183: 1-132.

Fravega P., Piazza M., Stockar R. & Vannucci G. (1994). Oligocene coral and algal reef and related facies of Valzemola (Savona, NW Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, 100: 423-456.

Frech F. (1890). Die Korallenfauna der Trias. *Palaeontographica,* 37: 1-116.

Fromentel L.É.G. de (1861). Introduction à l'étude des Polypiers fossiles. *Mémoires de la Société d'Émulation du Département du Doubs*, 5: 1-357.

Frost H. (1981). Oligocene reef coral biofacies of the Vicentin, northeast Italy. *In* Toomey D.F. (ed.), European fossil reef models. *Society of Economic Paleontologists and Mineralogists, Special Publication,* 30: 483-539.

Frost S.H., Harbour J.L., Beach D.K., Realini M.J. & Harris P.M. (1983). Oligocene reef tract development, southwestern Puerto Rico. *Sedimenta*, 11: 1-107.

Frost S.H. & Langenheim R.L. (1974). Cenozoic Reef Biofacies. 388 pp. Northern Illinois Press, Dekalb.

Gameil M. & Aly M.F. (2001). Paleontological studies on some Oligocene colonial corals from Gabal Hafit (Al Ain area, UAE). *Middle East Research Center, Ain Shams University, Earth Science Series*, 15: 156-183.

Geister J. & Ungaro S. (1977). The Oligocene formations of the Colli Berici (Vicenza, northern Italy). *Eclogae Geologicae Helvetiae*, 70: 811-823.

Gill G.A. & Coates A.G. (1977). Mobility, growth patterns and substrate in some fossil and Recent corals. *Lethaia,* 10: 119-134.

Ginsburg R.N. (1972). South Florida Carbonate Sediments. *Sedimenta,* 2: 1-71.

Glibert M. (1974). Quelques Turbinoliidae Cenozoiques des collections de l'Institut Royal des Sciences Naturelles de Belgique, I: Genre *Turbinolia* Lamarck, 1816. *Bulletin Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre,* 50: 1-27.

Gray J.E. (1847). An outline of an arrangement of stony corals. *Annals and Magazine of Natural History, Series 1*, 19: 120-128.

Gregory J.W. (1900). The corals. *In* The Jurassic fauna of Cutch. *Memoirs of the Geological Survey of India, Palaeontologia Indica, Series IX*, 2: 1-195.

Gruber A. (1995). Öffnung und Schliessung von Tertiärbecken im Bereich des Eiberger Beckens (Unterinntal, Tirol). Ein strukturgeologischer Beitrag zur Unterinntaler Scherzone. 144 pp. Unpublished Diploma thesis, University of Innsbruck.

Handy M.R., Ustaszewski K. & Kissling E. (2015). Reconstructing the Alps-Carpathians-Dinarides as a key to understanding switches in subduction polarity, slab gaps and surface motion. *International Journal of Earth Sciences*, 104: 1-26.

Hegedüs G. (1962). Magyarországi oligocen korallok (Oligocene corals of Hungary). *Annual Report of the Hungarian Geological Inststute, from the year 1959*: 231-261.

Hladil J., Otava J. & Galle A. (1992). Oligocene Carbonate Buildups of the Sirt Basin, Libya. *Geology of Libya,* 4: 1401-1420.

Ikeda E., Iryu Y., Sugihara K., Ohba H. & Yamada T. (2006). Bathymetry, biota and sediments on the Hirota Reef, Tane-gashima — the northernmost coral reef in the Ryukyu Islands. *Island Arc*, 15: 407-419.

Islamoglu Y. (2008). Molluscan biostratigraphy and paleoenvironmental reconstruction of Oligocene deposits in the Denizli and Kale-Tava subbasinbs (SW Turkey). *Geodiversitas*, 30: 261-285.

Johnson K.G. (2007). Reef-coral diversity in the Late Oligocene Atigua Formation and temporal variation of local diversity on Caribbean Cenozoic Reefs. *In* Hubmann B. & Piller W.E. (eds), Fossil Corals and Sponges. Proceedings of the 9th International Symposium on Fossil Cnidaria and Porifera. Österreichische Akademie der Wiisenschaften, Schritenreihe der Erdwissenschaftlichen Kommission, 17: 471-491.

Joly N. & Leymerie A. 1848. Memoire sur les *Nummulites*, considerees zoologiquement et geologiquement. *Memoire de l'Academie des Sciences de Toulouse* (3), 4: 149-218.

Koby F. (1889). Monographie des polypiers jurassiques de la Suisse (9). *Mémoires de la Société Paléontologique Suisse (=Abhandlungen der Schweizerischen Paläontologischen Gesellschaft),* 16: 457-586.

Kołodziej B. & Marcopoulou-Diacantoni A. (2003). Late Eocene-Oligocene corals from Evros (Thrace Basin, NE Greece). Abstracts of the 8th International Symposium on Fossil Cnidaria and Porifera, Graz, August 3-7, 2003. *Berichte des Institutes für Geologie und Paläontologie der Karl-Franzens-Universität Graz*, 7: 45.

Kolosvary G. (1966). Lutetian corals from Crni Kal in Yugoslavia. *Geologjia*, 10: 189-204.

Kolosvary G. (1967). Korallen und Balaniden aus den paläogenen Schichten Jugoslawiens [Corals and balanids from Paleogene beds of Yugoslavia]. *Geologija*, 10: 205-218.

Kühn O. (1954). Korallen des mitteldeutschen Mitteloligozäns. *Notizblatt des hessischen Landesamtes, Bodenforschung*, 82: 50-56.

Lamarck J.B.P. de (1801). Système des animaux sans vertèbres. 423 pp. Lamarck et Deterville, Paris.

Lamarck J.B.P. de (1816). Histoire naturelle des animaux sans vertèbres. 568 pp. Verdiére, Paris.

Linnaeus C. von (1758). Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. 1, 10th edition. 824 pp. Holmiae, Stockholm.

Löffler S.-B. (1999). Systematische Neubearbeitung und paläoökologische Aspekte der unteroligozänen Molluskenfauna aus den Zementmergeln von Bad Häring (Unterinntal, Tirol). *Tübinger geowissenschaftliche Arbeiten A*, 54: 1-207.

Lyell C. (1837). On the Cretaceous and Tertiary Strata of the Danish Islands of Seeland and Möen. *Transactions of the Geological Society, London, series 2*, 5: 243-257.

Mandl G.W. (1999). The Alpine sector of the Tethyan shelf - Example of Triassic to Jurassic sedimentation and deformation from the Northern Calcareous Alps. *Mitteilungen der Österreichischen Geologischen Gesellschaft*, 92: 61-77.

Marcopoulou-Diacantoni A., Fountoulis J. & Lekkas E. (1996). The occurrence of Oligocene (Rupelian) corals in west-central Peloponnesus (Greece), paleoecological and paleobiogeographic significance. *Geologie Mediterraneenne*, 23: 11-25.

Michelin H. (1842). Iconographie zoophytologique. Description par localités et terrains des polypiers fossiles de France. Volume 2, Bertrand, Paris: 41-72.

Michelotti G. (1841). Saggio storico dei rizopodi caratteristici dei terreni sopracretacei. *Memorie di matematica e di fisica della Società Italiana delle Scienze Residente in Modena*, 22: 253-302.

Milne Edwards H. & Haime J. (1848a). Observations sur les polypiers de la famille des astréides. *Comptes Rendus de l'Académie des Sciences*, 27: 465-469.

Milne Edwards H. & Haime J. (1848b). Note sur la classification de la deuxième tribu de la famille des astréides. *Comptes Rendus de l'Académie des Sciences*, 27: 490-497.

Milne Edwards H. & Haime J. (1848c). Recherches sur les polypiers (2). Monographie des turbinolides. *Annales de Sciences Naturelles, Série 3, Zoologie*, 9: 211-344.

Milne Edwards H. & Haime J. (1857). Histoire naturelle des Coralliaires ou polypes proprement dits. Volume 2. 560 pp. Librairie Encyclopédique de Roret, Paris.

Nebelsick J., Bassi D. & Drobne K. (2000). Microfacies analysis and palaeoenvironmental interpretation of Lower Oligocene, shallow-water carbonates (Gornji Grad beds, Slovenia). *Facies*, 43: 157-176.

Nebelsick J., Rasser M. & Stingl V. (2001). Autochthonous facies and debris flows compared: Lower Oligocene carbonates of the Lower Inn Valley (Tyrol, Austria). *Facies*, 44: 31-45.

Nielsen F. (1922). Zoantharia from Senon and Paleocene in Denmark and Skaane. *Biologiske skrifter*, 8: 199-233.

Oken L. (1815). Lehrbuch der Naturgeschichte. III Zoologie. 850 pp. August Schmid und Comp., Leipzig-Jena.

Oppenheim P. (1896). Die oligocäne Fauna von Polschitza in Krain. *Bericht über die Senckenbergische Naturforschende Gesellschaft in Frankfurt am Main,* 1896: 259-283.

Oppenheim P. (1912). Neue Beiträge zur Eozänfauna Bosniens. *Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients*, 25: 87-149.

Oppenheim P. (1914). Über *Porites polystyla* Reuss und die Gattung *Actinacis*. *Zeitschrift der Deutschen Geologischen Gesellschaft*, 65 [for 1913]: 159-180.

Orbigny A. d' (1849). Note sur des polypiers fossiles. 12 pp. Victor Masson, Paris.

Ortner H. & Stingl V. (2001). Facies and basin development of the Oligocene in the Lower Inn Valley, Tyrol/Bavaria. *In* Piller W.E. & Rasser M.W. (eds), Paleogene of the Eastern Alps. Österreichische Akademie der Wissenschaften, Schriftenreihe der Erdwissenschaftlichen Kommission, 14: 153-196.

Perrin C. & Bosellini F.R. (2012). Paleobiogeography of scleractinian reef corals: Changing patterns during the Oligocene–Miocene climatic transition in the Mediterranean. *Earth-Science Reviews*, 111: 1-24.

Pfister T. (1980a). Systematische und paläoökologische Untersuchungen an oligozänen Korallen der Umgebung von San Luca (Provinz Vicenza, Norditalien). *Schweizerische Paläontologische Abhandlungen (Mémoires Suisses de Paléontologie),* 103: 1-121.

Pfister T. (1980b). Paläoökologie des oligozänen Korallenvorkommens von Cascine südlich Acqui (Piemont, Norditalien). *Jahrbuch des Naturhistorischen Museums der Stadt Bern*, 7: 247-262.

Pfister T. (1985). Coral fauna and facies of the Oligocene fringing reef near Cairo Montenotte (Liguria, northern Italy). *Facies*, 13: 175-226.

Popov S.V., Rögl F., Rozanov A.Y., Steininger F.F., Shcherba I.G. & Kovac M. (2004). Lithological-paleogeographic maps of Paratethys, 10 maps late Eocene to Pliocene. *Courier Forschungsinstitut Senckenberg*, 250: 1-46.

Prever P.L. (1922). I coralli Oligocenici di Sassello nell'Appenino Ligure. Continuazione parte I. Corallari a calici confluenti. *Palaeontographia Italica,* 28: 1-40.

Quaranta F., Piazza M. & Vannucci G. (2009). Climatic and tectonic control on the distribution of the Oligocene reefs of the Tertiary Piedmont Basin (NW Italy). *Bollettino della Società Geologica Italiana*, 128: 587-591.

Reig Oriol J.M. (1988). Dos nuevos géneros de corales cretácicos. *Batalleria*, 1: 39-45.

Reig Oriol J.M. (1990). Madreporarios eocénicos de Castellolo y de la Sierra de Malvals. 71 pp. Reig Oriol, Barcelona.

Reis O.M. (1889). Die Korallen der Reiter Schichten. *Geognostische Jahreshefte*, 2: 91-162.

Reuss A.E. von (1864). Die fossilen Foraminiferen, Anthozoen und Bryozoen von Oberburg in Steiermark. Ein Beitrag zur Fauna der oberen Nummulitenschichten. *Denkschriften der Österreichischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe,* 23: 1-36.

Reuss A.E. von (1868). Palaeontologische Studien über die altern Tertiärschichten der Alpen. 1. Theil. Die fossilen Anthozoen und Bryozoen der Schichtengruppe von Crosara. *Denkschriften der kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe*, 28: 129-184.

Reuss A.E. von (1869). Zur fossilen Fauna der Oligocänschichten von Gaas. *Sitzungsberichte der Kaiserlichen Akademie der*

Wissenschaften. Mathematisch Naturwissenschaftliche Classe, 59: 446-488.

Reuss A.E. von (1874). Paläontologische Studien über die älteren Tertiärschichten der Alpen. III. Abtheilung. Die fossilen Anthozoen der Schichtengruppe von S. Giovanni Ilarione und von Ronca. *Denkschriften der Österreichischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe,* 33: 1-60.

Reuter M., Piller W.E., Harzhauser M., Mandic O., Berning B., Rögl F., Krog A., Aubry M.-P., Wieland-Schuster U. & Hamedani A. (2009). The Oligo/Miocene Qom Formation (Iran): evidence for an early Burdigalian restriction of the Tethyan Seaway and closure of its Iranian gateways. *International Journal of Earth Sciences,* 98: 627-650.

Romano S.L. & Cairns S.D. (2000). Molecular phylogenetic hypotheses for the evolution of scleractinian corals. *Bulletin of Marine Science*, 67: 1043-1068.

Sanders D. & Baron-Szabo R.C. (2005). Scleractinian assemblages under sediment input: their characteristics and relation to the nutrient input concept. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 216: 139-181.

Sanders D. & Baron-Szabo R.C. (2007). First Oligocene coral fauna of the Eastern Alps. Sediment 2007, Brixen/Bressanone (Italy), 12.9.2007, Abstract: 1 p.

Santodomingo N. (2014). Miocene reef-coral diversity of Indonesia: unlocking the murky origins of the Coral Triangle. *Utrecht Studies in Earth Sciences*, 63: 1-336.

Scherbacher M., Schmiedl G. & Hemleben C. (2001). Early Oligocene benthic foraminifera from the Lower Inn Valley area, Austria: Implications for the paleoenvironmental evolution of the Inneralpine Molasse. *In* Piller W. & Rasser M. (eds), Paleogene in Austria, *Schriftenreihe der Erdwissenschaftlichen Kommissionen*, 14: 611-640.

Schuster F. (2002a). Scleractinian corals from the Oligocene of the Qom formation (Esfahan-Sirjan fore-arc basin, Iran). *Courier Forschungsinstitut Senckenberg*, 239: 5-55.

Schuster F. (2002b). Early Miocene corals and associated sediments of the northwestern Gulf of Suez, Egypt. *Courier Forschungsinstitut Senckenberg*, 239: 57-81.

Schuster F. (2002c). Oligocene scleractinian corals from Doutsiko (Mesohellenic Basin, northwestern Greece). *Courier Forschungsinstitut Senckenberg*, 239: 83-127.

Silvestri G., Bosellini F.R. & Morsilli M. (2008). Turbid-water coral assemblages: A case study from the Oligocene Tertiary Piedmont Basin (N Italy). *Rendiconti online Società geologica Italiana,* 2: 177-180.

Silvestri G., Bosellini F.R. & Nebelsick J.H. (2011). Microtaphofacies analysis of lower Oligocene turbid-water coral assemblages. *Palaios,* 26: 805-820.

Sismonda E. (1871). Matériaux pour servir a la paléontologie du terrain tertiaire de Piémont. *Memorie della Reale Accademia delle Scienze di Torino (serie 2),* 25: 21-107.

Sokolow N. (1894). Die unteroligocäne Fauna der Glaukonitsande bei der Einsenbahnbrücke von Jekaterinoslaw. *Mémoires of the geological Commission, Russia*, 9: 1-138.

Solomko E. (1888). Die Jura- und Kreidekorallen der Krim. *Verhandlungen der Russisch-Kaiserlichen Mineralogischen Gesellschaft zu St. Petersburg (2)*, 24: 67-231.

Squires D.F. (1958). The Cretaceous and Tertiary corals from New Zealand. *New Zealand Geological Survey Palaeontological Bulletin,* 29: 1-107.

Squires D.F. (1962). Additional Cretaceous and Tertiary corals from New Zealand. *Transactions of the Royal Society of New Zealand (Geology),* 1: 133-150.

Stemann T.A. (2004). Reef corals of the White Limestone Group of Jamaica. *In* Donovan S.K. (ed.), The Mid-Cainozoic White Limestone Group of Jamaica. *Cainozoic Research*, 3: 83-107.

Stolarski J. (1995). Ontogenetic development of the thecal structures in caryophylliine scleractinian corals. *Acta Geologica Polonica*, 40: 19-44.

Stolarski J. & Taviani M. (2001). Oligocene scleractinian corals from CRP-3 drillhole, McMurdo Sound (Victoria Land Basin, Antarctica). *Terra Antartica,* 8: 1-4.

Tomes R.F. (1883). On some new or imperfectly known Madreporaria from the Coral Rag and Portland Oolite of the counties of Wilts, Oxford, Cambridge, and York. *Quarterly Journal of the Geological Society*, 39: 55-65.

Vannucci G., Testa M., Piazza M. & Pastorino P. (2010). *Subterraniphyllum* and free-living *Neogoniolithon* (coralline algae) from the Oligocene reef facies of Costa d'Ovada (Tertiary Piedmont Basin, Alessandria, NW Italy). *Italian Journal of Geosciences*, 129: 4-14.

Vaughan T.W. (1900). The Eocene and Lower Oligocene coral faunas of the United States with descriptions of a few doubtfully Cretaceous species. *Monographs of United States Geological Survey*, 39: 1-263.

Vaughan T.W. (1918). Some shoal-water corals from Murray Island (Australia), Cocos-Keeling Islands, and Fanning Island. *Papers from the Department of Marine Biology of the Carnegie Institution of Washington*, 9: 49-234.

Vaughan T.W. (1919). Fossil corals from Central America, Cuba, and Porto Rico, with an account of the American Tertiary, Pleistocene, and Recent coral reefs. *United States National Museum Bulletin*, 103: 189-524.

Vaughan T.W. & Wells J.W. (1943). Revision of the suborders, families and genera of the Scleractinia. *Geological Society of America, Special Paper*, 44: 1-363.

Veron J.E.N. (1992). Conservation of biodiversity: A critical time for the Hermatypic Corals of Japan. *Coral Reefs*, 11: 13-21.

Veron J.E.N. & Michin P.R. (1992). Correlations between sea surface temperature, circulation patters and the distribution of hermatypic corals of Japan. *Continental Shelf Research*, 12: 835-857.

Verrill A.E. (1901). Variations and nomenclature of Bermudian, West Indian, and Brazilian reef corals, with notes on various Indo-Pacific corals. *Transactions of the Connecticut Academy of Arts and Sciences,* 11: 63-168.

Verrill A.E. (1902). Notes on corals of the genus *Acropora* (Madrepora Lam.) with new descriptions and figures of types, and of several new species. *Transactions of the Connecticut Academy of Arts and Sciences*, 11: 207-266.

Vredenburg E. (1921). Comparative diagnoses of Pleurotomidae from the Tertiary formations of Burma. *Records of the Geological Survey of India*, 53: 83-129.

Wallace C.C. (2008). New species and records from the Eocene of England and France support early diversification of the coral genus *Acropora*. *Journal of Paleontology*, 82: 313-328

Weisbord N.E. (1973). New and little-known corals from the Tampa Formation of Florida. *Bulletin State of Florida Department of Natural Resources Division of Interior Resources Bureau of Geology*, 56: 1-146.

Wells J.W. (1941). Cretaceous and Eocene corals from northwestern Peru. *Bulletins of American Paleontology*, 26: 301-326.

Wells J.W. (1956). Part F, Coelenterata. *In* Moore R.C. (ed.), Treatise on Invertebrate Paleontology, Lawrence, Kansas: F328-F444.

Wells J.W. (1964). Fossil Corals from Eniwetok Atoll. *United States Geological Survey Professional Paper*, 260-DD: 1101-1111.

Wilson M.E.J. (1995). The Tonasa Limestone Formation, Sulawesi, Indonesia: Development of a Tertiary Carbonate Platform. 520 pp. PhD Thesis, University of London.

Zuffardi-Comerci R. (1937). Corallari oligocenici e miocenici della Somalia. *Palaeontographia Italica*, 32: 265-301.

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Revisiting reef models in the Oligocene of northern Italy (Venetian Southern Alps)

Francesca R. Bosellini, Alessandro Vescogni*, Wolfgang Kiessling, Alessandro Zoboli,
Dario Di Giuseppe & Cesare Andrea Papazzoni

F.R. Bosellini, Dipartimento di Scienze Chimiche e Geologiche, Università degli Studi di Modena e Reggio Emilia, Via Campi 103, I-41125 Modena, Italy; francesca.bosellini@unimore.it

A. Vescogni, Dipartimento di Scienze Chimiche e Geologiche, Università degli Studi di Modena e Reggio Emilia, Via Campi 103, I-41125 Modena, Italy; alessandro.vescogni@unimore.it **corresponding author*

W. Kiessling, GeoZentrum Nordbayern, Friedrich-Alexander Universität Erlangen-Nürnberg, Loewenichstrasse 28, D-91054 Erlangen, Germany; wolfgang.kiessling@fau.de

A. Zoboli, Dipartimento di Scienze Chimiche e Geologiche, Università degli Studi di Modena e Reggio Emilia, Via Campi 103, I-41125 Modena, Italy; 176695@studenti.unimore.it

D. Di Giuseppe, Dipartimento di Scienze Chimiche e Geologiche, Università degli Studi di Modena e Reggio Emilia, Via Campi 103, I-41125 Modena, Italy; dario.digiuseppe@unimore.it

C.A. Papazzoni, Dipartimento di Scienze Chimiche e Geologiche, Università degli Studi di Modena e Reggio Emilia, Via Campi 103, I-41125 Modena, Italy; papazzoni@unimore.it

KEY WORDS - Coral reefs, early Oligocene, euphotic barrier-lagoon system, coral assemblages.

ABSTRACT **-** *The lower Oligocene coral communities and reefs exposed in the Lessini Shelf of northern Italy may record one of the oldest well-developed barrier reef/lagoon systems of the Cenozoic. However, the rimmed-shelf interpretation has been repeatedly challenged in favour of a ramp model with scattered corals. Based upon a re-analysis of selected localities in the Lessini Shelf, we here provide support for the barrier reef model based on four key observations: 1) systematic changes of coral growth-forms from branching in the proximal areas to massive at the platform margin; 2) a progressive increase of the hydrodynamic energy from the proximal belt towards the more distal environments in the Berici Hills; 3) the occurrence of shallow-water, euphotic conditions throughout the whole depositional system; and 4) the presence of restricted circulation in the proximal environments during sea-level lowstands, with lack of coral colonies. These features, together with the evidence of coral frameworks located on the southeastern edge of the Lessini Shelf, substantiate the occurrence of a reef-rimmed margin. The reefal rim acted as an efficient barrier, with the formation of a landward, wide lagoon protected from the action of waves and currents.*

INTRODUCTION

Well-developed coral reefs were globally scarce during most of the Paleogene but increased in abundance, size, and biotic diversity during the Oligocene, perhaps related to an increasing Mg/Ca ratio in ocean water facilitating coral growth (Stanley & Hardie, 1998). The Lessini Shelf is a major Cenozoic paleogeographic element of the Southern Alps (Bosellini, 1989) (Fig. 1a) with shallow marine deposits ranging from the early Eocene to the early Miocene (Bosellini et al., 1967; Bassi et al., 2007, 2008; Bassi & Nebelsick, 2010). From paleontological and geological points of view, this area is famous for the extensive collections of the 19th century describing its rich coral fauna and has long been a global landmark for the study of Oligocene reefs.

Exceptional for the Oligocene, a Rupelian (early Oligocene) barrier-reef/lagoon complex is thought to have rimmed the Lessini Shelf. According to older models, a barrier reef rim was located in the southeastern side of the Berici Hills, with a wide lagoon extending for about 30 km northwestward into the Lessini Mountains (Frost, 1981; Bosellini & Trevisani, 1992). This barrier-reef/lagoon model has been repeatedly challenged, proposing a ramp depositional system instead of a reef-rimmed platform (Nebelsick et al., 2012; Pomar et al., 2017).

Here we evaluate these alternative reconstructions providing new data, especially focusing on microfacies analysis and types of coral assemblages, from three selected key localities (Castelgomberto, Bastia, and Lumignano), placed along a NW/SE transect through the Castelgomberto Limestone Formation depositional system (Fig. 1b).

GEOLOGICAL SETTING

The Lessini Mountains and Berici Hills are located in the Southern Alps, a geological domain that resulted from the collision of the northernmost margin of the Adria Plate with the European block (Bosellini, 1989). During the Jurassic, this area was occupied by the Trento Platform, a large shallow-water area bordered to the west by the Lombard Basin and to the east by the Belluno Trough (Fig. 1a) (Bosellini et al., 1981; Winterer & Bosellini, 1981). The Trento Platform drowned in the Middle to Late Jurassic to give rise to the Trento Plateau, with deep marine sedimentation until the Paleocene. In the Paleogene, the Alpine orogeny produced a gradual uplift with the segmentation of the plateau into several blocks. During the early Eocene, some of these structures reached the photic zone, with a progressive increase of carbonate production that eventually led to the formation of a vast platform called Lessini Shelf (Fig. 1a) (Doglioni & Bosellini, 1987; Bosellini, 1989; Luciani, 1989; Bassi et al., 2008).

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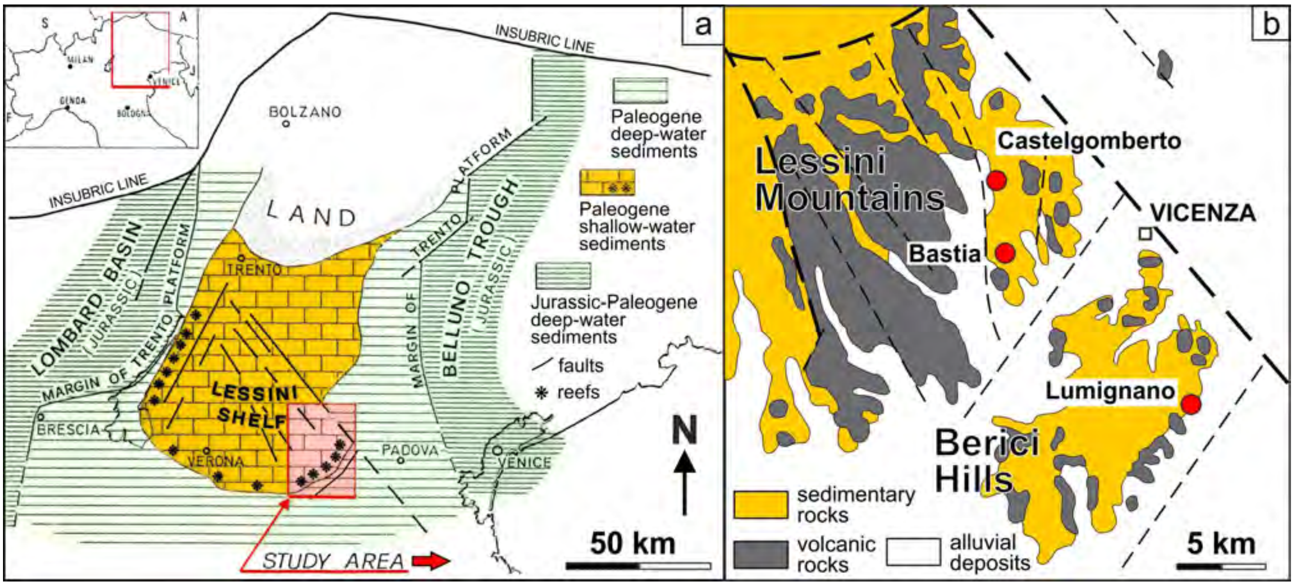

Fig. 1 - (color online) a) Paleogeographic reconstruction of the Lessini Shelf (modified from Bosellini et al., 1989). b) Simplified geological map of the south-eastern part of the Lessini Shelf (modified from De Vecchi & Sedea, 1995) showing the locations of the studied outcrops.

From the Paleocene to the Oligocene, the Lessini Shelf was limited northward by land and surrounded on the other sides by deeper marine basins (Bosellini, 1989). During this period, several pulses of volcanic activity took place, with the formation of basaltic intrusions and epiclastic horizons that interacted with the carbonate sedimentation (Barbieri et al., 1991; Barbieri & Zampieri, 1992; Zampieri, 1995). Carbonate deposits are concentrated in the eastern Lessini Shelf, initially represented by the middle Eocene "Calcari Nummulitici" (Nummulitic Limestone), an informal unit that includes a wide array of facies: larger foraminifera, coral and mollusc limestones, coralline algae breccias, and marly limestone with marine and freshwater fossils (Bosellini et al., 1967; Carraro et al., 1969; De Zanche et al., 1977; Sarti, 1980; Ungaro, 2001; Papazzoni et al., 2014, 2017; Vescogni et al., 2016). Volcanic activity over the Lessini Shelf area ceased nearly completely during the late Eocene, a phase characterised by the deposition of deep-platform, marly sediments (Barbieri et al., 1980; Mietto, 1992; Trevisani, 1997). However, volcanism started in the Euganean Hills area 42.0±1.5 Ma (Borsi et al., 1969), in the late Lutetian-Bartonian, with submarine mafic lavas, and continued until about 32-30 Ma in the early Oligocene with intermediate to felsic volcanism (Piccoli et al., 1981; Bartoli et al., 2015; Brombin et al., 2019). In the mid-Oligocene the volcanic activity started also in the Marostica Hills, east of the Lessini Shelf, reaching a peak during the early Miocene (Brombin et al., 2019).

Shallow-water carbonate sedimentation resumed in the Lessini area during the early Oligocene, with the deposition of the Castelgomberto Limestone Fm. (Geister & Ungaro, 1977; Frost, 1981; Bosellini & Trevisani, 1992; Mietto, 1992). The Castelgomberto Limestone Fm., developed in the south-eastern part of the Lessini Shelf, spans the entire Rupelian stage (Geister & Ungaro, 1977; Frost, 1981). Along the western sector, Oligocene sediments are lacking, probably due to emersion (Luciani, 1989). Lower Oligocene limestones are followed by the upper Oligocene-lowermost Miocene S. Urbano Sandstone (Bosellini et al., 1967; Bassi et al., 2007, 2008; Bassi & Nebelsick, 2010), which is further overlain by the lower Miocene Monte Costi Marlstone, a unit only a few meters thick (Bosellini & Dal Cin, 1966; Bassi et al., 2007, 2008) that represents the last marine sedimentary unit of the Lessini Shelf.

THE CASTELGOMBERTO LIMESTONE FORMATION

Known to pioneering workers as the "Strati di Castelgomberto" (Maraschini, 1824) and to modern authors as the "Calcareniti di Castelgomberto" (Bosellini et al., 1967) or "Calcare di Castelgomberto" (Coletti et al., 1973), the Castelgomberto Limestone Fm. is a 200 m thick formation made of different types of limestones (calcarenites, calcirudites, coral boundstones), marly limestones and clay horizons. This unit is mainly exposed in the south-eastern part of the Lessini Mountains and in the Berici Hills area (Fig. 1b). The number of extensive outcrops showing a luxuriant coral fauna has attracted the interest of many scientists and there were several attempts to reconstruct this lower Oligocene coral-rich depositional system (Rossi & Semenza, 1958; Geister & Ungaro, 1977; Frost, 1981; Bosellini & Russo, 1988; Bosellini & Trevisani, 1992; Nebelsick et al., 2012; Pomar et al., 2017).

Geister & Ungaro (1977) focused on the Berici Hills, where they identified two main paleoenvironmental settings and coral assemblages. In the central and NW Berici, under shallow-water, moderate hydrodynamic condition, prevalent ramose coral colonies formed low-relief patches, whereas along the SE margin, massive colonies thrived in a slightly deeper environment, rarely forming compact, wave-resistant frameworks. Taking into accounts the low-energy setting of the central-NW Berici sector, these authors postulated the presence of a coral reef barrier towards SE, acting as a protection from the open-sea. However, no certain evidence of its presence was identified, and considering that the same kind of protection could have been attained by a seaward extension of the platform, Geister & Ungaro (1977) left a detailed interpretation of the depositional paleoenvironment to future studies.

Some years later, Frost (1981) conducted a comprehensive study of the entire region where the Castelgomberto Limestone Fm. is exposed. According to Frost (1981), a shallow-water barrier reef developed in the southeastern portion of the Berici Hills, comprising a 150-200 m thick, 800-900 m wide and about 8 km long reef core mainly constructed by massive to columnar coral colonies. Corals with similar growth-forms built thickets and small patch reefs in a more protected lagoonal environment, which extended northwestward for about 30 km into the Lessini Mountains. The most proximal lagoonal areas received episodic terrigenous influxes and are characterised by ramose coral assemblages developing thicket-like structures.

Bosellini & Russo (1988) and Bosellini & Trevisani (1992) focused on the SE Lessini Mountains, in the most proximal portion of the Castelgomberto Limestone Fm. depositional system. These authors corroborated the Frost (1981) model by the recognition and interpretation of a cyclical depositional pattern. Well-bedded rhodolite-nummulitid grainstones alternate with nodular or wavy-bedded marly wackestones rich in ramose coral colonies sometimes forming thicket-like structures. Bosellini & Trevisani (1992) interpreted this cyclicity as related to alternating high-energy and low-energy hydrodynamic conditions, correlated to short-term sea-level fluctuations affecting the Lessini Shelf reef-lagoonal complex. The biocalcarenite facies represents relative highstand deposits with flooding and open circulation on the entire shelf, strong tidal currents, swells and periodic storms able to sweep the bioclastic sand masses into sand waves and subaqueous dunes. The marly facies, in contrast, was deposited during relative lowstands, when the shelf was more protected by the reefs in what is now the Berici Hills. These reefs possibly acted as a true barrier, shielding the quiet inner shelf lagoon from currents and waves and favouring colonisation by coral patches. During sea-level lowstands large inland areas were exposed to weathering, supplying fine, clay-rich detritus to the shelf-lagoon.

More recently, Nebelsick et al. (2012) studied a 100 m thick and about 280 m long section in the SE Berici Hills. They recognised a succession of coralline algal rudstones that developed within the photic zone and under relatively low hydrodynamic conditions, with corals represented only by variable amounts of fragments. Sedimentary fabrics, biofacies analysis and the lack of bioconstructions led these authors to interpret this portion of the Berici as an homoclinal ramp, with no evidence of a reef barrier.

Finally, Pomar et al. (2017), in a review of Cenozoic carbonate depositional models, considered the Castelgomberto Limestone Fm. as a low-angle ramp system, with a gradual, progressive deepening occurring from the euphotic settings of the proximal belt (present-day SE Lessini) to the oligophotic paleoenvironments in the distal areas (present-day SE Berici). According to this model corals are lacking in the shallower areas, which were instead dominated by seagrass. Isolated coral colonies were limited to the mesophotic to oligophotic paleoenvironments of the middle ramp, rarely forming small structures. In the more distal, oligophotic areas corals occur only as fragments.

A schematic summary of the different paleoenvironmental reconstructions obtained in these studies is reported in Tab. 1 and compared with the results of the present work. To facilitate the reading of the table, we replaced the terms originally used by the previous authors for the description of coral assemblages (e.g., coral carpets, biostromes, coppices) with others with similar meaning and used in this work.

MATERIALS AND METHODS

Stratigraphic, sedimentary and paleontological data have been acquired from three selected localities: Castelgomberto, Bastia and Lumignano (Fig. 1b).

The Castelgomberto section was studied along a fresh, 135 m long road cut about 1 km SW of the small town of Castelgomberto (45°34’27.6”N, 11°23’55.5”E). Here, a 27 m thick succession of Rupelian limestones and marls is exposed (Fig. 2a).

The Bastia outcrop is located about 3 km north of Montecchio Maggiore, along a small road connecting the locality of Bastia Bassa to the village of S. Urbano (45°31’26.7”N, 11°24’58.2”E). Despite a dense vegetation cover and intense faulting, this outcrop allows the observation of a 120 m long and ca. 5 m thick exposure of coral-rich limestone (Fig. 3a).

Lumignano is located in the Berici Hills at the southeastern margin of the Lessini Shelf. We studied the best exposed coral outcrop at the San Cassiano hermitage (45°27’57.1”N, 11°35’13.3”E), an antique, small monastery built on a suspended ledge carved on the cliff along the south-eastern side of the Berici Hills. There, a 100 m long and several meters thick exposure allows the characterisation of the coral facies (Fig. 4a), although intense karstification affects the assessment of primary facies patterns and prevents the measurement of a stratigraphic section.

We conducted macroscopic and microscopic observations. Coral-rich facies has been traced in the field focusing on prevalent growth-forms and dominant genera. Coral taxa have been identified directly in the field at the genus level. We also recorded growth-forms and colony size (maximum diameter and maximum height of corals in growth position). Additional data have been collected in Lumignano, where biostratinomic data (orientation, fragmentation) of 70 coral colonies were quantified from the bioconstructed portions of the outcrop. Microfacies analysis was conducted on a total of 73 thin sections (60 × 45 mm), providing data on textures and carbonate grains reported in the facies description. Rock textures were classified following Dunham (1962) and Embry & Klovan (1971). The nomenclature of Woelkerling et al. (1993), originally established for the description of coralline algae growth-forms, was slightly extended to also characterise peyssonneliacean algae.

In the Castelgomberto outcrop, some of the clay horizons have been sampled and analysed in order to ascertain their depositional origin: whether they can be

	Castelgomberto Limestone Fm.				
	SE Lessini/central-NW Berici		**SE Berici**		**Depositional model**
	Paleoenvironmental setting	Coral assemblage	Paleoenvironmental setting	Coral assemblage	
Geister & Ungaro (1977)	Within the fair weather wave base, moderate hydrodynamic conditions.	Ramose corals forming low-relief patches.	Below the fair weather wave base, close to the lower limit of the euphotic zone.	Patches of lens-shaped and massive corals, rarely forming a real framework.	Possible occurrence of a coral reef barrier in the SE of the Berici Hills protecting a lagoon towards the NW, but no direct evidence of its presence is observed.
Frost (1981)	Shallow-water environment, with marine carbonate deposition. Periodic terrigenous influxes limited to the proximal areas.	Massive corals prevail in thoroughly carbonate depositional settings, forming thickets and small patch-reefs. In proximal areas ramose corals form thicket-like structures during terrigenous/carbonate deposition.	Shallow-water conditions.	Reef framework with dominant massive-columnar corals.	A large, coral reef barrier along the SE margin of the Berici Hills protects a wide lagoon towards NE.
Bosellini & Trevisani (1992)	Shallow-water environment. Sea-level fluctuations control cyclic phases of high-energy carbonate deposition and lower-energy, mixed terrigenous/carbonate sedimentation.	Pure limestone intervals contain coral fragments and rare massive and laminar colonies. Ramose corals colonies prevail during terrigenous/carbonate deposition, forming also thicket-like structures.			The presence of a coral reef barrier in the SE of the Berici Hills is postulated, influencing the lagoon hydrodynamic conditions during sea-level variations.
Nebelsick et al. (2013)			Within the photic zone, relatively low hydrodynamic conditions.	Corals as fragments within a coralline algal rudstone.	The SE margin of the Berici Hill was represented by a homoclinal ramp. No evidence of a coral reef barrier has been identified.
Pomar et al. (2017)	Seafloor gradually downgrades from the euphotic to the meso-oligophotic zone. Presence of episodic terrigenous inputs.	Corals are absent in the shallower settings and occur as isolated colonies in the meso-oligophotic areas, where they can also form small mounds.	Oligophotic conditions.	Corals as fragments within a coralline algal rudstone.	The whole Castelgomberto Limestone Fm. depositional system is interpreted as a low-angle ramp, lacking a seaward coral reef barrier.
This study	Shallow-water, euphotic environment. In the proximal areas variations in water turbidity and terrigenous inputs are controlled by sea-level changes. Progressive seaward increase of hydrodynamic energy.	Ramose corals form thicket-like structures in the proximal areas. In more distal settings patch-reefs are made by massive and ramose colonies.	Shallow-water, euphotic setting, high-energy hydrodynamic conditions.	Massive-globose colonies form a wave-resistant framework.	A wave-resistant, shallow-water coral framework occurs at the SE margin of the Berici Hills, associated to a wide, euphotic lagoon towards the NW with scattered patch reefs.

Tab. 1 - Summary of the main interpretations of the Castelgomberto Limestone Fm. depositional models compared with the results of this study.

associated to the transport from the mainland of clays derived from the alteration of volcanic rocks, or if they can be rather related to the deposition of volcaniclastics following eruption events. Five samples (A1 to A5; Fig. 2a) have been dissolved in water and then passed through a series of sieves (1-0.5-0.25-0.125 mm) to check the presence of bioclasts and/or fragments of volcanic origin. In addition, two samples (A2 and A5) have been analysed by means of X-ray powder diffraction (XRPD), for a qualitative determination of the minerals forming the clay levels. Before the XRPD analysis both samples were air-dried and milled with an agate mortar. An aliquot of dried samples was suspended in deionised water and then casted on the aluminium sample-holder in order to obtain an oriented sample that allows a proper identification of the clay minerals (Zhou et al., 2018). Both randomly oriented samples (i.e., dry samples) and oriented samples were analysed using a conventional Bragg-Brentano Philips diffractometer (model PW-1729). A complete description of the instrumental set up is reported in Zoboli et al. (2019).

FACIES DESCRIPTION AND INTERPRETATION

Stratigraphic, sedimentary and paleontological features of the Castelgomberto Limestone Fm. facies are here reported from each of the studied localities, followed by an interpretation of the main paleoenvironmental factors controlling their deposition.

Castelgomberto

In the Castelgomberto locality, four main facies have been recognised (Fig. 2a). These are in stratigraphic order:

- Coralline rudstone: planar beds with massive to weakly stratified inner arrangement, few dm up to 3.5 m in thickness, characterised by the presence of a dense network of thin, discontinuous clay intercalations (Fig. 2b). Bioclastic components are mainly coralline algae (fragments and small rhodoliths) and small coral fragments, the latter frequently coated by coralline algae and encrusting foraminifera. The matrix is a marly wackestone/packstone (Fig. 2c) with fragments of echinoids, small concentrations of *Polystrata* sp. crusts, often showing hooked, hollow or foliose growth-forms (sensu Woelkerling et al., 1993), calcareous sponges, miliolid foraminifera, fragments of molluscs, bryozoans and rare dasycladacean algae. Within the coralline rudstone facies, the number of coral fragments increases from about 10 meters from the base of the section, with the initial appearance of scattered, ramose colonies in growth position that upward give way to more distinct, larger coral thickets.

- Bentonite layers: laterally continuous, planar clay layers of 5 to 15 cm in thickness (Fig. 2d-e). Bioclasts are mainly represented by miliolids, fragments of echinoids, ostracods and spicules. Very small fragments of volcanic glass have been also observed. XRPD analyses show that the facies contains mainly calcite, clay minerals (smectite, illite, chlorite and kaolinite) and quartz, with a minor amount of pyrite (Fig. 5a). XRPD patterns (Fig. 5b) reveal that smectite is the main group of clay minerals that characterises these deposits.

- Marly mudstone: planar beds up to 1.8 m in thickness (Fig. 2e) made of a compact, sometimes finely-laminated marly mudstone (Fig. 2f) with sparse bioclasts mainly represented by miliolids and coralline algae.

- Coral thickets: the facies is characterised by in situ coral colonies arranged in discontinuous, superimposed patches, each up to 20-50 cm thick and several meters wide. Coral thickets are covered by thin clay intervals (Fig. 2g) similar to those within the coral rudstone. The coral assemblage (Fig. 2h-j) is dominated by ramose *Actinacis rollei* Reuss, 1864 and phaceloid *Caulastraea*, especially *C. tenuis* (Reuss, 1868), with colonies up to 30 cm in size. Other corals, such as *Goniopora nummulitica* (Reuss, 1864) and *Astreopora tecta* (Catullo, 1856) are present but rare. Coral sticks are often coated by thin coralline algae and foraminiferal crusts. The matrix is a fine-grained marly limestone, with a prevalent mudstone-wackestone texture (Fig. 2k). Bioclasts are fragments of echinoderms, calcareous sponges, bivalves, gastropods, miliolid foraminifera, coralline algae, bryozoans, rare dasycladacean algae, and *Gypsina*. Coral thickets pass laterally into coralline rudstones.

INTERPRETATION - The stratigraphic arrangement of the identified facies suggests cyclical changes of controlling factors. We identified four main cycles, each starting with a marly mudstone followed by coralline rudstone and coral thickets facies (Fig. 2a). Considering the marly mudstone, the large amount of clay within this facies most probably derives from the alteration and erosion of Paleocene-Eocene volcanic rocks that cropped out in the mainland areas. Clay minerals were transported to the sea and deposited into a calm, shallow-water environment, as suggested by the occurrence of miliolids. This process must have been fully effective during lowstand phases, that controlled the periodic progradation of terrigenous-rich sediments in the Castelgomberto area. The deposition of the marly mudstone was followed by transgressive/highstand phases, accompanied by an increase of the hydrodynamic energy. This is testified by the sedimentation of the coarser, grain-supported coralline rudstone facies and by the colonisation of corals, as isolated colonies or grouped into coral thickets. In comparison to the marly mudstone, coralline rudstone and coral thickets facies may have developed in a slightly deeper setting, but always within the euphotic zone, as indicated by the presence of dasycladacean algae and by the occurrence of hollow, hooked and foliose *Polystrata* sp. crusts in the coralline rudstone. These types of growth-forms are usually associated with seagrass beds. Algal crusts develop on the surface of stems and leaves of seagrass (Beavington-Penney et al., 2004; Sola et al., 2013) that thrive in shallow-water, euphotic settings (e.g., Larkum et al., 2006; Mateu-Vicens et al., 2010). Despite the relatively high hydrodynamic conditions, coralline rudstone and coral thickets facies are associated with a considerable amount of clay, represented by thin intercalations (Fig. 2b, g) and by marly micrite that accumulate among the in situ coral colonies (Fig. 2k). This indicates how these facies were developing in a relatively proximal environment, under the influence of terrigenous inputs. The occurrence of a turbid environment is also suggested by the coral assemblage, which is dominated by *Actinacis rollei* (Fig. 2h), a pioneer, sediment resistant genus (Frost, 1981), and by the prevalent ramose growth-forms (Fig. 2i, l), interpreted as an acclimatisation to muddy, turbid-water conditions (Bosellini & Trevisani, 1992; Bosellini & Stemann, 1996; Sanders & Baron-Szabo, 2005). The clay layers covering the coral thickets (Fig.

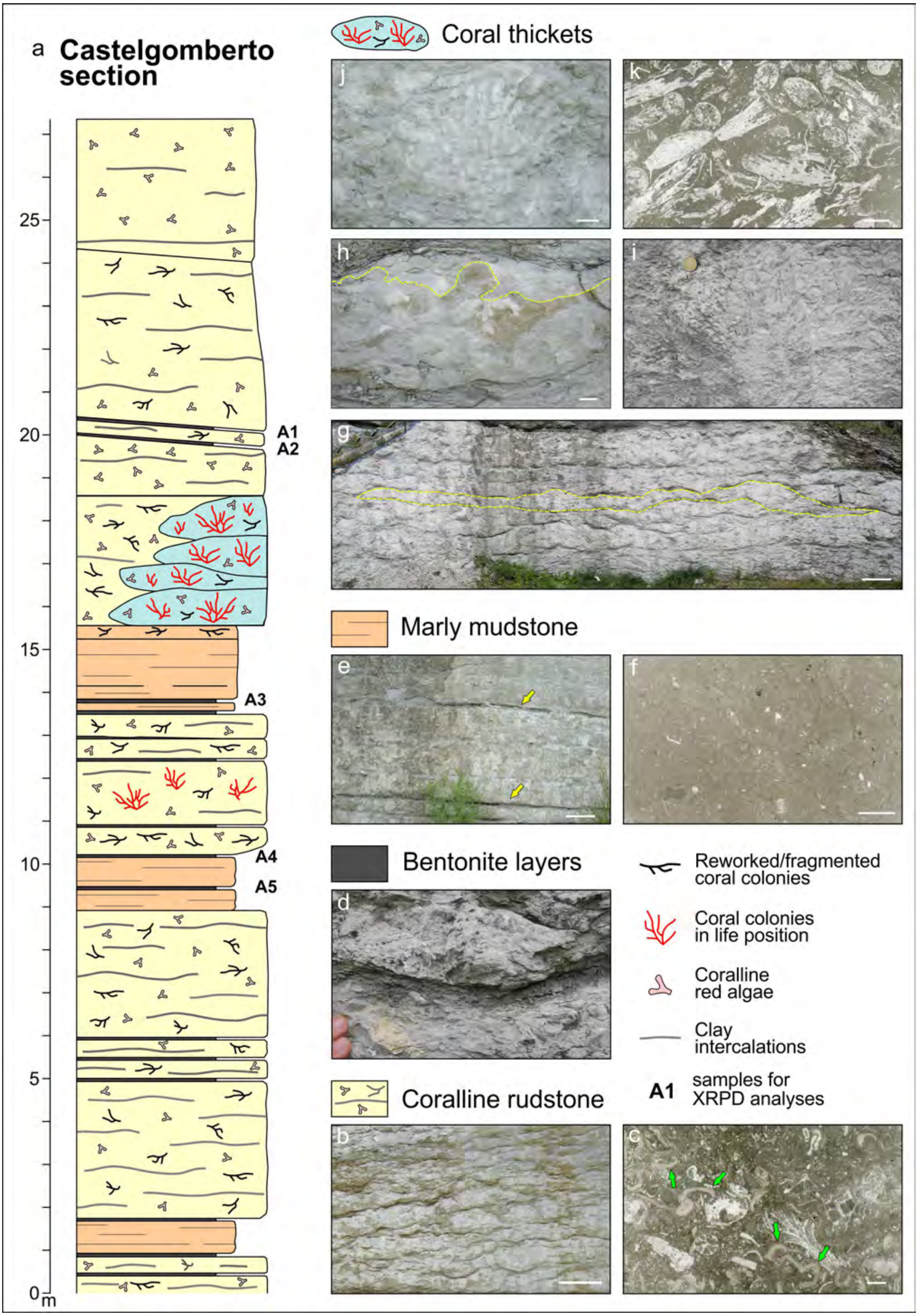
a Castelgomberto section
0 m
5
10
15
20
25
A1
A2
A3
A4
A5
Coral thickets
j
k
h
i
g
Marly mudstone
e
f
Bentonite layers
d
Reworked/fragmented coral colonies
Coral colonies in life position
Coralline red algae
Clay intercalations
A1 samples for XRPD analyses
Coralline rudstone
b
c

Fig. 2 - (color online) Castelgomberto outcrop. a) Stratigraphic column. b) Coralline rudstone facies, outcrop view showing clay intercalations among the bioclastic deposits, scale bar = 50 cm. c) Coralline rudstone facies, wackestone/packstone matrix in thin section; arrows indicate *Polystrata* sp. crusts with hooked growth form, scale bar = 2 mm. d) Bentonite layers facies, outcrop close-up. e) Marly mudstone facies with two bentonite layers (arrows), scale bar = 50 cm. f) Marly mudstone facies, mudstone texture in thin section, scale bar = 5 mm. g) Coral thickets facies, coral thickets separated by thin clay intercalations; dashed lines trace one of the coral thickets, scale bar = 50 cm. h) Coral thickets facies, *Actinacis rollei* colony with short, vertical branches (dashed line), scale bar = 1 cm. i-j) Coral thickets facies, phaceloid *Caulastraea* colonies, scale bar = 1 cm. k) Coral thickets facies, thin section showing floatstone with *Caulastraea* fragments, scale bar = 5 mm.

2g) suggest periodic mass accumulations of terrigenous sediments eventually causing the death and burial of the corals. Concerning the bentonite layers, the prevalence of smectite among the clay minerals (Fig. 5b), as well as the occurrence of fragments of volcanic glass, indicate their origin as directly related to eruption events (Cuadros et al., 1999; De la Fuente et al., 2000; Christidis & Huff, 2009). During the Rupelian, the supply of pyroclastic material in the Lessini Mountains can be associated with the volcanic activity located in the Euganei Hills, an area about 40 km SE from the Castelgomberto outcrop (Borsi et al., 1969; Brombin et al., 2019). At least 14 of these events are registered along the studied section (Fig. 2a), which probably had severe consequences for the survival of the communities. However, the presence of miliolids, ostracods and echinoids within these layers suggests a relatively fast recolonisation of the sea floor after each volcanic episode.

Bastia

Although the diverse coral assemblage of the Bastia section has been already studied, with the description of 16 genera and 20 species (Bosellini, 1988), a detailed facies analysis has never been performed. Here we identify three main facies (Fig. 3):

- Coral floatstone: stratified deposits with an overall thickness of 1.7 m, characterised by abundant fragments of *Caulastrea tenuis*, *Actinacis rollei* and *Astreopora* ramose colonies that accumulated parallel to the stratification (Fig. 3b). Fragments of coral sticks show an average diameter of about 1 cm and are frequently coated by coralline algae

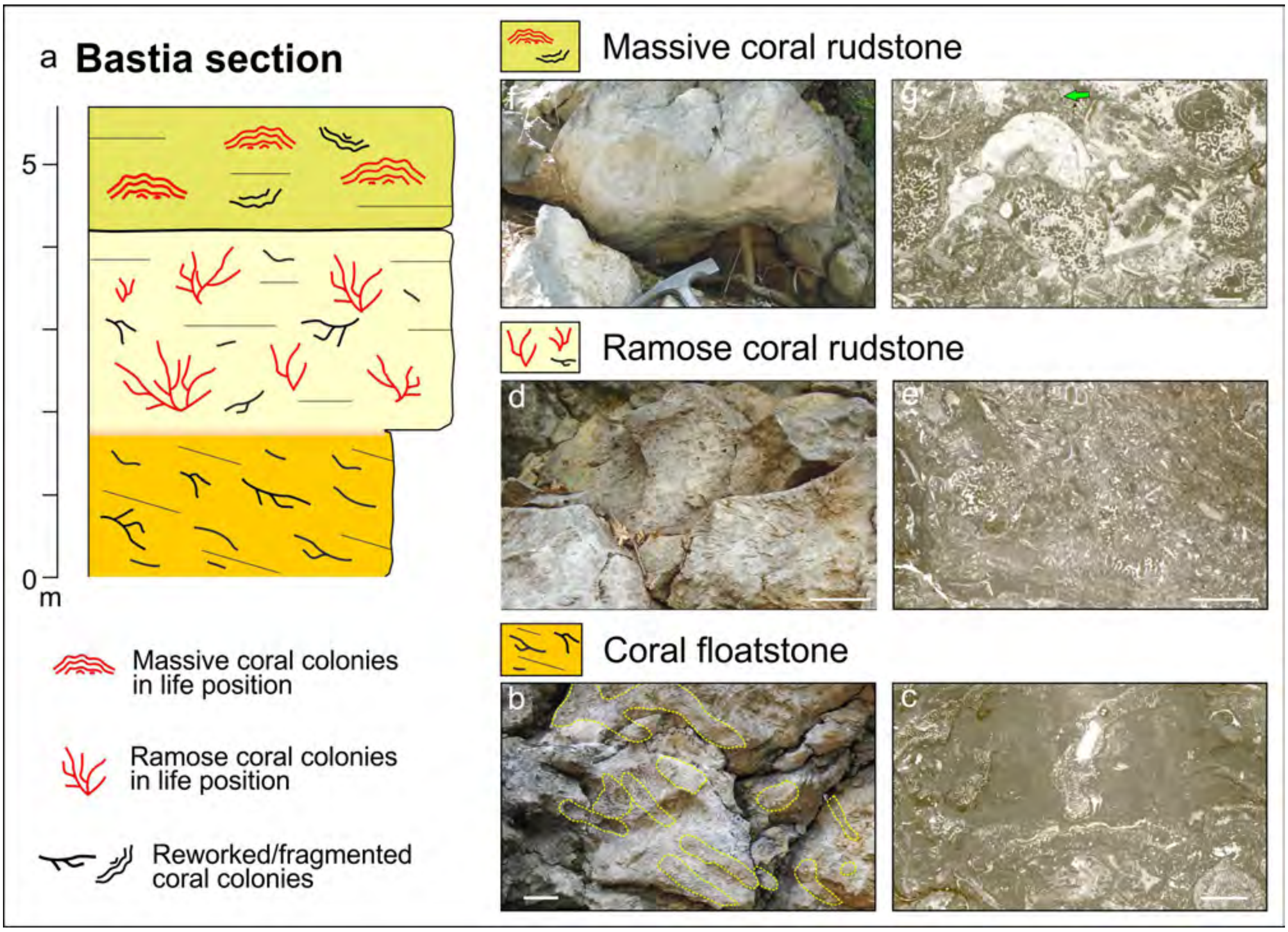

Fig. 3 - (color online) Bastia outcrop. a) Stratigraphic column. b) Coral floatstone facies, outcrop view; dashed lines outline the iso-oriented fragments of coral sticks, scale bar = 1 cm. c) Coral floatstone facies in thin section with numerous fragments of *Actinacis*, scale bar = 5 mm. d) Ramose coral rudstone facies, outcrop view with *Caulastraea* colonies in life position, scale bar = 10 cm. e) Ramose coral rudstone facies, packstone-wackestone matrix in thin section, scale bar = 5 mm. f) Massive coral rudstone facies, outcrop view with a globose *Variabilifavia* colony in life position. g) Massive coral rudstone facies in thin section; arrow indicates a dasycladacean algae, scale bar = 5 mm.

and encrusting foraminifera. The matrix is a mudstone (Fig. 3c) with fragments of coralline algae, echinoids and bryozoans.

- Ramose coral rudstone: with a gradual transition, the coral floatstone passes into an up to 2.4 m thick coral rudstone with massive appearance. Several colonies are preserved in growth position with prevailing ramose and phaceloid growth-forms (20 cm of average width and 20-35 cm in height) (Fig. 3d). *Actinacis rollei*, *Caulastrea tenuis* and other corals belonging to the genera *Acropora*, *Goniopora* and *Astreopora* are the main representatives of the coral assemblage. A minor amount of meandroid colonies, identified as *Variabilifavia,* has also been observed. In situ colonies are scattered in the sediment and associated with toppled specimens and coral rubble, thus not forming a compact framework. The rudstone matrix is a packstone-wackestone (Fig. 3e) with fragments of coralline algae, corals and minor amounts of bryozoans, miliolids, echinoids and molluscs.

- Massive coral rudstone: a sharp transition connects the ramose coral facies with coral rudstone deposits, which attain up to 1.5 m in thickness. Although mostly rudstones, massive and globose coral colonies in growth position occur in this facies (Fig. 3f). The coral assemblage, with colonies up to 50 cm in maximum diameter, is dominated by *Actinacis rollei*, associated with less common *Antiguastrea lucasiana* (Defrance, 1826) and corals belonging to the genera *Acropora, Astreopora* and *Hydnophyllia.* Although corals grew in close contact, they did not form an extensive framework. Toppled and fragmented colonies are also frequent. The matrix is a packstone (Fig. 3g) with abundant coral fragments, miliolids and rotaliid foraminifera, coralline algae, echinoids, and fragments of molluscs; *Polystrata* sp. and dasycladacean algae are also present.

Interpretation - The stratigraphic arrangement of the three Bastia facies point to a prograding, shallowing-upward depositional system. The lack of clay or marly sediments suggests development in a relatively distal setting. The basal coral floatstone can be associated with a calm, relatively deep environment, where fragments of coral sticks accumulated forming mud-supported deposits. Size and shape of these fragments, belonging to the genera *Actinacis*, *Caulastrea* and *Astreopora*, indicate their origin from the breakage of branching coral colonies that characterise the overlying ramose coral rudstone. The coral rudstone contains common miliolids, which suggests shallow water depth. Moderate wave exposure is supported by the prevalence of delicate, ramose growth forms of corals. The massive coral rudstone at the top of the section can be ascribed to very shallow water depths on the basis of an increase of miliolids and by the presence of dasycladacean algae. High-energy conditions are here indicated by the texture of the sediment and by the prevailing massive shapes of the coral colonies. In summary, the Bastia outcrop can be interpreted as a distal patch reef that grew on a topographic high in the Rupelian lagoon. In comparison to the Castelgomberto locality, this setting allowed the development of a more diverse coral fauna with larger colony sizes.

Lumignano

Despite the strong karstic overprint, two different facies could be distinguished at Lumignano:

- Coral framestone: the facies is represented by several meters wide areas occupied by a dense framework of massive-globose coral colonies (10-70 cm in width, 10-35 cm in height) (Fig. 4a, c-d), with a minor amount of branching growth-forms. Most of these corals are preserved in growth position (59%), while the rest are tilted (22%) or fragmented (19%) (Fig. 4b). The most

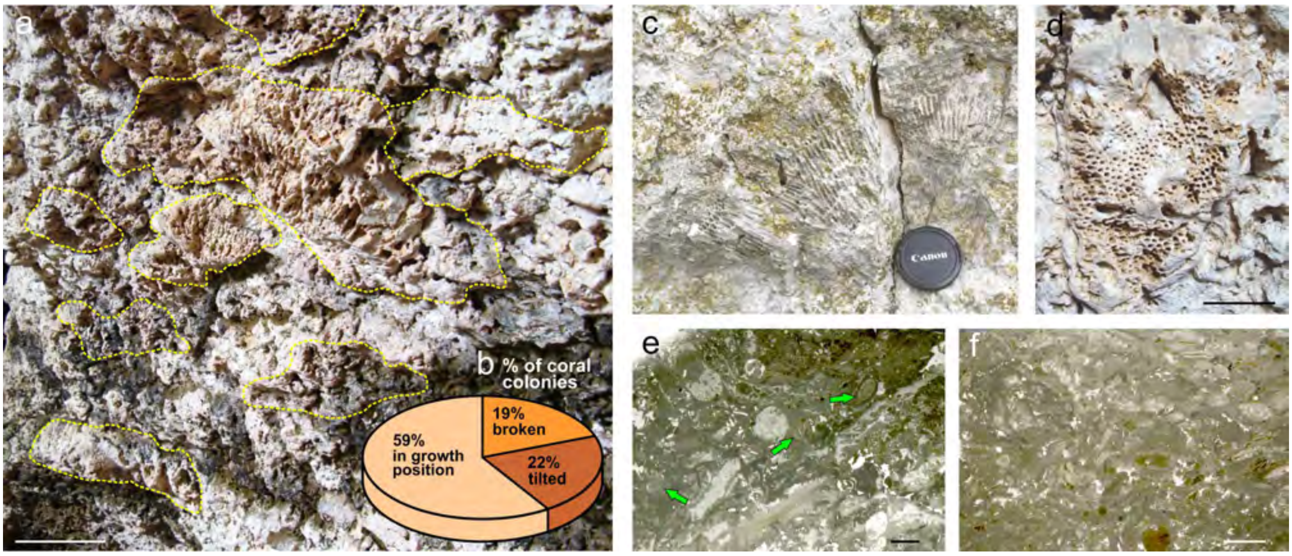

Fig. 4 - (color online) Lumignano outcrop. a) Coral framestone facies, outcrop view showing massive coral colonies in growth position, scale bar = 20 cm. b) Coral framestone facies, percentage of corals preserved as colonies in growth position, broken or tilted. c-d) Coral framestone facies, outcrop close-up of massive coral colonies, scale bar = 5 cm. e) Coral framestone facies, thin section of the rudstone deposits among the coral colonies, arrows indicate fragments of dasycladacean algae, scale bar = 2 mm. f) Coralline and bryozoan rudstone facies, microfacies assemblage in thin section, scale bar = 2 mm.

common coral taxa are *Actinacis rollei*, *Antiguastrea lucasiana* and coral colonies belonging to the genus *Montastraea.* A coarse coral rudstone can be found among the coral colonies in growth position and in close proximity of the framework. The matrix is a packstone (Fig. 4e) with abundant coral fragments associated with coralline algae, frequently represented by foliose growth-forms. Fragments of echinoids, bryozoans, molluscs, small nummulites and dasycladacean algae are also common.

- Coralline and bryozoan rudstone: the facies is found between the coral framework. Prevalent are coralline algae (foliose fragments and small rhodoliths) and bryozoans. Small nummulites, echinoids, miliolids, brachiopods, and coral fragments are associated. Micrite is present (Fig. 4f).

Interpretation - The extensive development of coral reef framework with massive corals leads us to interpret this facies as a coral reef rimming the Lessini Shelf. In situ, massive-globose colonies in close contact formed a wave-resistant framework that developed in a high-energy, euphotic environment, as testified by the abundant miliolids, the presence of dasycladacean algae and the foliose growth-forms of many coralline algae fragments. The occurrence in the nearby areas of rudstone deposits rich in coralline algae and bryozoans can be explained with the possible influx of nutrient-rich waters. The presence of a NE/SW oriented fault called Riviera dei Berici (Piccoli et al., 1976; Márton et al., 2011), bordering the southwestern side of the Berici Hills and passing close to the Lumignano locality, represented a sharp boundary during the Rupelian, which separated the southwestern margin of the Lessini Shelf from much deeper environments (Fig. 1a). Upwelling currents may have flowed from these deep areas, periodically affecting the Lumignano coral margin.

THE CASTELGOMBERTO LIMESTONE FM. DEPOSITIONAL SYSTEM

The position of the three studied localities within the Lessini Shelf (Fig. 1b) allows to trace a NE-SW oriented transect across the Castelgomberto Limestone Fm. depositional system. As already pointed out by previous authors (Geister & Ungaro, 1977; Frost, 1981), one main issue in the interpretation of the Castelgomberto Limestone Fm. is the impossibility of direct stratigraphic correlations among the different outcrops, that could not be synchronous and thus reflecting different time intervals and conditions in the depositional history of the platform. Frost (1981) however, identified a strong uniformity within the lower Oligocene carbonates of the SE Lessini and within those of the central-NW Berici. He suggested that the Castelgomberto Limestone Fm. lagoon developed within a relatively stable depositional environment throughout the existence of the barrier reef. For this reason, it seems appropriate to consider the three sections selected in the present study as representative of the environmental conditions during most of the Castelgomberto Limestone Fm. depositional history, from the innermost, proximal areas (Castelgomberto) to the most distal setting (Lumignano) (Fig. 6).

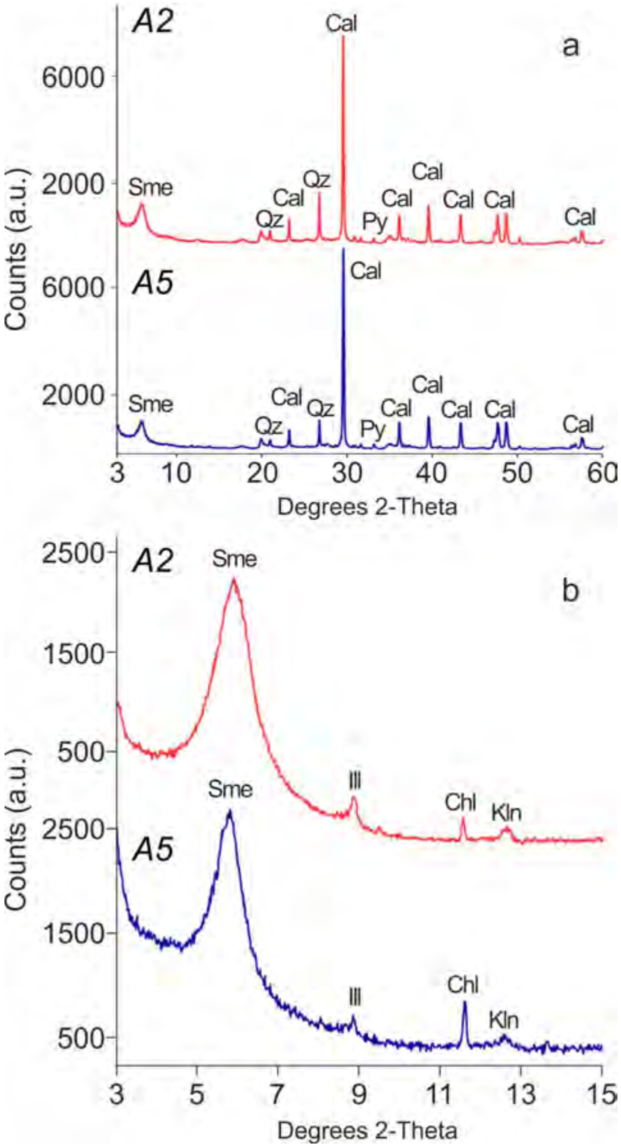

Fig. 5 - (color online) X-ray powder diffraction (XRPD) patterns of the two clay samples collected from Castelgomberto. a) XRPD patterns of the air dried and randomly oriented samples. b) Selected ranges (3-15 degrees 2-Theta) of the XRPD patterns of the orientated samples. Sme = smectite, Qz = quartz, Cal = calcite, Py = pyrite, Ill = illite, Kln= kaolinite and Chl = chlorite.

Depth

Information on the depth of the depositional system is provided by the occurrence of light-dependent organisms and porcelaneous foraminifera throughout the transect. The presence of dasycladacean algae and abundant miliolids in the coralline rudstone and coral thickets of Castelgomberto, in the massive coral rudstone of Bastia, and in the coral framestone of Lumignano, indicate a very shallow-water setting for all these facies. The same conclusion is provided by the *Polystrata* sp. crusts within the coralline rudstone of Castelgomberto, whose shapes can be associated with seagrass beds.

Turbidity

Evidence of high turbidity are limited to the Castelgomberto outcrop and can be attributed to clay influx

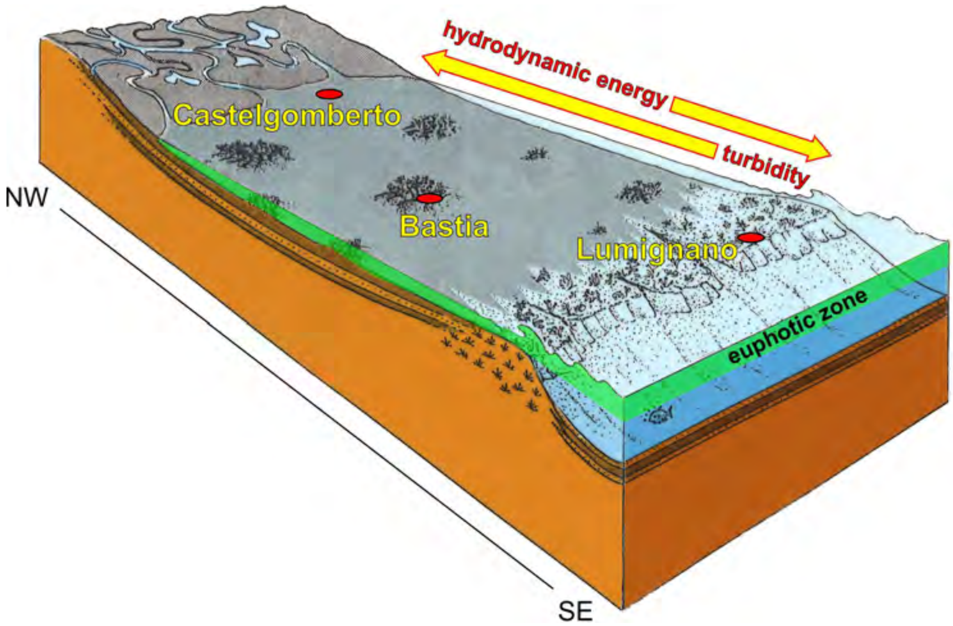

Fig. 6 - (color online) Reconstruction of the Castelgomberto Limestone Fm. depositional system with the position of the investigated sections and the variations of the main environmental stressors along the identified transect (modified from Bosellini & Trevisani, 1992).

from the mainland. These conditions were particularly strong during sea-level lowstand phases, represented by the marly mudstone facies, during which coral colonies were absent. Terrigenous sedimentation was active also during transgressive/highstand phases, affecting the coral assemblage and leading to the dominance of ramose growth-forms in the coral thickets facies. Terrigenous influx was still present but probably more episodic in the coral thickets facies. However, turbidity was not high enough to prevent coral and algal growth.

Hydrodynamic conditions

Changes in the sedimentary features indicate a progressive increase of hydrodynamic energy from the more proximal areas towards the margin of the Lessini Shelf in the Berici Hills. While the matrix of the coralline rudstone and coral thickets in Castelgomberto contains a considerable amount of clay and micrite (from wackestone/packstone to packstone/wackestone), the quantity of micrite decreases in Bastia, where the matrix of the massive coral rudstone is represented by a packstone. The sediment within the most distal coral framestone at Lumignano is characterised by a coarser rudstone with a packstone matrix. This trend in hydrodynamic conditions is also confirmed by the changes of the coral assemblages along the considered transect. In Castelgomberto, the delicate, ramose colonies are chiefly a response to high levels of turbidity but at the same time they could not have endured the impact of strong waves and currents. To the contrary, the sparse, massive colonies at the top of the Bastia patch reef are more adapted to higher energy conditions, and the Lumignano coral framestone, made of massive, in situ colonies, suggests intense hydrodynamic levels, typical of a rimmed shelf facing the open sea.

Oxygen and salinity

The highly diversified biotic assemblages that characterise all the considered outcrops indicate normal marine conditions throughout the whole depositional system. During transgressive/highstand phases, even the most proximal environment (Castelgomberto outcrop) displays a rich and diversified association that can be related to open circulation. The only exception is represented by the marly mudstone facies at Castelgomberto, which we ascribe to lowstand depositional phases, during which possible freshwater inputs may have contributed to the scarcity of fossil remains.

CONCLUSIONS

Comparing the results of the present study to the previous interpretations of the Castelgomberto Limestone Fm. (Tab. 1), three main aspects should be highlighted that improve the understanding of its depositional setting:

1. A barrier reef along the SE Berici margin. This interpretation has two issues; first, the coral framework is not particularly dense and continuous. There are larger areas with just rudstones and few corals. This observation led Geister & Ungaro (1977) to doubt the presence of a true barrier reef in Lumignano. Second, the presence of micrite, dasycladacean algae and miliolid foraminifera is not typical for a wave-swept barrier reef system. Following Geister & Ungaro (1977), we propose that the facies exposed at the Berici Hills represents the proximal back reef environment of the proper barrier reef that may have been destroyed by tectonic activity and weathering.
2. The presence of euphotic facies throughout the identified transect, from the SE Lessini to the SE Berici Hills, suggests the occurrence of a very shallow-water setting, without significant changes of the water depth.
3. Sedimentological and paleontological evidences point to a progressive increase of hydrodynamic energy from the proximal portions towards the most distal areas of the Lessini Shelf.

Features 2 and 3, as well as the presence of a distal framework, support the reef-lagoon model (Fig. 6) originally proposed by Frost (1981), whereas they are inconsistent with the interpretation of a low-angle ramp system with scattered coral colonisations limited to the meso-oligophotic zone. Considering the fundamental criteria reported in Flügel (2004) for the definition of a carbonate ramp setting, a ramp is a gently dipping sea-floor surface with progressive downslope transition from shallow-water, high-energy deposits to deeper-water, lower-energy sediments and finally to basinal, muddy deposits. A ramp geometry would thus predict for the Castelgomberto Limestone Fm. the occurrence of the shallower facies limited to the most landward portion, and a gradual deepening towards the basin, associated to a progressive decrease of the hydrodynamic conditions, which is clearly not the case.

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REFERENCES

Barbieri G., De Vecchi G.P., De Zanche V., Di Lallo E., Frizzo P., Mietto P. & Sedea R. (1980). Note illustrative alla Carta Geologica di Recoaro alla scala 1:20.000. *Memorie di Scienze Geologiche*, 34: 23-52.

Barbieri G., De Zanche V. & Sedea R. (1991). Vulcanismo paleogenico ed evoluzione del semigraben Alpone-Agno (Monti Lessini). *Rendiconti della Società Geologica Italiana*, 14: 5-12.

Barbieri G. & Zampieri D. (1992). Deformazioni sinsedimentarie eoceniche con stile a domino e relativo campo di paleostress (Monti Lessini). *Atti Ticinensi di Scienze della Terra*, 35: 25-31.

Bartoli O., Meli S., Bergomi M.A., Sassi R., Magaraci D. & Liu D.Y. (2015). Geochemistry and zircon U-Pb geochronology of magmatic enclaves in trachytes from the Euganean Hills (NE Italy): further constraints on Oligocene magmatism in the eastern Southern Alps. *European Journal of Mineralogy*, 27: 161-174.

Bassi D., Bianchini G., Mietto P. & Nebelsick J. (2008). Southern Alps in Italy: Venetian Pre-Alps. *In* McCann T. (ed.), The Geology of Central Europe, v. 2. *Geological Society of London, Special Volume*: 56-62.

Bassi D., Hottinger L. & Nebelsick J. (2007). Larger foraminifera of the Late Oligocene of the Venetian area, north-eastem ltaly. *Palaeontology*, 50: 845-868.

Bassi D. & Nebelsick J. (2010). Components, facies and ramps: redefining Upper Oligocene shallow water carbonates using coralline red algae and larger foraminifera (Venetian area, northeast Italy). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 295: 258-280.

Beavington-Penney S.J., Wright V.P. & Woelkerling W.J. (2004). Recognising macrophyte–vegetated environments in the rock record: a new criterion using "hooked" forms of crustose coralline red algae. *Sedimentary Geology*, 166: 1-9.

Borsi S., Ferrara G. & Piccoli G. (1969). Determinazioni col metodo K/Ar dell'età delle eruzioni euganee. *Rendiconti della Società Italiana di Mineralogia e Petrologia*, 25: 27-34.

Bosellini A. (1989). Dynamics of Tethyan carbonate platforms. *In* Crevello P.D., Wilson J.L., Sarg J.F. & Read J.F. (eds), Controls on Carbonate Platform and Basin Platform. *S.E.P.M. Special Publication*, 44: 3-13.

Bosellini A., Carraro F., Corsi M., De Vecchi G.P., Gatto G.O., Malaroda R., Sturani C., Ungaro S. & Zanettin B. (1967). Note Illustrative della Carta geologica d'ltalia alla scala 1:100.000, Foglio 49 Verona. 61 pp. Servizio Geologico d'Italia, Nuova Tecnica Grafica, Roma.

Bosellini A. & Dal Cin R. (1966). Analisi sedimentologica delle "Arenarie di S. Urbano" (Miocene inferiore, Lessini vicentini). *Bollettino della Società Geologica Italiana*, 85: 739-765.

Bosellini A., Masetti D. & Sarti M. (1981). A Jurassic "Tongue of Ocean" infilled with oolitic sands: the Belluno Trough, Venetian Alps, Italy. *Marine Geology*, 44: 59-95.

Bosellini F.R. (1988). Oligocene Corals from Monte Bastia (Vicentin Lessini Mountains, N. Italy). *Atti e Memorie della Accademia Nazionale di Scienze, Lettere e Arti di Modena*, Serie VII, 5: 111-157.

Bosellini F.R. & Russo A. (1988). The Oligocene *Actinacis* coral community of the Southern Alps (Italy): temperature vs. terrigenous control. *Proceedings of the 6th International Coral Reef Symposium*, 3: 385-391.

Bosellini F.R. & Stemann T.A. (1996). Autoecological significance of growth form in the scleractinian coral *Actinacis rollei* Reuss (Oligocene, Lessini Mountains, Northern Italy). *In* Cherchi A. (ed.), Autoecology of selected fossil organisms: Achievements and Problems. *Bollettino della Società Paleontologica Italiana, Volume Speciale*, 3: 31-43.

Bosellini F.R. & Trevisani E. (1992). Coral facies and cyclicity in the Castelgomberto Limestone (Early Oligocene, Eastern Lessini Mountains, Northern Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, 98: 339-352.

Brombin V., Bonadiman C., Jourdan F., Roghi G., Coltorti M., Webb L.E., Callegaro S., Bellieni G., De Vecchi G., Sedea R. & Marzoli A. (2019). Intraplate magmatism at a convergent plate boundary: The case of the Cenozoic northern Adria magmatism. *Earth-Science Reviews*, 192: 355-378.

Carraro F., Malaroda R., Piccoli G., Sturani C. & Venzo S. (1969). Note Illustrative della Carta Geologica D'Italia, Scala 1:100.000. Foglio 48, Peschiera del Garda. Poligrafica & Cartevalori Ercolano, Napoli.

Catullo T. A. (1856). Dei terreni di sedimento superiore della Venezie e dei fossili Bryozoari, Antozoari e Spongiari. 88 pp. Angelo Sicca, Padova.

Christidis G.E. & Huff W.D. (2009). Geological aspects and genesis of bentonites. *Elements*, 5: 93-98.

Coletti F., Piccoli G., Sambugar B. & Vendemiati dei Medici M.C. (1973). I molluschi fossili di Castelgomberto e il loro significato nella paleoecologica dell'Oligocene Veneto. *Memorie degli Istituti di Geologia e Mineralogia dell'Università di Padova*, 28: 1-32.

Cuadros J., Caballero E., Huertas F.J., de Cisneros C.J., Huertas F. & Linares J. (1999). Experimental alteration of volcanic tuff: smectite formation and effect on ^{18}O isotope composition. *Clays and Clay Minerals*, 47: 769-776.

Defrance M. (1823-1828). Dictionnaire des sciences naturelles. 17: 215-218, 42: 372-398, 56: 91-94, 60: 297-364.

De la Fuente S., Cuadros J., Fiore S. & Linares J. (2000). Electron microscopy study of volcanic tuff alteration to illite-smectite under hydrothermal conditions. *Clays and Clay Minerals*, 48: 339-350.

De Vecchi G.P. & Sedea R. (1995) The Paleogene basalt of the Veneto region (NE Italy). *Memorie degli Istituti di Geologia e Mineralogia dell'Università di Padova*, 47: 253-274.

De Zanche V., Sorbini L. & Spagna V. (1977). Geologia del territorio del Comune di Verona. *Memorie del Museo Civico di Storia Naturale di Verona*, 1: 1-52.

Doglioni C. & Bosellini A. (1987). Eoalpine and mesoalpine tectonics in the Southern Alps. *Geologische Rundschau*, 77: 734-754.

Dunham R.J. (1962). Classification of carbonate rocks according to depositional texture. *In* Hamm W.E. (ed.), Classification of carbonate rocks, a symposium. *AAPG Special Volumes*, 1: 108-121.

Embry A.F. & Klovan J.E. (1971). A Late Devonian reef tract on Northeastern Banks Island, N.W.T. *Bulletin of Canadian Petroleum Geology*, 19: 730-781.

Flügel E. (2004). Microfacies of carbonate rocks. 976 pp. Springer, Berlin.

Frost S.H. (1981). Oligocene reef coral biofacies of the Vicentin, northeast Italy. *In* Toomey D.F. (ed.), European fossil reef model. *S.E.P.M. Special Publication*, 30: 483-539.

Geister J. & Ungaro S. (1977). The Oligocene coral formations of the Colli Berici (Vicenza, northern Italy). *Eclogae Geologicae Helvetiae*, 70: 811-823.

Larkum A.W.D., Orth R.J. & Duarte C.M., eds (2006). Seagrasses: biology, ecology and conservation. 691 pp. Springer, Dordrecht.

Luciani V. (1989). Stratigrafia sequenziale del Terziario nella Catena del Monte Baldo (Provincie di Verona e Trento). *Memorie di Scienze Geologiche*, 41: 263-351.

Maraschini P. (1824). Sulle formazioni delle rocce del Vicentino. Saggio Geologico. 230 pp. Tipografia della Minerva, Padova.

Márton E., Zampieri D., Kázmer M., Dunkl I. & Frisch W. (2011). New Paleocene–Eocene paleomagnetic results from the foreland of the Southern Alps confirm decoupling of stable Adria from the African plate. *Tectonophysics*, 504: 89-99.

Mateu-Vicens G., Box A., Deudero S. & Rodriguez B. (2010). Comparative analysis of epiphytic foraminifera in sediments colonized by seagrass *Posidonia oceanica* and invasive macroalgae *Caulerpa* spp. *Journal of Foraminiferal Research*, 40: 134-147.

Mietto P. (1992). Monte di Malo. Aspetti Geologici. 109 pp. Comune di Monte di Malo & Centro Studi del Priaboniano "M° Antonio Marchioro", Monte di Malo, Vicenza.

Nebelsick J.H., Bassi D. & Lempp J. (2012). Tracking paleoenvironmental changes in coralline algal-dominated carbonates of the Lower Oligocene Calcareniti di Castelgomberto formation (Monti Berici, Italy). *Facies*, 59: 133-148.

Papazzoni C.A., Carnevale G., Fornaciari E., Giusberti L. & Trevisani E. (2014). 4. The Pesciara-Monte Postale Fossil-Lagerstätte: 1. Biostratigraphy, sedimentology, and depositional model. *In* Papazzoni C.A., Giusberti L., Carnevale G., Roghi G., Bassi D. & Zorzin R. (eds), The Bolca Fossil-Lagerstätten: A window into the Eocene World. *Rendiconti della Società Paleontologica Italiana*, 4: 29-36.

Papazzoni C.A., Fornaciari E., Giusberti L., Vescogni A. & Fornaciari B. (2017). Integrating shallow benthic and calcareous nannofossils zones: the lower Eocene of the Monte Postale section (northern Italy). *Palaios*, 32: 6-17.

Piccoli G., Bellati R., Binotti C., Di Lallo E., Sedea R., Dal Prà A., Cataldi R., Gatto G.O., Ghezzi G., Marchetti M., Bulgarelli G., Schiesaro G., Panichi C., Tongiorgi E., Baldi P., Ferrara G.C., Massari F., Medizza F., Iliceto V., Norinelli A., De Vecchi G.P., Gregnanin A., Piccirillo E.M. & Sbettega G. (1976). Il sistema idrotermale euganeo-berico e la geologia dei Colli Euganei. *Memorie degli Istituti di Geologia e Mineralogia dell'Università di Padova*, 30: 1-266.

Piccoli G., Sedea R., Bellati R., Di Lallo E., Medizza F., Girardi A., De Pieri R., De Vecchi G.P., Gregnanin A., Piccirillo E.M., Norinelli A. & Dal Prà A. (1981). Note illustrative della carta geologica dei Colli Euganei alla scala 1:25000. *Memorie dell'Istituto di Geologia e Mineralogia dell'Università di Padova*, 34: 523-566.

Pomar L., Baceta J.I., Hallock P., Mateu-Vicens G. & Basso D. (2017). Reef building and carbonate production modes in the west-central Tethys during the Cenozoic. *Marine and Petroleum Geology*, 83: 261-304.

Reuss A.E. von (1864). Die fossilen Foraminiferen, Anthozoen und Bryozoen von Oberburg in Steiermark. Ein Beitrag zur Fauna der oberen Nummulitenschichten. *Denkschriften der Osterreichischen Akademie der Wissenschaften, mathematisch naturwissenschaftliche Classe*, 23: 1-36.

Reuss A.E. von (1868). Paläontologische Studien über die älteren Tertiärschichten der Alpen. 1 Abtheilung. Die Fossilen Anthozoen der Schichten von Castelgomberto. *Denkschriften der mathematisch-naturwissenschaftlichen Classe*, 28: 129-180.

Rossi D. & Semenza E. (1958). Le scogliere oligoceniche dei Colli Berici. *Annali dell'Università di Ferrara, sezione 9, Scienze Geologiche e Minerarie*, 3: 49-70.

Sanders D. & Baron-Szabo R.C. (2005). Scleractinian assemblages under sediment input: their characteristics and relation to the nutrient input concept. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 216: 139-181.

Sarti M. (1980). Frane sottomarine e debris flowin una successione carbonatico torbiditica eocenica (Val d'Avesa, Verona). *Annali dell'Università di Ferrara, Sez. IX Scienze Geologiche e Paleontologiche*, 7: 65-89.

Sola F., Braga J.C. & Aguirre J. (2013). Hooked and tubular coralline algae indicate seagrass beds associated to Mediterranean Messinian reefs (Poniente Basin, Almería, SE Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 374: 218-229.

Stanley S.M. & Hardie L.A. (1998). Secular oscillations in the carbonate mineralogy of reef-building and sediment-producing organisms driven by tectonically forced shifts in seawater chemistry. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 144: 3-19.

Trevisani E. (1997). Stratigrafia sequenziale e paleogeografia del margine orientale dei Lessini Shelf durante l'Eocene superiore (Prealpi Venete, provincie di Vicenza e Treviso). *Studi Trentini di Scienze Naturali, Acta Geologica*, 71: 145-168.

Ungaro S. (2001). Le biofacies paleoceniche ed eoceniche dei Monti Lessini (Veneto, Italia). *Annali dell'Università di Ferrara, Sezione Scienze della Terra*, 9: 1-40.

Vescogni A., Bosellini F.R., Papazzoni C.A., Giusberti L., Roghi G., Fornaciari E., Dominici G. & Zorzin R. (2016). Coralgal buildups associated with the Bolca Fossil-Lagerstätten: new evidences from the Ypresian of Monte Postale (NE Italy). *Facies*, 62: 21.

Winterer E.L. & Bosellini A. (1981). Subsidence and sedimentation on Jurassic passive continental margin, Southern Alps, Italy. *Bulletin of the American Association of Petroleum Geologists*, 65: 394-421.

Woelkerling W.J., Irvine L.M. & Harvey A. (1993). Growth-forms in non-geniculate coralline red algae (Corallinales, Rhodophyta). *Australian Systematic Botany*, 6: 277-293.

Zampieri D. (1995). Tertiary extension in the southern Trento Platform, Southern Alps, Italy. *Tectonics*, 14: 645-657.

Zhou X., Liu D., Bu H., Deng L., Liu H., Yuan P., Du P. & Song H. (2018). XRD-based quantitative analysis of clay minerals using reference intensity ratios, mineral intensity factors, Rietveld, and full pattern summation methods: A critical review. *Solid Earth Sciences*, 3: 16-29.

Zoboli A., Di Giuseppe D., Baraldi C., Gamberini M.C., Malferrari D., Urso G., Gualtieri M.L., Bailey M. & Gualtieri A.F. (2019). Characterisation of fibrous ferrierite in the rhyolitic tuffs at Lovelock, Nevada, USA. *Mineralogical Magazine,* 83: 577-586.

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Lineages of *Acropora* (staghorn) corals in the Oligocene to Miocene of Florida and SW Georgia (USA)

Carden C. WALLACE[*], Roger W. PORTELL & Paul R. MUIR

C.C. Wallace, Biodiversity and Geosciences Program, Queensland Museum, Brisbane, Queensland 4101, Australia; carden.wallace@qm.qld.gov.au
[*]*corresponding author*
R.W. Portell, Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611, USA; portell@flmnh.ufl.edu
P.R. Muir, Biodiversity Section, Queensland Museum, Townsville 4811, Australia; paul.muir@qm.qld.gov.au

KEY WORDS - Acroporidae, Suwannee Limestone, Arcadia Formation (Tampa Member), coral reefs, climate change, Atlantic corals.

ABSTRACT - The staghorn coral genus Acropora *is the most diverse living genus of reef-building corals. From earliest records around the K-Pg event, the genus has a geo-history of strongly persistent morphological lineages, dating from 49 Mya to present and extending across the Eocene of England and Europe, Oligocene to early Miocene of Europe, Oligocene to present in the western Atlantic, and late Paleogene to present reef-bearing areas in the Indo-Pacific. Because of these records and the usually well-preserved* Acropora *fossils, it is regarded as an exemplar for studying modern diversity and distribution of reef corals and predicting their response to future climate change. Here we examine previously undocumented diversity of* Acropora *species groups present in Oligocene and Miocene (Suwannee Limestone and Tampa Member of the Arcadia Formation, respectively) deposits in Florida and southern Georgia, USA. We find evidence of both species-group lineages from the European region and novel, probably unique Atlantic lineages. Of 11 extant species-group lineages first present in the Eocene to Miocene of the European region, seven are present in this American material, including the* cervicornis *group, never recorded in the Indo-Pacific and now extant only in the western Atlantic. Two as yet undescribed species in the samples and the known species* Acropora tampaensis *Weisbord, 1973 could not be matched within the 19 species groups recognised in extant* Acropora*, and these may be lineages uniquely developed and lost in the Americas. The two species in the* cervicornis *species group, both now categorised as critically endangered, are the only surviving representatives of the family Acroporidae, which was previously represented by five genera in the western Atlantic.* Acropora *species from Florida and Georgia reefs clearly played a substantive role in the continuation and diversification of* Acropora *species groups during the Oligocene-Miocene in the western Atlantic and it is possible that this contributed to the success of the genus in the Indo-Pacific, as well as* cervicornis *group as a critical environmental feature of western Atlantic reefs.*

INTRODUCTION

The reef-building coral genus *Acropora* (phylum Cnidaria, order Scleractinia, family Acroporidae), with more than 150 recognised living species (Wallace, 1999; Veron, 2000; Wallace et al., 2012), has come to dominate coral diversity and even influence the architecture of modern coral reefs. With a rich and accessible fossil history (e.g., Baron-Szabo, 2006; Wallace & Rosen, 2006; Wallace, 2008; Wallace & Bosellini, 2014; Santodomingo et al., 2015), generally stable skeletal biomineralisation (Stolarski et al., 2016), and 19 (previously 20: see Wallace et al., 2007) morphologically recognisable species groups (Wallace, 1999), it has been seen as an exemplar for the study of diversification and change on coral reefs. Its species are also particularly vulnerable to some environmental impacts associated with elevated sea surface temperatures and other types of change on coral reefs (e.g., Bruckner & Hourigan, 2002; Vollmer & Palumbi, 2007; Aronson et al., 2008a, b; Faith & Richards, 2012; Renema et al., 2016). However, many have been found to extend into mesophotic (and thus somewhat protected) reef zones as well as shallow reef fronts (Muir & Wallace, 2016; Muir et al., 2018a, b; Turak & DeVantier, 2019).

A finding of representatives of nine of the 19 (previously 20) modern *Acropora* species groups in the Eocene (49-33.9 Mya) of England and France (Wallace & Rosen, 2006), was taken as evidence that pre-existing diversity contributed to modern high diversity of *Acropora* in the Indo-Pacific region, in a contradiction of the previous premise that modern *Acropora* diversity sprang from a single Pliocene ancestor (Stehli & Wells, 1971; Potts, 1985; Veron, 1995; Fukami et al., 2000). These species groups: *humilis* (as *humilis I* and *II*), *cervicornis*, *muricata*, *robusta*, *aspera*, *florida*, *hyacinthus*, and *latistella* were subsequently matched up with ten species (some new, others previously described), and another species was tentatively matched with the *elegans* group (Wallace, 2008), which can now be validated. A subsequent study of Oligocene (23.0-33.9 Mya) and early Miocene (16.0-23.0 Mya) fossils from continental Europe (Wallace & Bosellini, 2014) found new and continuing species from all these groups except *elegans*, plus two additional groups *horrida* and *rudis*. That study concluded that conditions in the western Tethys region during the Oligocene and early Miocene were compatible with survival and range expansion of Eocene species and species turnover or origination of new species within lineages (Wallace & Bosellini, 2014).

In the western Atlantic Ocean region (Caribbean and the Americas) a "cosmopolitan pan-Tethyan fauna" was recognised in the coral fossil record from the Late Cretaceous to end-Eocene (Edinger & Risk, 1994; Budd, 2000). The family Acroporidae shows this pattern, with genera *Astreopora*, *Alveopora*, *Acropora*, and the now globally extinct *Dendracis*, all previously present in the western Atlantic as well as elsewhere in the Tethyan seaway (Wallace, 2012). This period was followed by

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Locality	Estimated age (Mya)	Biostratigraphical age	References
Tampa Member of the Arcadia Formation, Tampa Bay, Hillsborough County, Florida	22.3 - 26 Mya	Miocene (Aquitanian) to Oligocene (Chattian) W 11541, W 15166	Brewster-Wingard et al., 1997
Little Horseshoe Bend, Flint River, Decatur County, Georgia	27.8 - 33.9 Mya	Oligocene (Rupelian)	Dall, 1916
Terramar 01, Polk County, Socrum Quadrangle, Florida	33.6 - 34.1 Mya	Oligocene (Rupelian) to Eocene (Priabonian)	Herbert & Portell, 2002 (references therein)

Tab. 1 - Localities from which the *Acropora* fossils in this study were collected. Sources of ages and/or coral facies are from references indicated.

the Oligocene/early Miocene turnover period (OMT) characterised by loss of species and genera in many families including Acroporidae and leading to a "more distinctive Caribbean fauna" (Johnson & Kirby, 2006). By the end of the OMT only *Acropora* remained of the Atlantic Acroporidae, although it was briefly joined by its sister genus *Isopora* in the Neogene (Budd & Wallace, 2008; Wallace & Budd, 2009). Living *Acropora* is represented by the two extant species of the *cervicornis* group, *A. cervicornis* and *A. palmata*, and an F1 hybrid, currently accepted as *A. prolifera* (Lamarck, 1816) (see Wallace, 1999, p. 178-179; Vollmer & Palumbi, 2002; Anguila-Perera & Hernánde-Lander, 2018; Nylander-Asplin, 2018; Hoeksema & Cairns, 2020). While the histories of other genera of Acroporidae are well-documented (Budd et al., 1994, 1995) the origination and turnover of many species of *Acropora* in the western Atlantic remain to be detailed from fossil material deposited in museums. This paper documents a small part of this record, by looking at the species group status of fossils from Oligocene and Miocene deposits in Florida and Georgia, USA.

Geological setting

The basement conformation of the Florida Platform includes land that was rifted from the African Plate during the Triassic breakup of Pangea and sutured onto the North American continent (Scott, 2001, 2011; Smith, 2015; Upchurch et al., 2019). In the Cretaceous to mid Eocene, most of Florida was separated from the rest of North America by the Suwannee Straits, a swift marine current running from the Gulf of Mexico to the Atlantic Ocean (Fig. 1; Scott, 2011). Following this, tectonic activity and erosion of the Appalachian Mountains caused siliciclastic sediments and carbonates to fill the channel, forming the Gulf Trough (Smith, 2015; Upchurch et al., 2019). The flow of materials continued southwards, forming the Suwannee Limestone, named by Cooke & Mansfield (1936), which now underlies a portion of southern Georgia and most of modern Florida. It encompasses the early Oligocene (Rupelian, 27.8-33.9 Mya) and is thought to straddle the Eocene/Oligocene boundary (Herbert & Portell, 2002).

The Suwannee Limestone is exposed in river banks and at Little Horse Shoe Bend on the Flint River, Decatur County, Georgia (Dall, 1916) or accessed by mining, e.g., as at the FLMNH Terramar 01 site in Polk County, Florida (Herbert & Portell, 2002). In the region of Tampa Bay, Hillsborough County, Florida, the Suwannee Limestone is overlain by a younger deposit, the Tampa Member of the Arcadia Formation, which is late Oligocene (Chattian) to mid Aquitanian (early Miocene) (22.3-26 Mya) (Brewster-Wingard et al., 1997). These three locations provided our samples (Tab. 1, Fig. 1).

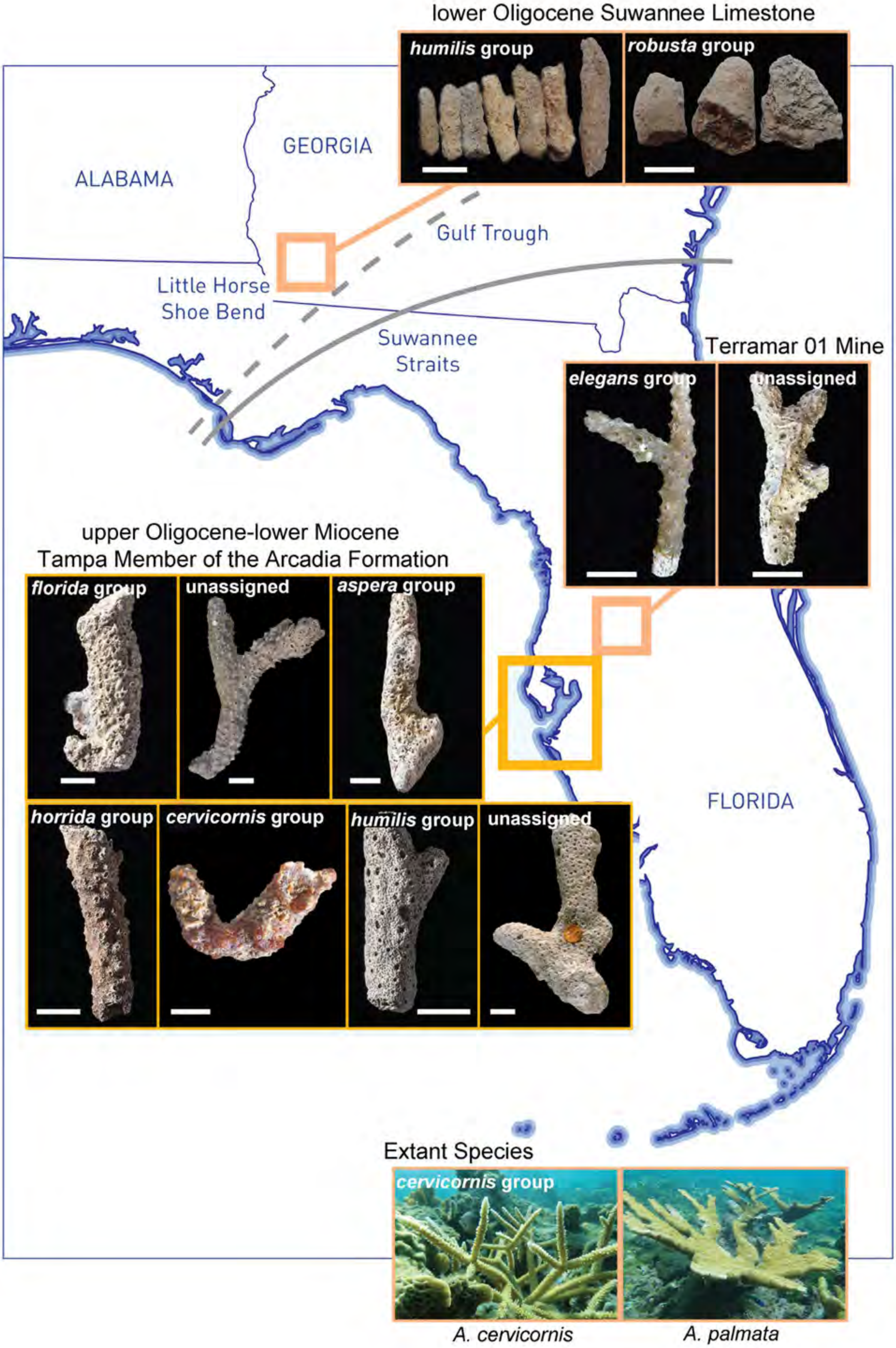
MATERIAL AND METHODS

Specimens were examined at the Florida Museum of Natural History (FLMNH), University of Florida, Gainesville, USA, the National Museum of Natural History (USNM), Smithsonian Institution, Washington DC, and at Queensland Museum, Brisbane, using a binocular dissecting microscope with eyepiece micrometer. We examined fossil fragments from 12 specimen lots, collected at the localities (Tab. 1, Fig. 1) from mid-nineteenth century to present. The fragments were studied for discernible skeletal characters at species-group level, as outlined in Wallace & Rosen (2006: Methods and tab. 2) and subsequent fossil studies (Wallace, 2008; Santodomingo et al., 2015).

RESULTS AND DISCUSSION

Eleven forms with characters consistent with separate species were found, two from Georgia and nine from Florida (illustrated in Fig. 1 by locality). One was *Acropora tampaensis* Weisbord, 1973, with the others interpreted as new to science. Eight of the as yet undescribed species were attributed to seven of the species groups, assumed to be lineages, recognised in modern *Acropora* (Wallace, 1999; Wallace et al., 2012): *humilis*, *cervicornis*, *robusta*, *aspera*, *florida*, *elegans* and *horrida* groups (Fig. 1), leaving the affinities of the other three

Fig. 1 - (color online) Map of Florida and southern Georgia, indicating features and locations mentioned in the text. Images of species identified to species group are superimposed and arranged according to collecting location in: Suwannee Limestone (top and centre right hand images) and Tampa Member of the Arcadia Formation (left hand images). Two extant Atlantic Ocean species from the *cervicornis* group are shown alive and in situ in the San Blas Islands on the bottom right. All scale bars are 10 mm.


lower Oligocene Suwannee Limestone
humilis group
robusta group
GEORGIA
ALABAMA
Gulf Trough
Little Horse
Shoe Bend
Suwannee
Straits
Terramar 01 Mine
elegans group
unassigned
upper Oligocene-lower Miocene
Tampa Member of the Arcadia Formation
florida group
unassigned
aspera group
horrida group
cervicornis group
humilis group
unassigned
FLORIDA
Extant Species
cervicornis group
A. cervicornis
A. palmata

Period	Epoch	Age	Mya	*latistella*	*humilis**	*cervicornis**	*muricata*	*florida**	*hyacinthus*	*aspera**	*horrida**	*robusta**	*elegans**	*rudis*
Neogene	Miocene	Burdigalian	16.0-20.4	Europe[2]				Europe[2]			Europe[2]			
		Aquitanian	20.4-23.0	Europe[2]	Florida[1]	Florida[1]		Florida[1] Europe[2]		Florida[1] Europe[2]	Florida[1]	Europe[2]		
Paleogene	Oligocene	Chattian	23.0-28.1	Europe[2]	Europe[2]	Europe[2]		Florida[1]	Europe[2]	Florida[1] Europe[2]		Europe[2]		Europe[2]
		Rupelian	28.1-33.9		Georgia[1] Europe[2]	Europe[2]					Florida[1]	Georgia[1]	Florida[1]	
	Eocene	Priabonian	33.9-37.8		England, France[3]	Europe[2,3]		England[3]			Florida[1]	England[3]	Florida[1]	
		Bartonian	37.8-41.2	France[3]	England, France[3]	Europe[2] France[3]	France[3]	England[3]	France[3]	France[3]				
		Lutetian	41.2-47.8	France[3]		France[3]				France[3]			France[3]	

Fig. 2 - Occurrence of identified *Acropora* species groups (columns) from the strata (rows) studied in: the Oligocene and Miocene of USA (superscript 1 = this paper), compared with the Oligocene and Miocene of continental Europe (superscript 2 = Wallace & Bosellini, 2014) and the Eocene of England and/or France (superscript 3 = Wallace & Rosen, 2006 + Wallace, 2008). Strata represented as in the Geologic Time Scale (Walker et al., 2012). Europe records include France, Italy, Spain and Slovenia. Each record is for one or two species in the species group indicated. Asterisk = species group found in this study.

species (including *A. tampaensis*) undetermined. Tab. 2 lists the main characteristics by which these species groups were determined from the fossil fragments.

Fig. 2 compares the age of the species-group distributions in Florida and Georgia with known species-group presence in the *Acropora* fossil record from the western Tethys. The identified Atlantic lineages also occur in the Eocene, Oligocene and early Miocene of Europe, with the exception of *horrida* group, which has only a late Miocene record in Europe to date (Wallace & Rosen, 2006; Wallace, 2008; Wallace & Bosellini, 2014). All the groups except *cervicornis* group are also represented in the Miocene or younger of Indonesia in the central Indo-Pacific (Santodomingo et al., 2015). At this stage of interpretation, up to three unnamed species groups can be hypothesised to be uniquely American. A more complete description of the fossil material in this study is in preparation and this will describe the new species and further examine their lineages.

All Florida and Georgia records of *Acropora* lineages identified in this study, except *horrida* group, postdate their appearance in the western Tethys region. The presence of these species groups in northern America indicates that, from early diversification in the Eocene of England and Europe (Wallace & Rosen, 2006; Wallace, 2008), followed by range extension, species longevity and turnover in the European Oligo-Miocene (Wallace & Bosellini, 2014), the *Acropora* lineages were able to extend into the Atlantic and leave a diverse species record in mainland USA. This is a clear indication that *Acropora* played a role in the cosmopolitan pan-Tethyan fauna of the western Atlantic to end-Eocene (Budd et al., 1994). The possibility that it also played a role in "the development of a more distinctive western Atlantic fauna by diversification during the Oligo-Miocene" (Johnson & Kirby, 2006, p. 283) may be hypothesised from the survival of the *cervicornis* group and presence of up to three novel species groups.

The diversity of species groups derived from the western Tethys in the Oligo-Miocene of the Atlantic is indicative of the presence of suitable conditions for *Acropora* survival in a variety of habitat types. The unique geological and biological features involved in the development of reefs in the region and the deposition of the fossil-bearing Suwannee Limestone and Arcadia Formation are described in many publications (e.g., Mansfield, 1937; Scott, 2001, 2011; Smith, 2015; Upchurch et al., 2019 and numerous others). Few of the species groups recorded here have been seen to date in the Caribbean fossil fauna (Budd et al., 1994; Budd, 2000; Wallace, 2012), so it is possible that this USA fauna played a unique role, perhaps in parallel to that played out in the Caribbean, and that this contributed to the maintenance and extension of many *Acropora* lineages into the Indo-Pacific.

Four other sister genera of *Acropora* in the family Acroporidae: *Astreopora*, *Alveopora*, *Isopora* and *Dendracis* (now extinct worldwide) are also present in the fossil record of the western Atlantic region (Wallace, 2012), but extinct there today, making *A. cervicornis* and *A. palmata* and their F1 hybrid (the *cervicornis* group) the only remaining representatives of the family. These species are known for their rapid growth and

Species group	**Main visible characteristics**
humilis	Radial corallites short, thickened tubular with dimidiate openings, evenly sized or two sizes. Coenosteum throughout reticulate with laterally flattened spinules, sometimes reticulo-costate. Colonies corymbose or digitate, branch diameter axial dominated.
cervicornis	Radial corallites approximately tubo-nariform, evenly sized. Coenosteum reticulate between, costate on radial corallites, with laterally flattened spinules more or less in lines (costae). Colony shape various, branch diameter axial dominated.
robusta	Radial corallites dimorphic, one form long tubular with dimidiate opening, the other subimmersed. Coenosteum reticulate between, costate on radial corallites. Colonies sub-arborescent, branch diameter axial dominated.
aspera	Radial corallites labellate, upper wall absent, lower wall developed into a flaring lip, evenly sized or two sizes. Coenosteum open reticulate with few simple spinules between radial corallites, costate on radial corallites. Colonies corymbose or arborescent, branch diameter axial dominated.
florida	Radial corallites appressed tubular with thickened lip-like lower wall and round openings, evenly sized. Coenosteum between radial corallites reticulate and simple, with few simple spinules, on radial corallites costate or reticulo-costate. Colonies based on simple hispidose branching, branch diameter 50/50 axial: radial.
elegans	Radial corallites tubular or appressed tubular, evenly sized, sometimes alternate- sympodially arranged on the branch. Coenosteum throughout formed by elaborate spinules, densely to moderately densely arranged. Colonies with light structure, mostly horizontal branching and sparsely arranged branches, branch diameter axial: radial domination various.
horrida	Radial corallites simple tubular with round openings, evenly sized. Coenosteum throughout with simple to moderately elaborated spinules, parts of coenosteum fused. Colonies arborescent to hispidose, branch diameter 50/50 axial: radial.

Tab. 2 - Main characteristics of the seven modern *Acropora* species groups that could be recognised in the fossil fragments examined and allow comparison with material from other fossil studies, in particular Wallace (2008), Wallace & Bosellini (2014), Santodomingo et al. (2015).

contribution to reef front structure. The *cervicornis* group is not represented elsewhere in the world after the Miocene, and never recorded from the Indo-Pacific. Current evidence suggests that this species group has a lineage of up to 45.8 million years, making its critically endangered status a serious threat to future phylogenetic diversity and habitat integrity of the reef ecosystems of the western Atlantic. *Acropora* species from the fossil record of Florida and Georgia reefs clearly played a substantive role in the diversification of *Acropora* during the Oligocene-Miocene in the western Atlantic and it is possible that this contributed to the success of the genus in the Indo-Pacific, as well as to the establishment of the surviving *cervicornis* group as a critical environmental feature of western Atlantic reefs.

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REFERENCES

Aguilar-Perera A. & Hernández-Landa R.C. (2018). Occurrence of large thickets of *Acropora prolifera* (Scleractinia: Acroporidae) in the southern Gulf of Mexico. *Marine Biodiversity*, 48: 2203-2205.

Aronson R., Bruckner A., Moore J., Precht B. & Weil E. (2008a). *Acropora cervicornis*. *The IUCN Red List of Threatened Species 2008*: e.T133381A3716457.

Aronson R., Bruckner A., Moore J., Precht B. & Weil E. (2008b). *Acropora palmata*. *The IUCN Red List of Threatened Species* 2008: e.T133006A3536699.

Baron-Szabo R.C. (2006). Corals of the K/T boundary: Scleractinian corals of the suborders Astrocoeniina, Faviina, Rhipidogyrina and Amphiastaena. *Journal of Systematic Palaeontology*, 4: 1-108.

Brewster-Wingard G.L., Scott T.M., Edwards L.E., Weedman S.D. & Simmons K.R. (1997). Reinterpretation of the peninsular Florida Oligocene: an integrated stratigraphic approach. *Sedimentary Geology*, 108: 207-228.

Bruckner A.W. & Hourigan T.F. (2002). Proactive management for conservation of *Acropora cervicornis* and *Acropora palmata*: Application of the US Endangered Species Act. Proceedings 9th International Coral Reef Symposium, Bali, Indonesia 23-27 October 2000, 2: 661-665.

Budd A.F. (2000). Diversity and extinction in the Cenozoic history of Caribbean reefs. *Coral Reefs*, 1: 25-35.

Budd A.F., Johnson K.G. & Edwards J.C. (1995). Caribbean reef coral assemblages during the early to middle Miocene: An example from the Anguilla Formation. *Coral Reefs*, 14: 109-117.

Budd A.F., Stemann T. & Johnson K. (1994). Stratigraphic distributions of genera and species of Neogene to Recent Caribbean reef corals. *Journal of Paleontology*, 68: 951-997.

Budd A.F. & Wallace C.C. (2008). First record of the Indo-Pacific reef coral genus *Isopora* in the Caribbean region: Two new species from the Neogene of Curaçao, Netherlands Antilles. *Palaeontology*, 5: 1187-1401.

Cooke C.W. & Mansfield W.C. (1936). Suwannee Limestone of Florida (abstract): *Geological Society of America Proceedings*, 1935: 71-72.

Dall W.H. (1916). A contribution to the invertebrate fauna of the Oligocene beds of Flint River, Georgia. *Proceedings of the U.S. National Museum*, 51: 486-524.

Edinger E.N. & Risk M.J. (1994). Oligocene-Miocene extinction and geographic restriction of Caribbean corals: Roles of turbidity, temperature, and nutrients. *Palaios,* 9: 576-598.

Faith D.P. & Richards Z.T. (2012). Climate change impacts on the tree of life: Changes in phylogenetic diversity illustrated for *Acropora* corals. *Biology*, 1: 906-932.

Fukami H., Omori M. & Hatta M. (2000). Phylogenetic relationships in the coral family Acroporidae, reassessed by inference from the mitochondrial genes. *Zoological Science*, 17: 689-696.

Herbert G.S. & Portell R.W. (2002). A new species of *Antiliosa* (Muricidae: Neogastropoda) from the upper Eocene/lower Oligocene Suwannee Limestone of Florida. *The Veliger*, 45: 303-308.

Hoeksema B.W. & Cairns S. (2020). World List of Scleractinia. *Acropora prolifera* (Lamarck, 1816). Accessed through: World Register of Marine Species at: http://www.marinespecies.org/aphia.php?p=taxdetails&id=288235 on 2020-03-23

Johnson K.G. & Kirby M.X. (2006). The Emperador Limestone rediscovered: Early Miocene corals from the Culebra Formation, Panama. *Journal of Paleontology*, 80: 283-293.

Lamarck J.B.P.A. de M. de (1816). Histoire naturelle des animaux sans vertebres. Paris, 2: 1-568.

Mansfield W.C. (1937). Mollusks of the Tampa and Suwannee limestones of Florida. *Florida Geological Survey Geological Bulletin*, 15: 1-334.

Muir P.R., Pichon M., Squire L. Jr. & Wallace C.C. (2018b). *Acropora tenella*, a zooxanthellate coral extending to 110 m depth in the northern Coral Sea. *Marine Biodiversity*, 49: 1-6.

Muir P.R. & Wallace C.C. (2016). A rare 'deep-water' coral assemblage in a shallow lagoon in Micronesia. *Marine Biodiversity*, 46: 543-544.

Muir P.R., Wallace C.C., Pichon M. & Bongaerts P. (2018a). High species richness and lineage diversity of reef corals in the mesophotic zone. *Proceedings Royal Society B*, 285: 20181987.

Nylander-Asplin H.F. (2018). Population dynamics and genotypic richness of the Threatened *Acropora* spp. and their hybrid in the U.S. Virgin Islands. Master's thesis. Nova Southeastern University. Retrieved from NSUWorks. 47 pp.

Potts D.C. (1985). Sea-level fluctuations and speciation in Scleractinia. In Hamelin V. & Salvat B. (eds), Proceedings 5th International Coral Reef Congress. Volume 4. International Society of Reef Studies, Tahiti: 127-132.

Renema W., Pandolfi J.M., Kiessling W., Bosellini F.R., Klaus J.S., Korpanty C., Rosen B.R., Santodomingo N., Wallace C.C., Webster J.M. & Johnson K.G. (2016). Are coral reefs victims of their own past success? *Science Advances*: e1500850 22.

Santodomingo N., Wallace C.C. & Johnson K.G. (2015). Fossils reveal a high diversity of the staghorn coral genera *Acropora* and *Isopora* (Scleractinia: Acroporidae) in the Neogene of Indonesia. *Zoological Journal of the Linnean Society*, 175: 677-763.

Scott T.M. (2001). Text to accompany the Geological Map of Florida. Open-file Report 80, Florida Geological Survey, Tallahassee, Florida: 1-28.

Scott T.M. (2011). Geology of the Florida Platform – Pre-Mesozoic to Recent. *In* Buster N.A. & Holmes C.W. (eds), Gulf of Mexico: Origins, water, and biota, Vol. 3 Geology, Texas A&M University Press, College Station, TX, Chapter 2: 17-31.

Smith K. (2015). A study of the lithological and petrographical changes across the Eocene-Oligocene transition of the Ocala and Suwannee formations in northern Florida and southern Georgia. 51 pp. The Florida State University, ProQuest Dissertations Publishing: 1600084.

Stehli F.G. & Wells J.W. (1971). Diversity and age patterns in hermatypic corals. *Systematic Zoology*, 20: 115-126.

Stolarski J., Bosellini F.R., Wallace C.C., Gothmann A.M., Mazur M., Domart-Coulon I., Gutner-Hoch E., Neuser R.D., Levy O., Shemesh A. & Meibom A. (2016). A unique coral biomineralization pattern has resisted 40 million years of major ocean chemistry change. *Scientific Reports,* 6: 27579.

Turak E. & DeVantier L. (2019). Reef-building corals of the upper mesophotic zone of the central Indo-West Pacific. *In* Loya Y. et al. (eds), Mesophotic Coral Ecosystems, Coral Reefs of the World 12, Springer Nature Switzerland AG 2019: 621-651.

Upchurch S.B., Scott T.M., Alfieri M.C., Fratesi B. & Dobecki T.L. (2019). The Karst Systems of Florida. *In* Geologic framework of Florida: 59-91.

Veron J.E.N. (1995). Corals in space and time: Biogeography and evolution of the Scleractinia. 321 pp. University of New South Wales Press, Sydney.

Veron J.E.N. (2000). *Corals of the World*. Townsville, Australia. Three volumes. 1382 pp. Australian Institute of Marine Science, Melbourne.

Vollmer S.V. & Palumbi S.R. (2002). Hybridization and the evolution of reef coral diversity. *Science*, 296: 2023-2025.

Vollmer S.V. & Palumbi S.R. (2007). Restricted gene flow in the Caribbean staghorn coral *Acropora cervicornis*: Implications for the recovery of endangered reefs. *Journal of Heredity*, 98: 40-50.

Walker J.D., Geissman J.W., Bowring S.A. & Babcock L.E., Compilers (2012). Geological Time Scale V. 4.0: Geological Society of America.

Wallace C.C. (1999). Staghorn Corals of the World. 421 pp. PMID: 25506965. CSIRO Publishing, Melbourne.

Wallace C.C. (2008). New species and records from the Eocene of England and France support early diversification of the coral genus *Acropora*. *Journal of Paleontology*, 82: 313-328.

Wallace C.C. (2012). Acroporidae of the Caribbean. *Geologica Belgica*, 15: 388-393.

Wallace C.C. & Bosellini F.R. (2014). *Acropora* (Scleractinia) from the Oligocene and Miocene of Europe: Species longevity, origination and turnover following the Eocene–Oligocene transition. *Journal of Systematic Palaeontology*, 13: 447-469.

Wallace, C.C. & Budd A.F. (2009). Mirror-image fossils reveal colony form of extinct Curaçao *Isopora. Coral Reefs*, 28: 715.

Wallace C.C., Chen C.A.C., Fukami H. & Muir P.R. (2007). Recognition of separate genera within *Acropora* based on new morphological, reproductive and genetic evidence from *A. togianensis,* and elevation of the subgenus *Isopora* Studer, 1878 to genus (Scleractinia: Astrocoeniidae; Acroporidae). *Coral Reefs*, 26: 231-239.

Wallace C.C., Done B. & Muir P.R. (2012). Revision and catalogue of worldwide staghorn corals *Acropora* and *Isopora* (Scleractinia: Acroporidae) in the Museum of Tropical Queensland. *Memoirs of the Queensland Museum Nature*, 57: 1-255.

Wallace C.C. & Rosen B.R. (2006). Diverse staghorn corals (*Acropora*) in high-latitude Eocene assemblages: Implications for the evolution of modern diversity patterns of reef corals. *Proceedings of the Royal Society B*, 273: 975-982.

Weisbord N.E. (1973). New and little-known fossil corals from the Tampa Formation of Florida. *Florida Bureau of Geology, Geological Bulletin*, 56: 1-147.

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