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J. Reitner. M. Reich. J.-P. Duda

Fossillagerstätten and Taphonomy

New Ideas and Approaches

Abstractband zum Symposium 23.-25.11.2023

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Abstract

Fossil lagerstätten are excellent windows into the geological past and are characterized by excellent preservation as well as abundance of fossils. However, in most cases the conditions of formation are unclear and poorly understood.

The concept of „fossil Lagerstätten“ was developed in 1970 by Prof. Dr. Adolf Seilacher (corresponding member of the Göttingen Academy) and was a milestone of paleobiological research.

At the symposium new ideas on the formation of different fossil sites will be presented by members of the research commission and invited specialists, combined with questions on fossilization processes (taphonomy) and fossil preservation.

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New ideas and approaches

Abstracts of the Symposium Nov. 23-25, 2023

Joachim Reitner, Mike Reich, Jan-Peter Duda (Eds.)

Symposium der Forschungskommission „Origin of Life“

(Nov. 23-25, 2023)

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Programm Symposium Fossillagerstätten 23.11.-25.11.2023

Beginn Donnerstag den 23.11.2023 um 14 Uhr
Akademiehaus in der Geiststrasse 10

Mod. **Joachim Reitner**

14:00
Begrüßung

14:15
Jan-Peter Duda (Geobiologie, Univ. Göttingen)
Glimpses in the deep shadow of time: Precambrian fossil lagerstätten and their significance for understanding early eukaryote evolution

14:45
Christina Ifrim (Museum Willibaldsburg, Eichstätt)
The Cretaceous Platy Lime-stones of Mexico

15:15 Kaffeepause

15:45
Volker Thiel (Geobiologie, Univ. Göttingen)
Lower Jurassic concretions: a treasure trove for molecular fossils?

16:15
Mike Reich (Staatliches Naturhistorisches Museum Braunschweig)
Micro- and nannofossil Lagerstätten – What can they contribute?

Ende ca. 17:00

18:15
Vortrag in der Aula der Universität Göttingen:

Grußwort: Prof Dr. **Daniel Göske**, Präsident der Niedersächischen Akademie der Wissenschaften zu Göttingen

Joachim Reitner (Geobiologie, Univ. Göttingen; Akademie Göttingen):
Fossillagerstätte Willershausen bei Northeim: Einblicke in eine Welt vor
3 Millionen Jahre

Mike Reich (Staatliches Naturhistorisches Museum Braunschweig)
& **Jan-Peter Duda** (Geobiologie, Univ. Göttingen)
Einführung in Fossillagerstätten

Freitag den 24.11.2023, ab 9:00 Uhr
Akademiehaus in der Geiststrasse 10

Mod. **Jan-Peter Duda**

9:00
Xingliang Zhang & **Yuheng Qiao** (Department of Geology, Northwest University, Xi'an China)
Thermal maturity of Cambrian Burgess Shale-Type Lagerstätten

9:30
Sonja Wedmann (Senckenberg Museum Frankfurt/Main)
The UNESCO world heritage "Messel Pit Fossil Site" – taphonomical issues

10:00
Cui Luo (NIGPAS, Nanjing, China)
Unsettle the affinity *Vauxia*: a challenge from taphonomic studies (Zoom)

10:30 Kaffeepause

11:00
Hans Hagdorn (Muschelkalkmuseum Ingelfingen) & **Mike Reich** (Staatliches Naturhistorisches Museum Braunschweig)
Echinoderm Fossillagerstätten in the Triassic Muschelkalk – Adolf Seilacher's early observations and current overview

11:30
Günter Schweigert (Staatliches Museum für Naturkunde, Stuttgart)
The Nusplingen Plattenkalk – observations, assumptions and enigmas of a Late Jurassic fossil Konservat-Lagerstätte

12:00
Hao Yun (Department of Geology, Northwest University, Xi'an, China) et al.
Adaptive evolution of hexactinellid sponges from the Cambrian black shale Lagerstätten of China

12:30 Mittagsbuffet

Mod. **Mike Reich**

13:30
Liuyi Lu (Geobiologie, Univ. Göttingen) et al.
Unlocking Vestiges of Microbial Life Hidden within Ediacaran Phosphorites of the Doushantuo Formation in South China

14:00
Hans Kerp (Geologisch-Paläontologischen Institut, Universität Münster) & **Michael Krings** (SNSB, München)
The Early Devonian Rhynie chert – The world's oldest and most complete terrestrial ecosystem

14:30
Michael Krings (SNSB, München) & **Hans Kerp** (Geologisch-Paläontologischen Institut, Universität Münster)
The fidelity of microbial preservation in the Lower Devonian Rhynie cherts of Scotland

15:00 Kaffepause

15:30
Thomas Terberger (Seminar für Ur- und Frühgeschichte Universität Göttingen)
Underestimated? Selected examples of the taphonomy of prehistoric sites in northern Germany

16:00
Derek Briggs (Yale Peabody Museum, Yale University, New Haven, USA)
The taphonomy of Konservat-Lagerstätten – now and next (Zoom)

16:30
Martin Röper (Museum Solnhofen) & **Mike Reich** (Staatliches Naturhistorisches Museum Braunschweig)
The Late Jurassic Plattenkalk deposits (Kimmeridgian/Tithonian) of the 'Solnhofen Archipelago', Bavaria, Germany

17:00
Julien Kimmig (Staatliches Museum für Naturkunde Karlsruhe) & **James D. Schiffbauer** (Department of Geological Sciences, University of Missouri Columbia)
Finding and describing the exceptional: A modern definition of Fossil-Lagerstätten

Ende ca. 17:30

19:00 Abendbuffet
Akademiehaus in der Theaterstrasse 7

Samstag, den 25.11.2023

Exkursion nach Willershausen
Abfahrt 10 Uhr von der Geiststr. 10 – zurück ca. 13 Uhr

Fossillagerstätten Symposium
Localities:

1 B&B Hotel Göttingen City
Machmühlenweg 19-21

2 Hotel Stadt Hannover
Goetheallee 21

3 Bahnhof

4 Akademie Haus Geiststr. 10
(Vorträge)

5 Aula, Universität, Wilhelmsplatz 1

6 Akademie Haus, Theaterstr. 7

Abstracts

The taphonomy of Konservat-Lagerstätten – now and next

Derek E.G. Briggs

Department of Earth and Planetary Sciences, and Yale Peabody Museum, Yale University,
New Haven, CT 06520-8109, USA; derek.briggs@yale.edu

Seilacher (1970) formulated the concept of Fossil-Lagerstätten more than 50 years ago. These fossil assemblages were initially considered curiosities confined to unusual environmental settings, but have long since been incorporated into mainstream paleontological research. Nonetheless there remains scope for a better understanding of the nature and biases in the assemblages they preserve. The occurrence of Konservat-Lagerstätten is favored at particular times in earth history and they are more common in certain environmental settings. The chemistry and microbiology of their enclosing sediments play a critical role in taphonomic processes, and the anatomy and tissue composition of the organisms they capture influences which survive decay and to what extent (Briggs 2003, Saleh et al. 2020). Environmental variables exercise a major control on the composition of communities through time, but taphonomic factors determine which taxa are incorporated into the fossil record.

Konservat-Lagerstätten are rarely unique. Exploration in the area of classic localities such as the Cambrian Burgess Shale of British Columbia and Ordovician Beecher's Trilobite Bed of upper New York State have demonstrated that similar settings in their vicinity host additional soft-bodied fossil occurrences (Caron et al. 2014, Farrell et al. 2009). A great deal of information about the early radiation of animals has been revealed by capitalizing on this approach particularly in the region of Walcott's Burgess Shale. Analyses of microstratigraphy and sedimentology, combined with geochemical analyses of fossils and lithological samples have revealed conditions during deposition (Gaines 2014). Analyses of the sedimentary matrix associated with a range of Cambrian arthropods, including trilobites, have allowed a comparison between those with and without preserved soft parts (Anderson et al. 2018). The results indicate that clays play a role in the preservation of organic cuticle and other anatomical features. Kaolinite appears particularly effective as indicated by its association with soft-bodied fossils or the presence of its diagenetic products berthierine and chamosite. Experiments involving the addition of various clays to bacterial cultures have confirmed that kaolinite and berthierine are effective in inhibiting the growth of decay bacteria (McMahon et al. 2016). The antibacterial properties of clays have also long been known in medicine.

The taphonomy of the Ediacara Biota, the familiar large organisms characteristic of multiple areas across the planet including Newfoundland, the White Sea, South Australia and Namibia, is very different to that of the Burgess Shale (e.g., Tarhan et al. 2016), not least because clays are not the primary host. The earlier pre-Ediacaran history of animals, however, is less known not least because of the challenge of discovering microscopic remains in older rocks in more remote part of the world. A major gap in rocks of Cryogenian age awaits further exploration and new discoveries. In the meantime, where depositional conditions similar to those in the Burgess Shale prevailed during the Tonian they have yielded a diversity of exceptionally preserved multicellular and filamentous organisms but animals are absent constraining their likely origin to no more than ~789 million years ago (Anderson et al. 2023). Further refinement of this age requires exploration of suitable sedimentary sequences of Cryogenian age.

Comparisons of the taxa represented in living and fossil assemblages on both a local and global scale indicate that only 40% of animals, i.e. those with biomineralized or organically strengthened tissues, are routinely preserved in the fossil record (Shaw et al. 2021). This percentage is lower where the concern is not simply whether the living animal is known as a fossil but whether it is represented in an ancient environment similar to the one it occupies today – only 15% of taxa in pelagic assemblages, for example, are represented anywhere in the fossil record and the percentage preserved in pelagic settings drops to zero. Completeness is obviously higher in Konservat Lagerstätten but there remains the challenge of determining what was truly absent from a fossil assemblage and what is simply not preserved.

Fossils are rarely if ever pristine representatives of the original organism – some decay is often intrinsic to the chemical conditions that favor preservation. Thus 'atlases' of decay (or at least illustrations of decay stages), generated by monitoring the process in the laboratory, provide helpful insights for the interpretation of soft-bodied fossils (Sansom et al. 2013). They also provide a guide to preservation thresholds (Briggs and Kear 1993) – if certain soft-bodied animals or specific tissues are preserved, for example, then the absence of others of similar structure or composition is likely to be real rather than taphonomic. Such considerations are important for moderating assessments of the composition of original communities based on fossil assemblages, but also for judging the utility of rare soft-bodied fossil occurrences for calibrating the molecular clock.

Arthropods have been the most diverse group of animals on Earth since the Cambrian and they provide a remarkable fossil record due to the biomineralized skeletons of trilobites and decapod crustaceans, for example, the durability of the chitin-protein exoskeleton even among arthropods (the majority) that lack biomineralization, and their growth by molting which ensures over-representation in the fossil record. Annelids, in contrast, are essentially soft-bodied and their presence in Konservat-Lagerstätten provides a threshold indicating which other soft-bodied organisms have the potential to be preserved. Their heavily sclerotized or even biomineralized jaw elements provide evidence of their presence even where the rest of their anatomy is lost through decay. Arthropods are, of course, ubiquitous in Konservat-Lagerstätten, annelids less so even taking their marine habitat into consideration. However, details of the taphonomy of these two groups, or at least their tissue type, provide a guide to likely preservation biases affecting fossil assemblages (Saleh et al. 2020).

Preservation of soft-bodied fossils, as illustrated by arthropods and annelids, involves two major types of process (Briggs 2003). The first is the precipitation of authigenic minerals, particularly apatite and pyrite, in association with decay-prone tissues such as digestive organs, muscle, and nerve tissue, for example, before they are lost through decay. Authigenic mineralization of such features often counters expectations based on decay experiments which predict that they are the least likely to survive (Parry et al. 2018). The second is the survival of features such as cuticle (arthropods) and non-biomineralized jaw elements (annelids) which are carbonaceous but relatively decay resistant. Their original chemical composition (dominated by chitin and proteins) is transformed through diagenesis over time into more stable organic compounds, a process that is accelerated by elevated temperature (Briggs 1999, Briggs and Summons 2014). The internal layering of cuticle is eventually destroyed over time by this chemical transformation but structural colors can even survive in younger fossil insects, for example, even though the color may have been modified by diagenetic changes (McNamara et al. 2012).

The processes involved in exceptional preservation are well illustrated by examples from the remarkable list of Konservat-Lagerstätten in Germany. The pyritized arthropods of the Devonian Hunsrück Slate (Bartels et al. 1998) preserve not only the sclerotized dorsal exoskeleton, but the morphology of the limbs. The cellular structure of muscle tissue does not survive but the exoskeleton of the limbs provided an envelope that was infilled with authigenic pyrite prior to collapse and flattening. Polychaete annelids preserve features of the jaws, parapodia and bristles (Briggs and Bartels 2010). The Hunsrück Slate quarries are no longer active and this source of new material has dried up. Mechanical preparation and x-radiography have revealed remarkable features of the animals. However, application of 3-dimensional scanning of known specimens (Clark et al. 2020) and unprepared material in various institutions has the potential to reveal much new information and even usher in a new phase of investigation (Gueriau et al. 2023).

Whereas the Hunsrück Slate fossils are dominantly pyritized those of the Jurassic Solnhofen Limestone and similar plattenkalk settings such as Nusplingen include more carbonaceous remains. Commercial exploitation has all but ceased in the famous quarries but there is an abundance of specimens in institutions around the world that will repay future study. A combination of microbial mats and high concentrations of phosphate have resulted in the capture of anatomical details of muscle tissue, for example, in polychaetes and horseshoe crabs in authigenic apatite (Briggs et al. 2005). Analysis of ink sacs from cephalopods from Holzmaden demonstrated the remarkable durability of the molecular composition of melanin (Glass et al. 2012).

Younger Konservat Lagerstätten including lake deposit such as Messel (Eocene), Enspel (Oligocene) and Willershausen (Pliocene) preserve a diversity of fossils providing a source of terrestrial animals and vegetation to illuminate aspects of climate change, for example. Such Tertiary deposits also offer opportunities to relate organic composition to taxonomic identity and environment, and to investigate the early stages of organic diagenesis through time (Briggs et al. 1998). The lava flows at Enspel even provide a natural maturation experiment (Illing et al. 2019).

Seilacher et al. (1985, p.5) noted that "there is a finite number of situations that lead to the formation of fossil Lagerstätten and that prospecting for them is therefore a realistic objective". Nonetheless, with few exceptions, prospecting is a somewhat haphazard affair which has often relied on serendipitous discoveries, sometimes by gifted and enthusiastic collectors. New discoveries are important, however, for improving our knowledge of the history of life on the planet and for calibrating phylogenies. The development and application of criteria for targeting Konservat-Lagerstätten is an important challenge particularly in the quest to understand the evolution of life prior to the appearance of the Ediacara Biota.

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Glimpses in the deep shadow of time: Precambrian fossil lagerstätten and their significance for understanding early eukaryote evolution

Jan-Peter Duda

Department of Geobiology, University of Göttingen, Göttingen, Germany
jan-peter.duda@geo.uni-goettingen.de

In the long and eventful history of life on our planet, the emergence of eukaryotes was one of the most striking evolutionary developments. During the Precambrian, unicellular eukaryotic clades established, sexual reproduction developed, and complex macroscopic life diversified, ultimately culminating in the emergence of animals (e.g., Butterfield 2015; Knoll 2014; Porter 2011). Although the Proterozoic rise of eukaryotes has been intensely studied, the timing of significant evolutionary key-developments and, perhaps more importantly, their relationship to environmental change are still poorly understood. Fossil lagerstätten (Seilacher 1970) provide valuable insights into ancient ecosystems and hence can help to shed light on the interconnections between biological and environmental evolution on the early Earth. In this presentation, I attempt to illustrate the complex relationships between early eukaryote evolution and environmental dynamics through the lens of selected Precambrian fossil lagerstätten. One example is the uppermost Mesoproterozoic Lakhanda Lagerstätte (ca. 1.00–1.03 Ga, Siberia, Russia), which contains a wealth of exquisitely preserved eukaryotic fossils as well as sedimentary hydrocarbons diagnostic for specific source organisms (i.e., molecular fossils) (e.g., Hermann 1990; Duda et al. 2021; Shuvalova et al. 2021). Another example is the terminal Ediacaran Khatyspyt Lagerstätte (ca. 550–544 Ma, Arctic Siberia, Russia), which preserves diverse assemblages of Ediacara-type fossils (e.g., rangeomorphs and arboreomorphs), carbonaceous compression fossils ("mega-algae"), trace fossils (including ichnofabrics produced by vertical burrowers), and molecular fossils (Grazhdankin et al., 2008; Rogov et al., 2012; Duda et al. 2016, 2020). I will demonstrate that such glimpses – although covered by the deep shadow of time – provide valuable insights into early eukaryote evolution and, consequently, the dawn of our modern world.

Acknowledgements

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Echinoderm Fossillagerstätten in the Triassic Muschelkalk Adolf Seilacher's early observations and current overview

Hans Hagdorn[1], Mike Reich[2]

[1] Muschelkalkmuseum Ingelfingen, Schloss-Str. 11, 74653 Ingelfingen
e-mail: encrinus@hagdorn-ingelfingen.de

[2] Staatliches Naturhistorisches Museum Braunschweig, Gaußstr. 22, 38106 Braunschweig, e-mail: m.reich@3landesmuseen.de

Introduction

Adolf Seilacher (1925–2014) coined the term Fossillagerstätten and framed its meaning and diversification as Projektbereich I *Fossillagerstätten* of the Tübingen SFB 53 *Palökologie* (Seilacher & Seilacher 1976, Seilacher et al. 1985). Since that time the term is internationally used in palaeontology. However, Seilacher already encountered basic types of fossil preservation as a schoolboy aged 15 in the Triassic Muschelkalk and Keuper of his home area in northern Württemberg (SW-Germany). In the Muschelkalk he found bedding planes with articulated brittle stars and sea lilies, as well as meter-thick crinoidal limestone beds with their accumulated fragments. He also collected amassed isolated bones and fish scales in the famous bonebeds, and he was aware that the Muschelkalk contained no black shales with complete vertebrate skeletons, which he knew from the Jurassic Posidonia Shale. His observations are documented in his diary kept during the year 1940, which is being edited and will be published at the occasion of the 100th anniversary of his birthday.

Hence, one can rightly state that Muschelkalk bonebeds and echinoderm deposits were crucial for the distinction of the conservation lagerstätten type from the concentration type of multielement fossils such as echinoderms or vertebrates (Seilacher 1970, 1993). A newly discovered deposit of articulated echinoderms on top of the erosive basal bed of the Jurassic near Schwäbisch Gmünd was described as prototype of an obrution echinoderm fossil lagerstätte by Rosenkranz (1971) in his doctoral thesis supervised by Seilacher. Other echinoderm lagerstätten throughout the Phanerozoic revealed identical features, namely (1) articulated echinoderm skeletons embedded in fine argillaceous sediment (2) covering a shell bed with autochthonous epibenthic fauna (3) deposited in a shallow water palaeoenvironment. The deposition of the muddy sediment cover is thought to be triggered by extraordinary events such as ground-touching storms indicating a fundamental change of environmental conditions lethal for benthic organisms.

The tripartite Muschelkalk Group was deposited in the Central European Basin under subtropical climate between ca. 25–35° N during Anisian and early Ladinian times. Water exchange with the open Palaeotethys shelf occurred through changing marine straits or gates from the Southeast during Lower Muschelkalk and from Southwest during Upper Muschelkalk times. The sedimentary record of abundant tempestitic shell beds in a cyclic context indicates shallow marine depositional environments and a subtropical climate with occasional storms (Aigner 1985). Hence, mud suspension and redeposition following ground-touching storms were prerequisite for the emergence of obrution lagerstätten. Echinoderms and other stenohaline benthic fauna lived exclusively in the Lower and Upper Muschelkalk seas. Restricted water exchange during the Middle Muschelkalk with cyclical dolomite, anhydrite and rock salt deposition left the central parts of the basin widely barren and uninhabitable for stenohaline organisms such as echinoderms. For more detailed descriptions and analyses see the respective chapters in DSK (2020) and Hauschke et al. (2021).

Muschelkalk echinoderm lagerstätten

Many Muschelkalk echinoderm lagerstätten have been described in detail. The following overview is intended to subdivide lagerstätten types according to faunal composition considering biological reactions and taphonomic, sedimentological and diagenetic features, with respect of stratigraphical and palaeogeographical occurrences. Depending on the faunal composition, low and high diversity echinoderm lagerstätten can be differentiated.

Low diversity conservation lagerstätten

Ophiuroidea – Steinbach Type

Mass occurrence of monospecific brittle stars on top of thin tempestite beds with pavements of convex-up shells in the Tonplatten and Wellenkalk facies. Uniform size, commonly of juvenile or semiadult individuals indicates breeding seasonality (Fig. 1a). *Aspiduriella* is the most abundant genus, less common are *Aplocoma* (Fig. 1b), *Arenorbis* and others. Individuals preserved under bivalve shells or in empty ceratite body chambers indicate negative phototropic hiding behaviour. Such individuals were trapped and unable to escape even when smothered by relatively coarse sediment. Lower Muschelkalk: Gogolin, Jena, Rüdersdorf formations, Upper Muschelkalk: Trochitenkalk and Meißner formations (up to *nodosus* biozone); Germany, France, Poland. Selected references: Kutscher (1940), Hagdorn (1985, 1999, 2021), Salamon et al. (2012), Seilacher (1988).

Asteroidea

(1) Single *Trichasteropsis weissmanni* or groups of individuals under thin mud cover on top of thick skeletal shell beds, usually dorsal side up and dorsoventrally compressed (Fig. 2a), occasionally topping late diagenetic stylolites (similar to Steinbach Type, but shellbeds thicker). (2) Individuals in thick marl beds uncompressed within early diagenetic concretions, commonly with arm tips bent upwards and

preserved outside of nodule (Bindlach Type) (Fig. 2b, c). Evidence of autotomy by isolated arm tips (Fig. 2d). Occasionally associated with *Aspiduriella*. Most common in Trochitenkalk and Meißner formations (*nodosus* biozone); Germany. Selected references: Blake & Hagdorn 2003, Hagdorn (1985, 2021), Hildner (2010).

Holothuroidea

Only one Muschelkalk obrution lagerstätte known (Steinbach Type), possibly due to the difficult to find tiny ossicles. More than a hundred individuals of a still undescribed member of the Holothuriidae with articulated calcareous pharyngal and anal rings and with dermal body wall ossicles (Fig. 3). Together with a brittle star arm and an isopod. Meißner Formation (*spinosus* biozone); SW-Germany. Isolated sclerites to be identified only in micropalaeontological samples. Selected references: Reich (2004), Reich et al. (2023).

Crinoidea

Most crinoid lagerstätten contain additional echinoderm clades. Among the monospecific lagerstätten, such of permanently holdfast-attached Encrinida differ from those of cirrus-attached Holocrinida.

Gogolin Type

Juvenile and adult individuals of the small softground and hardground dwelling Dadocrinidae (*Dadocrinus, Aszulcicrinus*) in the Gogolin Formation (Poland) and Formazione à gracilis (Recoaro, Vicentinian Alps), embedded in clusters generally in shaving brush position, sometimes in bunches of a number of equal-sized individuals with their holdfasts (Fig. 4a). Dadocrinid lagerstätten rarely contain brittle stars (*Aspiduriella* in Poland, *Arenorbis* in Recoaro). The Freyburg ‚Blumennester' (flower nests) of the large dadocrinid *Carnallicrinus* (Jena Formation) conform with the same patterns. Crinoids therein in shaving brush and rarely in starburst down positions. Selected references: Baumiller et al. (2008), Hagdorn (1996, 2019, 2021), Jaekel (1894).

Neckarwestheim Type

The largely monospecific *Encrinus liliiformis* lagerstätten best known from Neckarwestheim, Alverdissen, Lamerden and Driburg (Trochitenkalk Formation) contain mostly detached individuals preserved devoid of their holdfasts. Individuals commonly with regenerating terminal columnals. Autotomized distal arms may be indicative of ecological stress by smothering or predator attack. The Neckarwestheim Type is characterized by a decimeter-thick crinoidal limestone within a sequence of thin micrite beds intercalating with marls. The crinoidal limestone was deposited during a low sedimentation or even omission period that was terminated by a ground touching storm that extinguished the fixisessile epibenthic palaeocommunity. Subsequently no re-colonisation by crinoids but return of endobenthic mud ground palaeocommunities. Trochitenkalk, Meißner formations. Germany, France, Poland. Selected references: Hesse (1991), Linck (1965), Weissmüller (1998).

Udelfangen Type

Holocrinus lagerstätten have not yet been investigated in detail. Fully or partly articulated individuals indicating lateral transport accumulated at the base of marine sandstone sheets or lenses in the Lower Muschelkalk marginal facies (Ralingen Formation). Rupture of distal stem parts below the nodals and autotomy of complete arm crowns are typical patterns of proceeding decay (Fig. 4b). Crowns in shaving brush and in starburst up preservation. Another Holocrinus lagerstätte preserving countless individuals on top of the hardground surface of a big block entangled with one another correlates to the Herberhausen Type (Jena Formation). Germany, Luxembourg. Reference: Baumiller et al. (2008), Hagdorn & Baumiller (1998).

High diversity conservation lagerstätten

Herberhausen Type

Articulated crinoid, echinoid, ophiuroid and asteroid lagerstätten on top of tempestitic coquinas with isolated echinoderm ossicles and patchy hardgrounds (Fig. 5a) that may be fragmented and reworked (Jena Formation). Bored hardground may be incrusted by encrinid holdfasts. Crinoid percentages are generally higher than those of other echinoderms. Storm induced permanent extinction of the epibenthic palaeocommunity and post-event recurrence of largely barren Wellenkalk deposition. Göttingen-Herberhausen, Elvese, Großenlüder-Bimbach. Germany. Bielert & Bielert (2004), Ernst & Löffler (1993), Hagdorn & Schulz (1996).

Crailsheim Type

Lensoid bioherms of a few square meters and up to 1.5 m thickness with a frame of Muschelkalk oysters encrusted by crinoid root callus (Trochitenkalk Formation, Crailsheim Member) (Fig. 5c). Other than in the above described lagerstätten, crinoids and other echinoderms persisted through long time periods. Subsequently to lethal storm events, the seafloor was repopulated by identical epibenthic palaeocommunities from nearby unaffected areas. In the basinward facies of the Hassmersheim Member, bioherms reaching several meters thickness persisted through the depositional cycles of Trochitenbank 3 to 4. A thick marl layer smothered the lower parts of the bioherms and embedded its fauna (Fig. 5d). The top part remained unaffected. The large *Encrinus liliiformis* contributed estimated more than 95 % of the echinoderm biomass. Articulated crinoids from juvenile to adult stage are common fossils, whereas articulated echinoids and asteroids are much less abundant and ophiuroids were preserved only under sheltering bivalve shells. Articulated echinoderms are preferentially preserved next to the bioherm (Fig. 5b). Juveniles are even found in original attachment to the bioherm frame. Regenerating arms are indicative of ecological stress or predator attacks. Crowns are usually closed and upside arms are spread under sediment upload, more rarely in starburst down position. Echinoderms in their specific progressive disarticulation stages on top of bedding planes a few meters distant from neighbouring bioherms. Selected references: Hagdorn (1978), Hagdorn & Ockert (1993).

Echinoderm concentration lagerstätten

Erkerode Type

Up to 1.5 m thick crinoidal limestones (encrinites) of unsorted crinoidal and other echinoderm skeletal elements, brachiopod and bivalve shells (packstones, grainstones). Predominantly complete disarticulation, with single pluricolumnals and rare articulated crowns with column parts attached. Due to early lithification of the sediment, crowns were not compressed. This is the prevalent preservation in the Erkerode member at the classic sites near Erkerode, Schöningen and Uehrde; Lower Saxony. This preservation also occurs in comparable encrinites within the Crailsheim member (Fig. 6a). Deposition in shallow water of palaeogeographic shoals. Selected references: Hagdorn (1978), Hagdorn & Ockert (1993).

Karchowice Type

Thick skeletal grainstones with patchy sponge and coral bioherms, dominated by diverse echinoderm ossicles (predominantly Encrinidae, more rarely Holocrinidae, Eckicrinidae, Silesiacrinidae), and in some layers by Echinoidea (predominantly Triadocidaridae). Echinoderms in their specific progressive disarticulation stages (Fig. 6b). Rarely articulated Encrinidae. Deposition under shallow water close to the SE gate connecting the Muschelkalk sea with the open Palaeotethys shelf. Lower Muschelkalk Karchowice Formation; Poland. Due to deep weathering, loose rock samples allow picking echinoderm ossicles. Selected references: Assmann (1937), Hagdorn et al. (2021).

Marbach Type

Thick oolithic encrinite beds or single sheets within Erkerode Type encrinites with prefossilised ossicles abraded by continuous rolling transport (Fig. 6c, d). Commonly size-sorted. Deposition in extremely shallow, agitated water above shoals, e.g. Marbach oolite member at southeastern margin of Black Forest; SW-Germany. Selected references: Linck (1965), Seilacher (1993).

Ophiurites

Ophiurites originate from reworked lagerstätten of Steinbach type. Ophiuroid ossicles disarticulated and concentrated (1) in thin sheets on top of coquinas Fig. 6e), (2) as thin tempestite beds (Fig. 6f, h), (3) as fill material of gutters, (4) as fill material in cephalopod body chambers (Fig. 6g). Rarely single articulated arms or discs, complete individuals protected under convex-up bivalve shells (Fig. 6f). Common in Tonplatten facies of Meißner Formation; Germany. References: Kutscher (1940), Aigner & Futterer (1978), Seilacher (1988).

The unique role of the Muschelkalk echinoderm lagerstätten

Strangely, in spite the semi-enclosed palaeogeographic situation of the Muschelkalk sea and its temporarily divergent salinity with peaks towards hypersalinar and hyposalinar conditions, the Muschelkalk is crucial for the post-Palaeozoic record of the surviving echinoderm classes (Hagdorn 2000). The current knowledge of Middle Triassic echinoderms has almost entirely been gathered from the Central European Muschelkalk and from similar facies elsewhere, e.g. in the Vicentinian Prealps and Spain. Middle Triassic echinoderms from Palaeotethys and Neotethys open shelf areas were certainly more diverse, however, their fossil record is mostly based on isolated skeletal elements that provide only limited data. Exceptions are the Anisian *Dadocrinus* beds of the Vicentinian Prealps around Recoaro, Italy (Hagdorn 1996) and a still unknown fossil site in the Lombardian Alps that yielded articulated individuals of *Encrinus aculeatus* (Hagdorn et al. 2018). Each of these lagerstätten belongs to the Muschelkalk obrution type and yielded only taxa that also occur in the Germanic Muschelkalk. The Collbató lagerstätte of the Catalonian Muschelkalk (Spain) containing holothurian, echinoid, ophiuroid and crinoid skeletons (Gallemí 1990) is of special interest because of its Ladinian age and its palaeogeographic position open to the Neotethys shelf (Smith & Gallemí 1991). Another lagerstätte (plattenkalk) in Catalonia (Montral-Alcover; see Hemleben & Freels 1977; Víá Boada et al. 1977) yielded a few articulated Holothuroidea (Cherbonnier 1978). After more than 200 years of Muschelkalk research and collecting, spectacular new finds in conservation lagerstätten caused modifications of the post-Palaeozoic history of phylum Echinodermata. This has been demonstrated by Palaeozoic-type hangovers such as the Upper Muschelkalk proterocidarid echinoid *Lazarechinus* (Thuy et al. 2017, Hagdorn 2018), or by disarticulated material of Palaeozoic-type echinoderms (e.g. Ophiocistioidea) in Triassic liberation fossil lagerstätten (Reich et al. 2018).

Unfortunately, Lower and Upper Triassic benthic echinoderm lagerstätten comparable to the Muschelkalk have not yet been described. The upper Ladinian/lower Carnian *Traumatocrinus* beds of South China and Afghanistan are stagnation lagerstätten correlating to the Lower Jurassic Posidonia Shale preserving pseudoplanktonic and planktonic crinoids (Wang et al. 2008). The highly diverse upper Ladinian and lower Carnian echinoderm faunas of the Dolomites (Italy) were transported with turbiditic currents from reef platforms into deep basins and yielded predominantly disarticulated material leaving a puzzle that has not yet been completely resolved (Hagdorn 2011).

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Figures

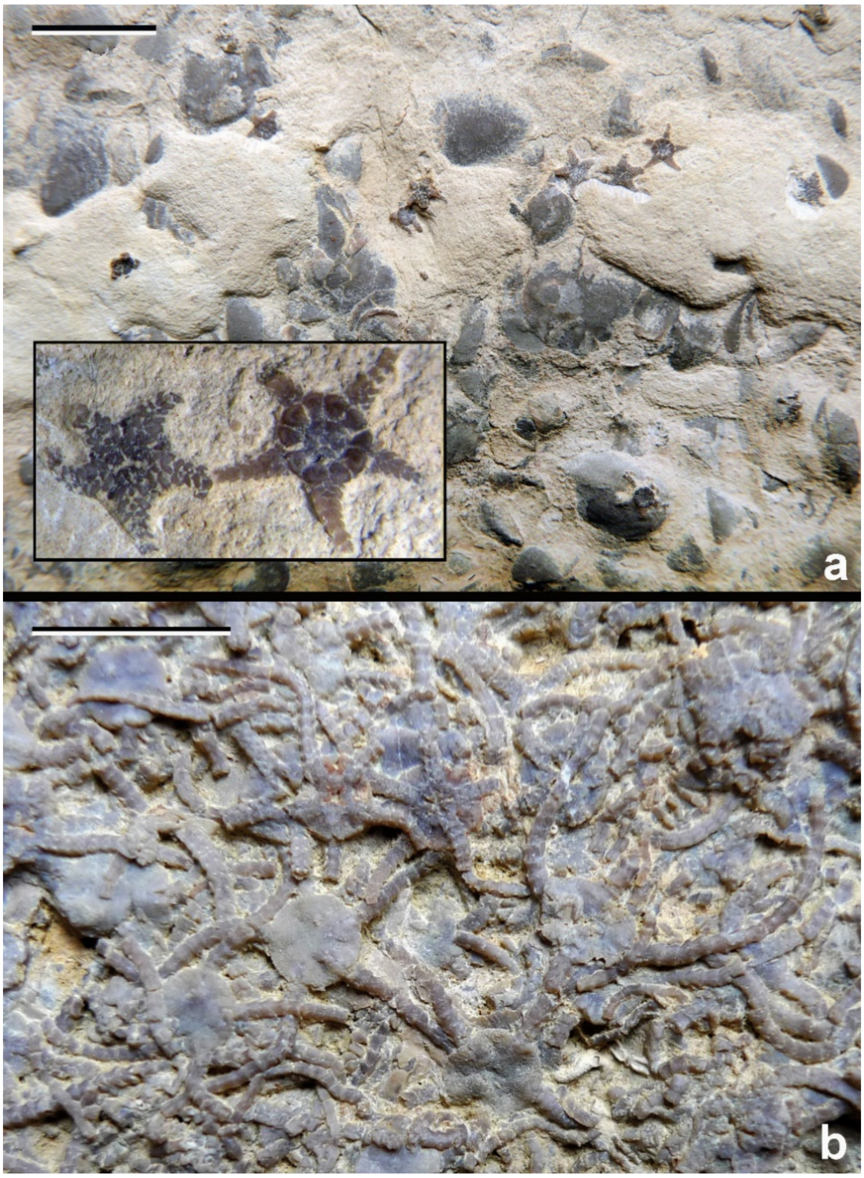

Fig. 1: Ophiuroid conservation lagerstätten (Steinbach Type). **a** Shell pavement (*Entolium discites*) with juvenile *Aspiduriella scutellata* of one breeding season smothered in mud cover. Meißner Formation (spinosus biozone), Schwäbisch Hall-Steinbach (Baden-Württemberg, Germany). MHI 518/1. **b** *Aplocoma agassizi* on top of thin tempestitic shell bed (endobenthic bivalves). Calcaire à Cératites (evolutus biozone), Eyviller (France). MHI 1206/1. Scale bars 10 mm.

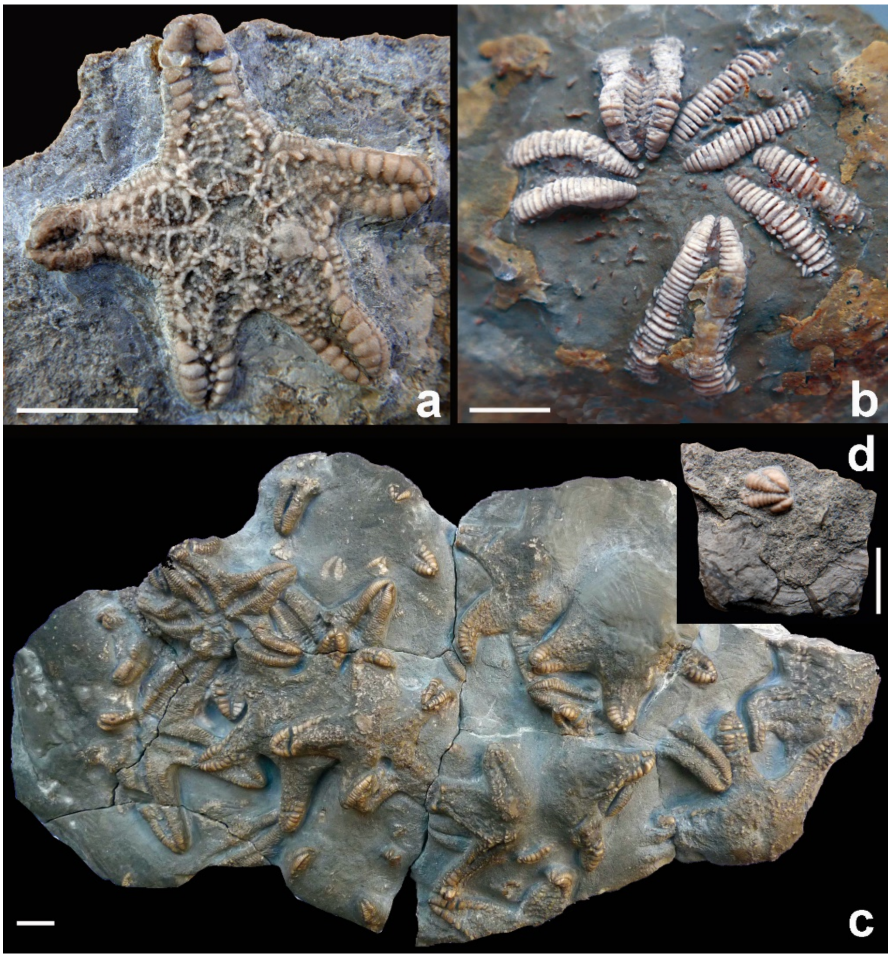

Fig. 2: Asteroid (*Trichasteropsis weissmanni*) conservation lagerstätten. **a** dorsoventrally compressed, on top of thick skeletal shell bed. Meißner Formation (nodosus biozone), Bölgental (Baden-Württemberg, Germany). MHI 843/1. **b** in concretion (Bindlach Type), dorsally arms recurved, outside nodule (nodosus biozone), Bayreuth-Bindlach (Upper Franconia, Bavaria, Germany). MHI 1857/22. **c** individuals transported and deposited both ventral and dorsal sides up, arms of some individuals recurved. nodosus biozone, Rothenburg-Gattenhofen (Middle Franconia, Bavaria, Germany). MHI 2062/1. **d** autotomized arm tip. Trochitenkalk Formation (pulcher biozone), Crailsheim-Wollmershausen (Baden-Württemberg, Germany). MHI 770/2. Scale bars 10 mm.

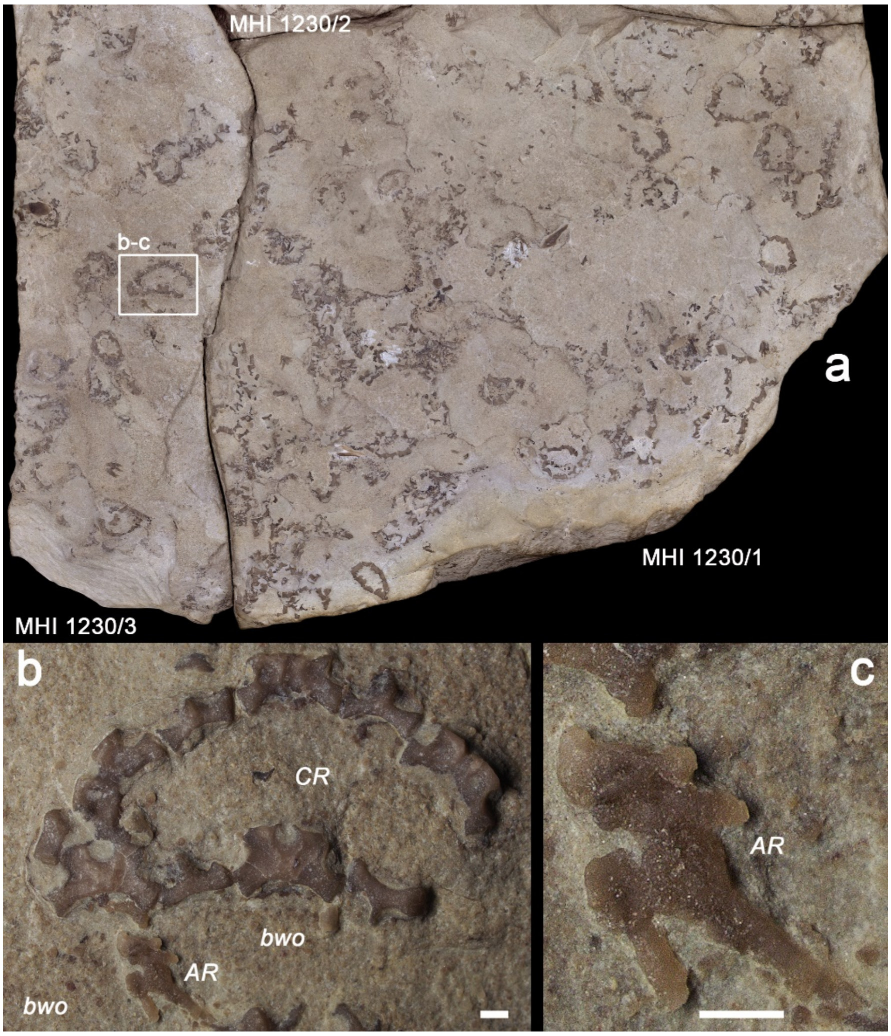

Fig. 3. Holothuroid conservation lagerstätte (Steinbach Type). **a** More than 100 specimens of undescribed holothurians are on the slab (MHI 1230), which was broken into three pieces. **b-c** Holothuriid sea cucumber (Actinopoda: Holothuriida) with articulated calcareous (*CR*) and anal (*AR*) ring as well as corresponding microscopic body wall ossicles (*bwo*). Lower Muschelkalk, Meißner Formation (spinosus biozone), Künzelsau-Nitzenhausen (Württemberg, Germany). MHI 1230/3 (specimen 40). Scale bars 1 mm.

Fig. 4: Crinoid conservation lagerstätten. **a** *Dadocrinus kunischi*, lensoid cluster bed (Gogolin Type). Lower Muschelkalk, Gogolin Formation, Gogolin (Poland). MHI 1284/1. **b** *Holocrinus* cf. *dubius* in different decay stages at base of tempestite bed (Udelfangen Type). Column fragments and autotomized crowns, transported. Lower Muschelkalk, Udelfangen Formation, Ralingen-Kersch (Rhineland-Palatinate, Germany). MHI 1276/12. Scale bars 10 mm.

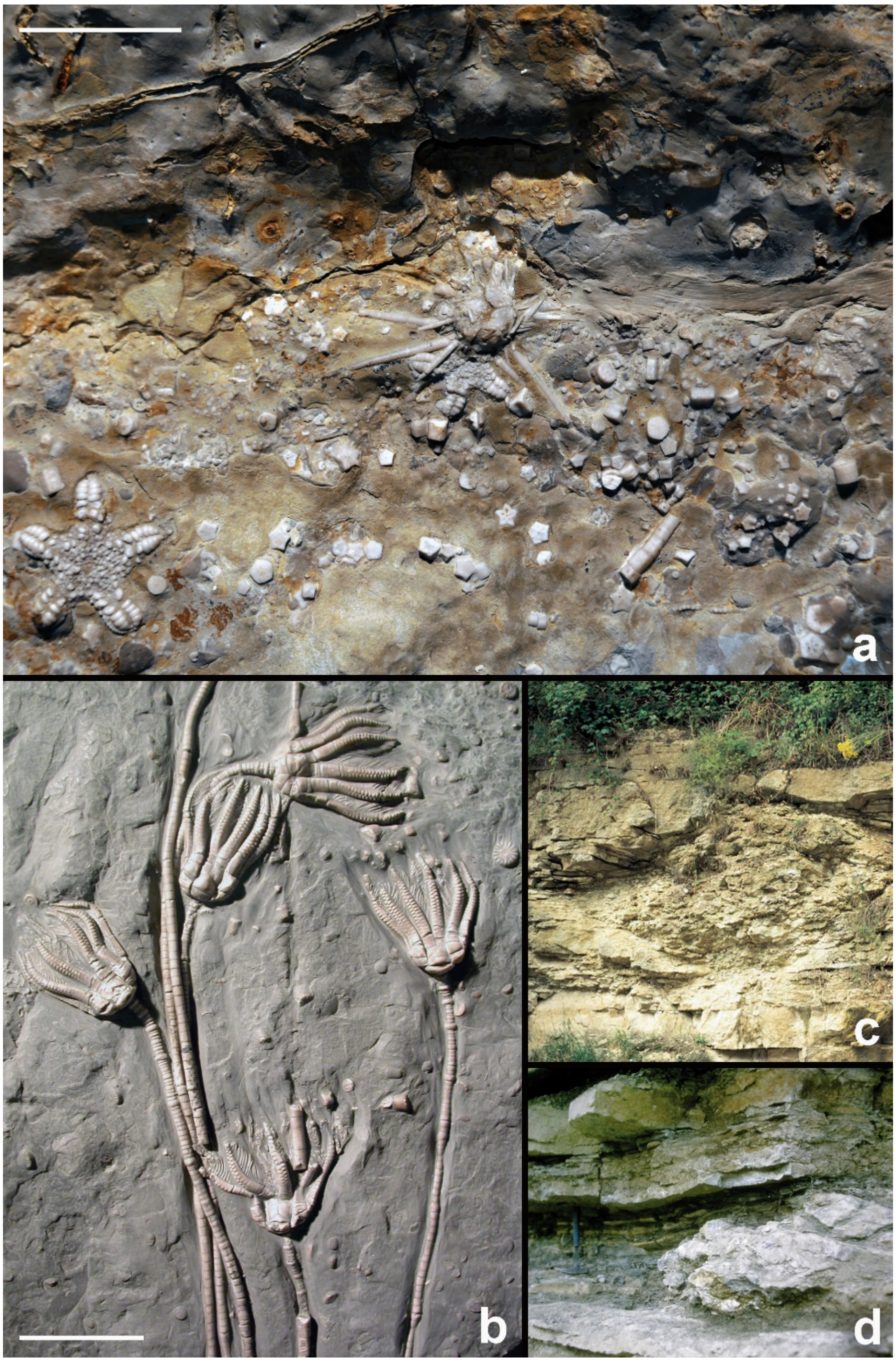

Fig. 5 (legend see p. 27)

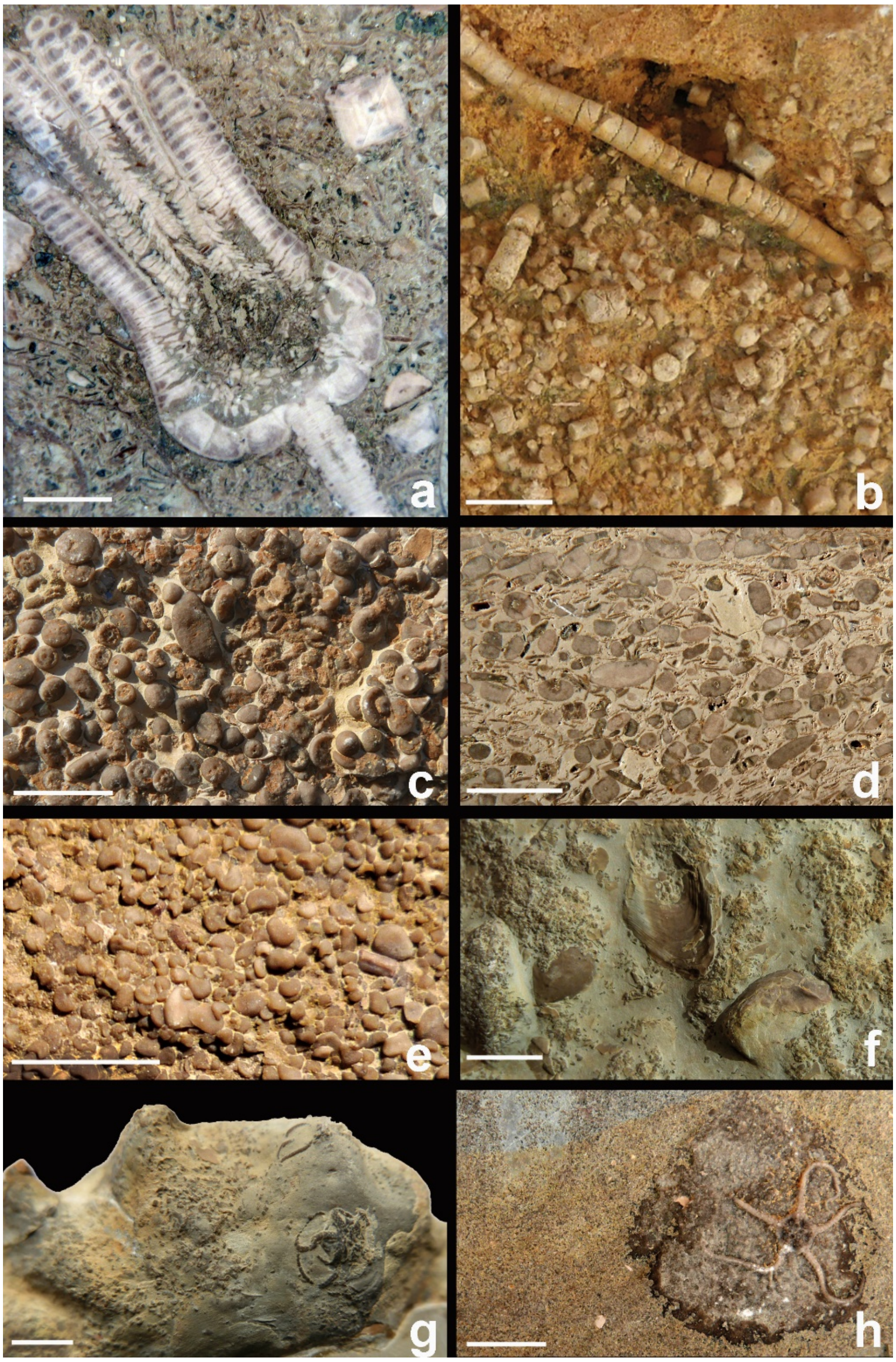

Fig. 6 (legend see p. 27)

Legends to figures 5 and 6

Fig. 5: Crinoid conservation lagerstätten. **a** *Trichasteropsis bielertorum, Migmaster angularis, Serpianotiaris coaeva, Holocrinus dubius* (disarticulated), on top of tempestitic shell bed and patchy hardground with*Trypanites* borings, (Herberhausen Type). Lower Muschelkalk (Jena-Formation), Göttingen-Herberhausen (Lower Saxony, Germany). MHI 1752–1754. **b** *Encrinus liliiformis*, bunch of equally sized individuals, columns pointing at bioherm. Trochitenkalk Formation (Crailsheim Member), Satteldorf-Neidenfels (Baden-Württemberg, Germany). MHI Ku-2006/1. **c** Crinoid bioherm, lateral transition into tempestitic crinoidal limestone intercalated with thin marl layers. Crailsheim Member, Wollmershausen (Baden-Württemberg, Germany). **d** Crinoid bioherm, lateral transition into thick marls with thin tempestitic crinoidal limestones intercalated. Hassmersheim Member, Schwäbisch Hall-Steinbach (Baden-Württemberg, Germany). Scale bars 10 cm.

Fig. 6: Echinoderm concentration lagerstätten. **a** poorly sorted crinoidal limestone (packstone) with articulated *Encrinus liliiformis*, due to early lithification crown uncompressed (Erkerode Type). Polished surface. Trochitenkalk Formation (Crailsheim Member), Satteldorf-Neidenfels (Baden-Württemberg, Germany). MHI 2208. **b** poorly sorted crinoidal limestone with hexactinellid sponge fragments, surface strongly weathered below Tertiary land surface (Karchowice Type). Strzelce Opolskie (Poland). MHI 2209. **c**, **d** prefossilized and abraded encrinid ossicles (Marbach Type). Bedding plane (c) and polished section (d). Crailsheim Member, Satteldorf-Neidenfels (Baden-Württemberg, Germany). MHI 2210. **e** Ophiurite of size-sorted *Aspiduriella* ossicles (mostly laterals and radials). Upper Muschelkalk (nodosus biozone), Satteldorf-Neidenfels (Baden-Württemberg, Germany). MHI 1225. **f** Ophiurite of *Aplocoma* and *Aspiduriella* ossicles, base of thin tempestite with convex-up bivalves (*Hoernesia*, *Entolium*). spinosus biozone, Künzelsau-Nitzenhausen (Baden-Württemberg, Germany). MHI 2211. **g** Ceratite body chamber with *Aplocoma* ossicles and articulated individual in curl position. spinosus biozone, Künzelsau-Garnberg (Baden-Württemberg, Germany). MHI 2212. **h** Ophiurite of size-sorted *Aplocoma* ossicles with articulated individual protected under bivalve shelter. evolutus biozone, Künzelsau-Nitzenhausen (Baden-Württemberg, Germany). MHI 2013. Scale bars 10 mm.

The Cretaceous Platy Limestones of Mexico

PD Dr. Christina Ifrim

Wiss. Museumsleitung Jura-Museum – SNSB Willibaldsburg, Burgstr. 19, 85072 Eichstätt, Germany; Christina.Ifrim@jura-museum.de

Introduction

Platy Limestones are famous for their excellently preserved fossils. They provide windows into the past because many details are preserved of ancient ecosystems.

The Platy Limestones of Mexico have been explored scientifically for ca. 50 years, now, with increasing number of studies dedicated to them. They are present over a large area in the northeast of the country, and were formed repeatedly on the shelf of the Ancient Gulf of Mexico. This paper intends to provide an overview over the localities currently known.

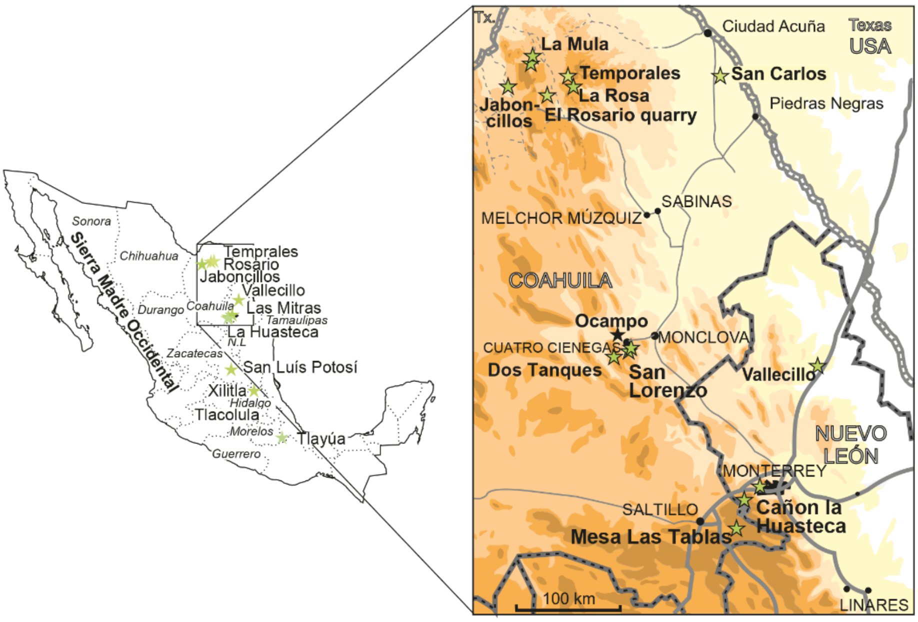

Fig. 1: Map of Mexico with the platy limestone localities in Mexico.

During the Cretaceous, there was an active volcanic arc in the west, preserved in today Sierra Madre Occidental (Fig. 1). To the east, a wide shelf opened towards the Cretaceous Ancient Gulf of Mexico. Enormous carbonate platforms developed there during the Cretaceous, including the Cupido Platform in the North of Mexico, the Valle San Luis Potosí Platform in east-central Mexico, and the Guerrero-Morelos Platform in Southwest Mexico.

A change in subduction style led to an increased coupling of the lower and upper slab, resulting in regional uplift, increased erosion and a progradation of the coastline towards the East, a process which continues until today (Salvador, 1991). The age of marine clastic sediments and the amount of marine carbonates decreases thus roughly through space and time, i.e. eastwards and through the Cretaceous in today surface and outcrops.

The platy limestone localities of the Cretaceous of Mexico

Albian, Tepexi de Rodríguez, Puebla

The first platy limestone discovered in Mexico was that of Tlayúa, also known as Tepexí de Rodriguez (Cantú-Chapa, 1987; Pantoja-Alor, 1990; Seibertz and Buitrón, 1987), situated in the state of Puebla.

This platy limestone is red and about 34 m thick, being distinguished as Middle Member of the Tlayúa Formation. It is exposed along the ravine Tlayúa and other small outcrops near Tepexi de Rodríguez (Applegate, 1992, 1996; Cantú-Chapa, 1987; Pantoja-Alor, 1990; Seibertz and Buitrón, 1987).

It has been studied extensively for its fishes (Alvarado-Ortega et al., 2007; Applegate, 1992, 1996) and arthropods (Feldmann et al., 1998; Vega et al., 2003), but ammonites (Cantú-Chapa, 1987), belemnites (Seibertz and Buitrón, 1987; Seibertz and Spaeth, 2005) are also known.

The paleoenvironment is under debate. Early studies suggested formation in a marine lagoon (Pantoja-Alor, 1990), but Kashiyama et al. (2004) suggested formation of this platy limestone in a deeper, open marine basin with scarce influence of continental to transitional paleoenvironment.

A recent study dates it to the early Albian radiometrically (Riquelme et al., 2021). This is in temporal correlation with OAE 1b (Ifrim, accepted-a) and might indicate that its formation could be related to this oceanographic event, but further study is needed. The formation of other platy limestone and the associated fossil Lagerstätten can be related to OAEs (Ifrim, 2006, accepted-a).

Since the discovery of this first locality, increasing interest has been generated to explore the fossil Lagerstätten associated with platy limestones in Mexico and their paleoenvironmental signals.

Muhi quarry

The Muhi quarry is located in the state of Hidalgo (fig. 1). A composite section of 7.2 m gray to light gray, thin bedded biomicritic and micritic limestone with frequent interbedding of chert related to platy limestone formation still needs to be discussed in detail. It is questionable whether this is a platy limestone but it is included here tentatively due to the presence of well-preserved fossils on the slabs quarried there. Scarce stylolitic suture planes are observed. Macrofossils have been recovered from five limestone strata, whereas microfossils are present in all levels.

The age of the Muhi quarry strata hinges on its stratigraphic relationship with the other Mesozoic rock units that outcrop in the Zimapán area, and the biogeochronologic dating afforded by the marine fish fauna that it bears. Based on stratigraphic relationships of the Muhi quarry, this sequence is post-Las Trancas Formation (late Jurassic – early Cretaceous) and pre-Soyatal-Méndez Formation (late Cretaceous); thus the Muhi quarry sequence probably originated during Mid-Cretaceous (late early Cretaceous to early late Cretaceous) (Bravo-Cuevas et al., 2009).

A recent study of ammonoids suggests it to be late Albian in age (López-Palomino et al., 2021). It is a fossil deposit with great richness in fishes {Baños-Rodríguez, 2020 #2339;e.g. \González-Rodríguez, 2009 #2517} and arthopods (Vega et al., 2022). Miliolids, planktic foraminifera, radiolarians, ammonites (López-Palomino et al., 2021), comatulid and echinoid echinoderms, chondrichthyes, osteichthyes (15 families) and reptiles were collected from a light gray micritic limestone unit with intercalated black chert lenses (Baños-Rodríguez et al., 2020; González-Rodríguez and Fielitz, 2009). The interpretation of the paleoenvironment is that of an open marine basin with hypersaline and/or poorly oxygenated bottom (Bravo-Cuevas et al., 2009).

Mid-Cenomanian Oceanic Anoxic Event (OAE)

A short mid-Cenomanian OAE was recognized from the Tethys (Coccioni and Galeotti, 2003), western Interior and North (Scaife et al., 2017) and tropical Atlantic (Friedrich, 2009) and the epicontinental European Cretaceous (Andrieu et al., 2015). In the Cañon la Huasteca (fig. 1) it is recognized as grey-pinkish platy limestone unit similar to the Turonian Vallecillo Member (Straub, 2012), but at lower stratigraphic level (Beckmann, 2012). Nannofacies analysis has shown that framboid pyrite size decreases to ca. 2 µm within this unit indicating deposition under oxygen-deficient conditions, similar to the early Turonian Vallecillo Member (Margulies, 2013).

This short, local event of platy limestone formation ceased but was repeated in the latest Cenomanian and continued during the early and into the middle Turonian in the aftermath of Oceanic Anoxic Event 2 (Ifrim, 2006, 2015; Ifrim et al., 2011a; Ifrim and Stinnesbeck, 2007, 2008).

OAE 2

OAE 2 is not described explicitely from Mexico until Ifrim (2006, 2015); Ifrim et al. (2011a). This may be because few outcrops exist where obvious black shales related to OAE2 crop out. It is now known that many platy limestones may be related with this event

Vallecillo, Nuevo León

The Vallecillo Member of the Agua-Nueva Formation is the best-known platy limestone and a very well studied fossil deposit in the Upper Cretaceous of Mexico. The lithostratigraphic assignation is used in the sense of Ifrim (2006). It is named after the small village Vallecillo ca 100 km north of Monterrey in the State of Nuevo León. Ca. 8 m of platy limestone are mined as flagstone in a series of quarries near the village. The platy limestone frequently yields fossils which allowed for quantitative analysis of the fossil assemblage through time. It yields a rich assemblage of fish fossils (Giersch et al., 2010; Ifrim, 2006; Ifrim et al., 2005; Ifrim et al., 2010; Stinnesbeck et al., 2019), ammonoids (Ifrim and Stinnesbeck, 2007, 2008), stramentids growing on them (Ifrim et al., 2011b), and benthic inoceramids (Ifrim et al., 2011a; Ifrim and Stinnesbeck, 2008).

Vallecillo is very well studied regarding the quantitative change in fossil content (Ifrim, 2015; Ifrim et al., 2011a). The macrofossil assemblage is dominated by nektonic organisms such as ammonoids, fishes and marine reptiles. The fossil distribution showed a pulsed recovery of the marine ecosystem together with insight into the paleoecology of ammonoids and inoceramid bivalves and their modes of dispersal (Ifrim, 2015; Ifrim et al., 2011a). Ammonoids show pulses of migration related to the expansion and shrinking of the oxygen minimum zone (Ifrim, 2015). Few ammonoids from Vallecillo show overgrowth epizoic oysters and cirripedians. They grew during the life of the ammonoid, because the oysters need some time to reach the preserved size and the cirripedians show two generations in their size distribution (Ifrim et al., 2011b). The good preservation even allowed insight into the growth of spines on ammonoid shells (Ifrim et al., 2018). The quantitative distribution of inoceramids correlates with the quantitative distribution of planktonic foraminifers (Ifrim et al., 2011a).

Fishes shows no significant changes, their quantitative distribution rather seems to reflect preservation potential. Marine reptiles are too rare.

The abundance of fishes even allows for taphonomic studies of the most abundant fishes (Stinnesbeck et al., 2023; Stinnesbeck et al., 2019; Stinnesbeck et al., 2020; Stinnesbeck et al., 2022). The good preservation allows the detailed studies of sharks (see summary in Ifrim et al., 2010), including spectacular forms (Vullo et al., 2021).

The other localities of the Vallecillo member are mainly identified by the lithology and frequent finding of the same fossils. One outcrop was found like that in the Cañon la Huasteca (Straub, 2012) where it is of same age than at Vallecillo (Beckmann, 2012) and formed under same conditions (Margulies, 2013). It was also found near Arteaga (own data). In 2000 there was an outcrop in Las Mitras, Monterrey, where the Vallecillo Platy Limestone is underlain by a black shale. The outcrop and section are documented in detail by Ifrim (2006). Today it is overgrown and a highway passes by, so access is much more difficult.

At Vallecillo only the uppermost Cenomanian was exposed, and relation to OAE 2 is detectable in geochemical data {Ifrim, 2006 #2006}. It was clearly visible in the Las Mitras section in the west of Monterrey when it was fresh in the 2000s (Ifrim, 2006). It is today rather overgrown. In the section, 26 m crop out. The lower 22.2 m are from the upper part of the Indidura Formation, a monotonous limestone-marl alternation which occurs widespread in the region and laterally grades into the also widespread and superficially similar Agua Neva Formation above an abrupt change to 2.2 m of black shale. This is currently the only Cretaceous black shale related to an OAE currently known in Mexico. At Las Mitras, it grades into the grey-pink Vallecillo Platy Limestone Member (Ifrim, 2006). This unit, however, has a widespread occurrence in north-eastern Mexico and is here considered as indirect evidence. For OAE 2. It occurs near Las Mitras, Monterrey (Ifrim, 2006), Vallecillo (Ifrim, 2006, 2015; Ifrim et al., 2011a), the Cañon la Huasteca (Beckmann, 2012), and Arteaga (own data).

La Mula, Múzquiz, Coahuila

Limestone with a suggested relation to OAE 2 are also exposed in the La Mula quarries of Múzquiz, (Giersch et al., 2011; González-Rodríguez and Fielitz, 2009). This quarry was frequently cited to be Turonian in age, but it is late Cenomanian based on the presence of *Inoceramus pictus* and the absence of *Mytiloides* (own data). The good preservation of the fishes point to oxygen-deficient conditions most probably related to OAE 2.

Xilitla, San Luís Potosí

The Xilitla quarry has been known for fossils for decades (Maldonado-Koerdell, 1956; Seibertz, 1988). A more recent study by Núñez-Useche (2016) shows that the Xilitla section spans the latest Cenomanian–earliest Turonian interval. According to these authors, high marine productivity was associated with organic matter burial and oxygen depletion in the Tampico–Misantla Basin, analogous to that occurring in modern coastal upwelling areas. Fluctuations in primary production controlled bottom water oxygen conditions at the seafloor, which remained mostly oxygen-deficient (anoxic–dysoxic) and were interrupted by punctuated, short-lived oxic events (Núñez-Useche et al., 2016). The platy limestone of Xilitla was tentatively assigned to the Vallecillo Member by Ifrim (accepted-b). It formed during the same time than the Vallecillo Platy Limestone and under same conditions (Núñez-Useche et al., 2016).

First studies show that the Vallecillo Platy Limestone may even extend as far as Puebla (Alvarado-Ortega et al., 2019) although precise biostratigraphic studies are pending. The platy limestone formation then ceases for the rest of the Turonian.

Coniacian-Santonian

Organic carbon-rich sediments related to the Coniacian-Santonian OAE 3 have been recorded from both sides of the Atlantic Basin (Wagner *et al.*, 2004), and also in Mexico . In the Coniacian and Santonian, a relation to the formation of the platy limestones of Rosario and Temporales to OAE 3 is suggested here.

The limestone succession of the El Rosario quarry in the Sierra San Carlos is well described (Stinnesbeck et al., 2005). It comprises a platy limestone interval in its middle part. Fossil preservation is excellent in these yellow platy limestones, shown e.g. by a nyctosaurid pterosaur (Frey et al., 2006), marine reptiles (Buchy, 2007), fossil fishes (Giersch, 2014), crustaceans (Vega et al., 2022; Vega et al., 2007), ammonoids (Ifrim, 2020; Ifrim et al., 2019) and inoceramid bivalves (Ifrim et al., 2014). The latter two allow for long distance correlation, accomplished by a stable carbon isotope curve. This is why El Rosario is an Associated Stratotype Section and Point for the base of the Coniacian (Walaszczyk et al., 2022).

The limestone exposed at Temporales yields fishes, ammonites and inoceramid bivalves (Alvarado-Ortega et al., 2016; Nyborg et al., 2014). It is of middle Santonian age due to the presence of abundant *Reginaites* indicative of middle Santonian age, and *Cordiceramus* cf. *bueltenensis* (Nyborg et al., 2014). The good preservation is here related to a later stage of OAE 3.

Conclusions

Many of the platy limestones of Mexico formed under Oceanic Anoxic Events. This is remarkable because these events are characterized by a breakdown of the marine carbonate factory. It was shown that a layered water body with oxygen chemoclines influenced both the faunas and the sediment formation (Ifrim, 2015; Ifrim et al., 2011a), a model which might be transferrable to more platy limestones of Mexico.

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The Early Devonian Rhynie chert – The world's oldest and most complete terrestrial ecosystem

Hans Kerp[1] and Michael Krings[2,3]

[1] Forschungsstelle für Paläobotanik am Geologisch-Paläontologischen Institut, Universität Münster, Heisenbergstraße 2, 48149 Münster, Germany
[2] SNSB-Bayerische Staatssammlung für Paläontologie und Geologie, Richard-Wagner-Straße 10, 80333 Munich, Germany
[3] Department of Earth and Environmental Sciences, Palaeontology & Geobiology, Ludwig-Maximilians-Universität München, Richard-Wagner-Straße 10, 80333 Munich, Germany

The Rhynie chert was discovered in 1912, more than 110 years ago near the small village of Rhynie in Aberdeenshire, Scotland. The first of the five parts of the monograph on the plants and fungi from the Rhynie chert published by Kidston & Lang between 1917 and 1921 was a real sensation. Even before the last parts of their monograph were published, a special chapter dealing with Rhynie chert plants was added to the third edition (1920) of D.H. Scott's famous textbook on fossil plants. Early terrestrial plants were preserved in unprecedented detail, showing the cellular organization, including subterranean parts and upright axes with reproductive organs, often still in life position. Initially, fives species of land plants were recognized, which all except for *Asteroxylon* that is now classified as an early lycopsid, appeared to belong to extinct groups. These early studies were based on thin sections, a method still used today. From the early 1920s onwards, soon after the publication of the seminal papers on the fossil flora, a series of papers on the fossil fauna, including the spider-like triginotarbids, freshwater crustaceans and a springtail, appeared. Initially, faunal remains were primarily studied from small chips of chert glued on microscope slides.

The first cherts were found as in stone walls and as loose blocks. Immediately after its discovery, in 1912 a first trench was dug that that yielded all the material described during the first 50 years. In 1964 and 2003 two other trenches exposed the chert. Until the mid-1990s hardly anything was known about the thickness of the chert-bearing sequence and its lateral extension. A first deep drilling was made in 1995 followed by additional ones in 1997. Meanwhile, another fossiliferous chert occurrence was discovered in the immediate vicinity of the nearby Windyfield farm. Nigel H. Trewin and Clive A. Rice from Aberdeen studied the geology of the Rhynie outlier and could confirm that Mackie's (1913) original interpretation that the Rhynie chert was a hot-spring deposit was correct. In the Early Devonian the Rhynie Basin formed a lowland floodplain, situated within the Old Red Sandstone continent, distant from marine influences, at 20–30° south of the Equator. The chert was dated palynologically dated as late Pragian to early Emsian; recent radiometric data reveal an age of ca. 407 Ma. For a review of

Rhynie chert, the geology and the research history refer to Trewin (2004), Trewin & Kerp (2017) and Edwards et al. (2018).

In addition to the five plant taxa described by Kidston & Lang, in recent years two more species of higher land plants were described from the Rhynie and Windyfield cherts, as well as several new animals. A remarkable find is an early opilionid, a long-legged spider with reproductive organs and more importantly – with trachea; it is one of the oldest animals fully adapted to permanent life on land. Another amazing find is a nematode of which several dozens of specimens are known in various developmental stages, ranging from embryos and young ones hatching from the egg to adult animals. These nematodes are the first soft-bodied animals known from the Rhynie chert. A sensation was the description of the life cycle of several Rhynie chert plants by Remy & Remy (1980a,b), this so-called alternation of generations was immediately incorporated in (palaeo)botanical textbooks. Now, gametophytes of four of the five sporophyte taxa originally described by Kidston & Lang are known (Kerp 2018); one of these taxa grew on sandy soils where the preservation was less ideal for these very delicate structures. The two more recently described taxa are rather poorly preserved. Of several species germinating spores are known, and of two gametophytes even the release of sperm cells from the antheridia has been captured in the chert.

Although the attention in the Rhynie chert had never really ceased, the 1990s were a period during which Rhynie chert studies gained new interest, both from palaeobotanists, palaeozoologists, sedimentologists and geochemists. Research groups started to collaborate. One of the first collaborations on the Rhynie chert was with the late Thomas N. Taylor from Lawrence KS, who spent one year in Münster to work with our team on fossil fungi from the chert. Michael Krings, his former postdoc, continues the research on micro-organisms in the chert and in soils, a field often neglected by palaeoecologists. Cooperative research of colleagues from research institutes, in e.g., Berlin, London, Cardiff, Sheffield, Aberdeen, Edinburgh and Oxford resulted in a large number of papers on Rhynie chert organisms, their ecology, food webs, growth and reproductive strategies of plants, plant functional morphology, plant-animal and plant-fungal interactions, and – last but not least – the Rhynie chert ecosystem as a whole. New taxa are still found, but primarily micro-organisms, and during the last century the research goals shifted from mainly taxonomic work to an integrated approach, using traditional methods such as thin sections studies, but also micro-CT and numerical modeling. Due to the renewed interest in the chert, the number of publications on the chert has increased dramatically in recent years with as highlights two special volumes on the Rhynie chert published by the Royal Society of Edinburgh [Trewin & Rice (eds.) 2004] and the Royal Society of London [Edwards et al. (eds) 2018]. These and the publications that appeared thereafter demonstrate that after more than hundred years after its discovery, the Rhynie chert continues to provide new and exciting results.

This presentation will focus on the Rhynie chert ecosystem, its formation and will show examples of selected animals and plants, their preservation, their growth and development, and their ecology as part of this unique early, pristinely preserved fossil ecosystem.

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Figures

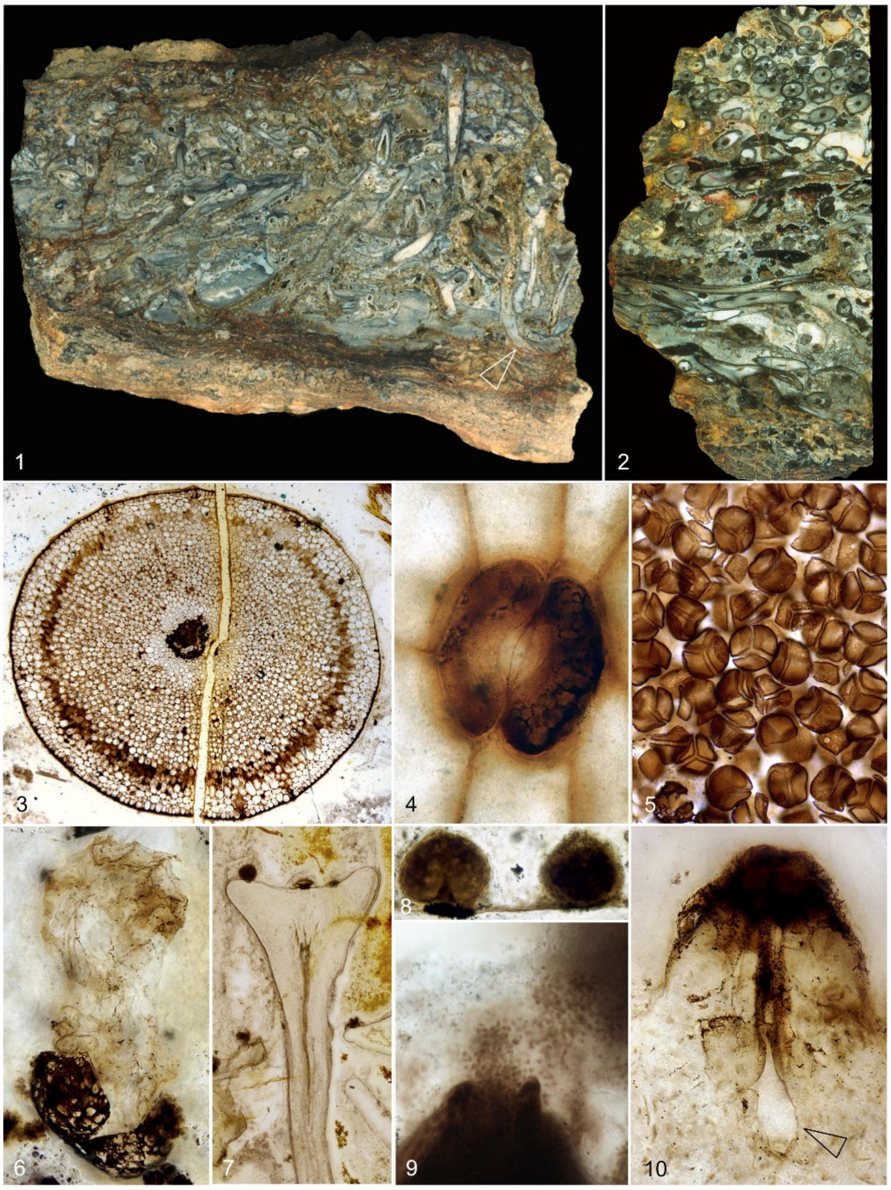

Plate 1 – Rhynie chert flora – *Aglaophyton major*
(description see page 45)

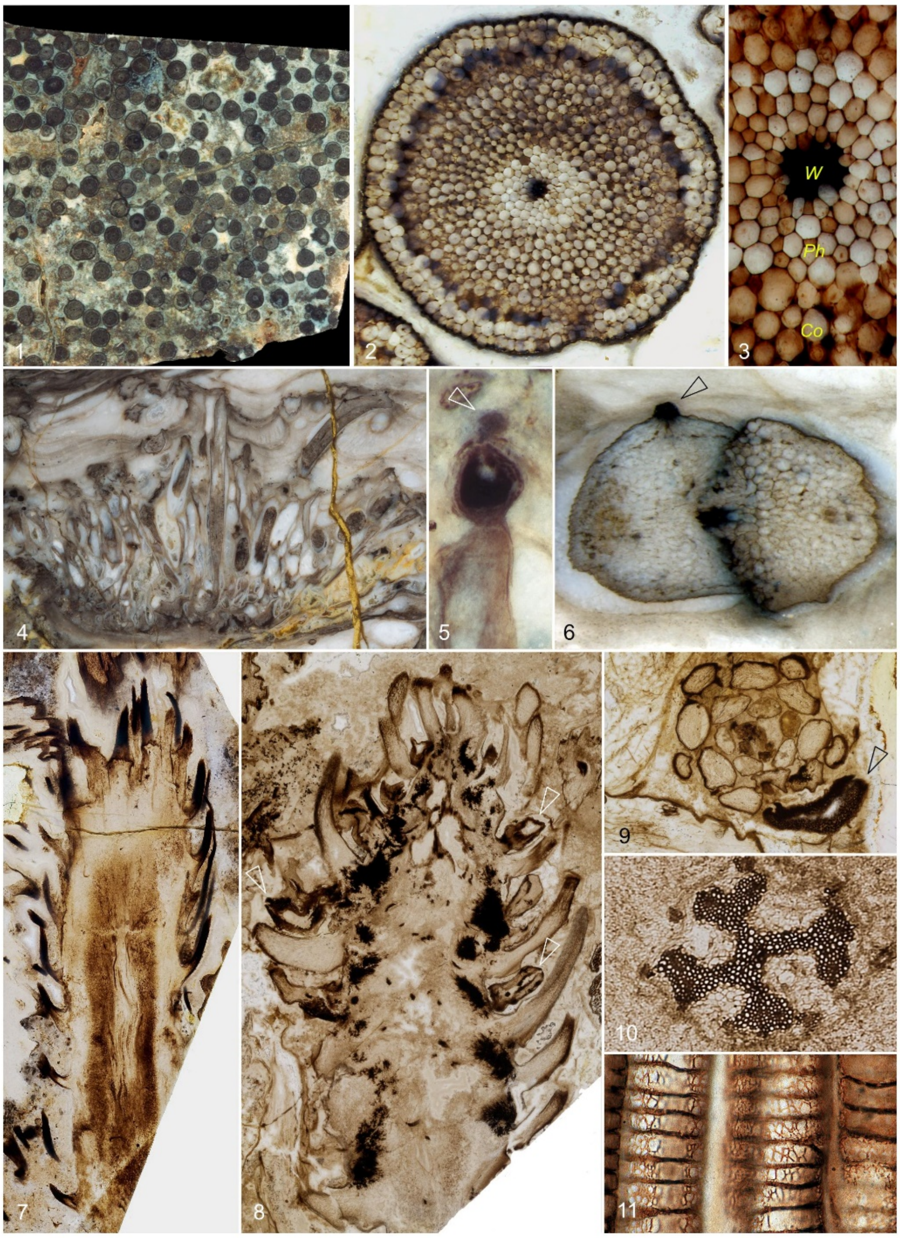

Plate 2 – Rhynie chert flora – *Rhynia gwynne-vauganii* (1–6) and *Asteroxylon mackiei* (7–11) (description see page 45)

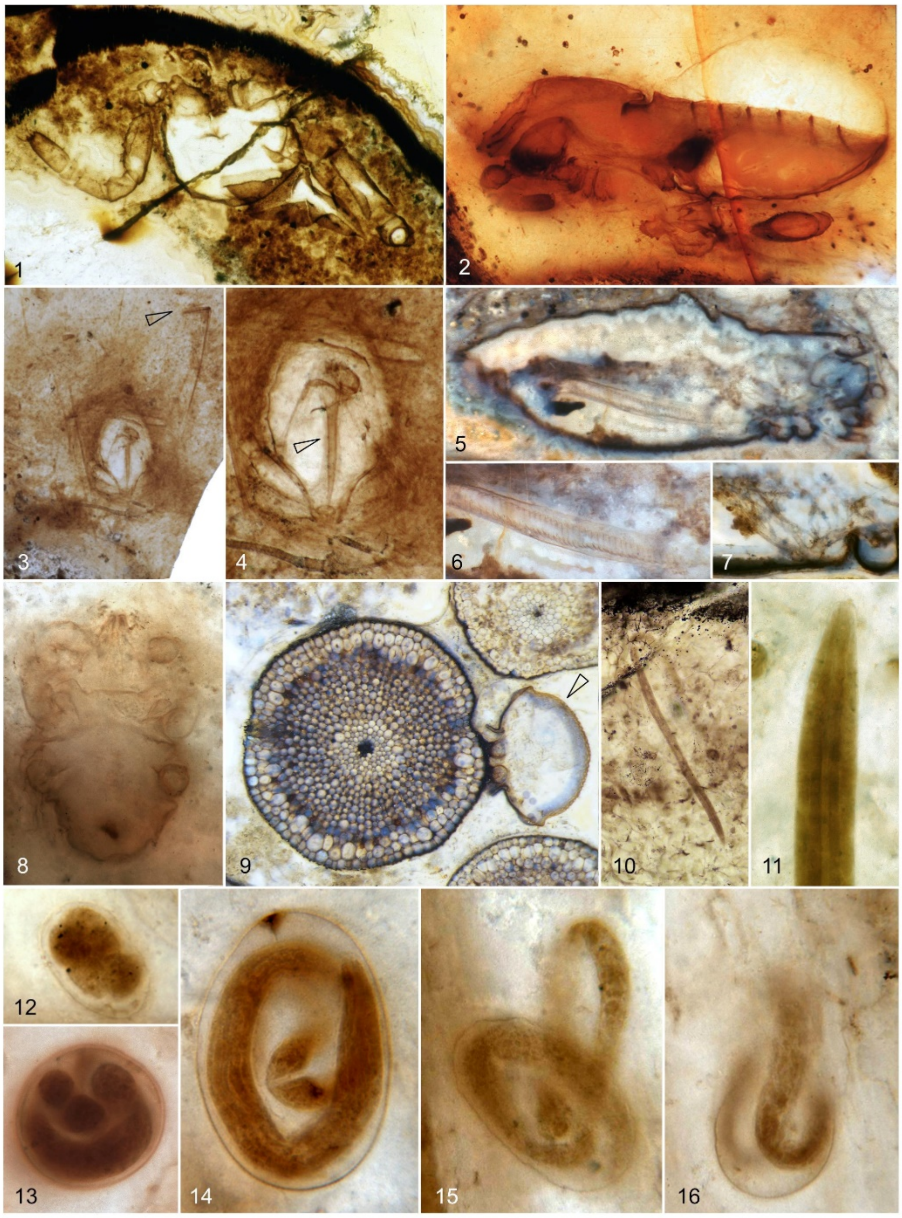

Plate 3 – Rhynie chert fauna
(description see page 45)

Plate 1

(1) Vertical section through a chert block with a sandy soil below and an *in situ* stand of with upright axes and the typical U-shaped axis lying on the substrate (arrow); (2) Block of chert with several generations of *Aglaophyton major*; (3) Cross section through an axis; (4) Stoma; (5) Spore tetrads inside a sporangium; (6) Germinating spore of with the first cell divisions of the young gametophyte; (7) Full-grown gametophyte with sperm-producing antheridia on top of the slightly bowl-shaped apex; note the presence of a conducting strand; (8) Two antheridia; (9) Antheridium showing the release of sperm cells; (9) Archegonium with the egg cell (arrow).

Plate 2

(1) Chert block cut parallel to the stratification showing a dense stand of *Rhynia gwynne-vauganii*; (2) Cross section through an axis; (3) Detail of 3 showing the water-conducting tissue (*W*), phloem-like tissue (*Ph*) and the cortex with large intercellular spaces (*Co*); (4) An *in situ* stand of gametophytes; (5) Antheridium showing the release of sperm cells; (6) Sporophyte-gametophyte junction with the gametophyte axis (left) with small cells and an archegonium (arrow), and the young sporophyte with larger cells (right). (7) Longitudinal section through a sterile, aerial leafy axis of *Asteroxylon mackiei*, the largest and most complex plant from the Rhynie chert; (8) Longitudinal section through a fertile axis showing the sporangia (arrows) interspersed with sterile leaves; (9) Cross section through the apex of an axis with leaves and a sporangium (arrow): (10) The typical cross-shaped xylem strand; (11) Tracheids in longitudinal section showing the typical annular thickenings.

Plate 3

(1–2) The trigonotarbid spider *Palaeocharinus rhyniensis* inside a sporangium of *Aglaophyton major* amidst its own coprolites consisting of undigestible mite skins (1), and seen in longitudinal section (2); the abdomen has collapsed, probably due to dehydration in silica; the original rounded outline is still visible. (3–6) The opilionid *Eophalangium sheari:* (3–4) male specimen showing the long legs (3, arrow) and the penis (4, arrow); (5–7) female specimen in longitudinal section, showing the ovipositor (6) and the trachea (7). (8) The mite *Protacarus crani.* (7) The branchiopod-like crustacean *Ebullitiocaris oviformis* (arrow) sitting on an axis of *Rhynia gwynne-vauganii.* (10–16) The nematode *Palaeonema phyticum*: (10) a complete specimen entered a decomposing axis of *Aglaophyton major* through the stomatal pore, (11) head part with mouth, gastro-ventricular tract and musculature, (12–16) nematode eggs with young embryo (12), nearly full-grown individuals inside the egg cases (13–14) and young hatching ones (15–16).

Finding and describing the exceptional: A modern definition of Fossil-Lagerstätten

Julien Kimmig[1] and James D. Schiffbauer[2,3]

[1] Abteilung Geowissenschaften, Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe, 76133, Germany; ORCID: 0000-0001-8032-4272; julien.kimmig@smnk.de

[2] Department of Geological Sciences, University of Missouri, Columbia, MO 65211, USA; ORCID: 0000-0003-4726-0355; schiffbauerj@missouri.edu

[3] X-ray Microanalysis Core, University of Missouri, Columbia, MO 65211, USA

Seilacher coined the term Fossil-Lagerstätte in his 1970 paper '*Begriff und Bedeutung der Fossil-Lagerstätten*'. In this paper he defined Fossil-Lagerstätten as "Rock bodies, which in quality and quantity preserve an unusual amount of paleontological information". He borrowed the term Lagerstätte from economic geology, where it refers to 'an unusually high, local concentration of one or multiple chemical elements in the Earth's crust'. The paper included a first attempt at the classification of Lagerstätten into Konservat-Lagerstätten and Konzentrat-Lagerstätten. These in turn where subcategorized based on the fossilization processes. Seilacher also emphasized that Fossil-Lagerstätten are created under exceptional circumstances and will therefore present a distinct but perhaps atypical view of the contemporary life it preserves.

This view changed by the time Seilacher presented his ideas on patterns in the preservation and distribution of Fossil-Lagerstätten some 15 years later, as he emphasized the potential of Konservat-Lagerstätten: "conservation deposits … reveal(s) ecological replacements, as well as trends related to the evolution of the biosphere, through geological time" (Seilacher et al., 1985; Briggs 2014). In his 1985 publication, Seilacher also elaborated on the classification of Konservat-Lagerstätten and brought it in the context of the sedimentary facies and the major agents involved in the preservation of the fossils.

Since 1985, there have been multiple attempts to build on Seilacher's Konservat-Lagerstätten classification, while the Konzentrat-Lagerstätten classification has mostly been left standing as an unusually abundant fossil deposit. Seilacher (1990) himself acknowledged that the problem with the term Lagerstätte is, that it defines no boundary, and he suggested that they be not treated as a separate class of rocks, but as end members with additional paleontological information.

An early attempt building on Seilacher's Konservat-Lagerstätten classification was presented by Allison (1988). He suggested: "Since diagenetic mineral growths are the most important factor in the formation of exceptionally preserved fossil biotas, it is logical to erect a causative classification based upon mineral paragenesis." Allison's introduced mineralogy based classification was fleshed-out by Muscente et al. (2017) with sedimentary geochemistry and microbial metabolic pathways and is one of the more quantitative approaches at classification to date.

Currently most authors use a classification scheme of Konservat-Lagerstätten that follows a site-based nomenclature, referring to localities with a typical kind of fossil preservation (Butterfield 2003), e.g. Doushantuo-type, Ediacara-type, Orsten-type, Burgess Shale-type, Beechers-type, Posidonia-type, just to name a few. In addition, some authors have tried to subdivide some of these types into tiers (e.g., Gaines 2014), moving further away from the end member idea of Seilacher (1990).

Considering the massive increase of Konservat-Lagerstätten in the literature from 44 in 1993 (Allison and Briggs 1993) to 650 in 2017 (Muscente et al. 2017), it is important to reconsider the term Fossil-Lagerstätte and find a modern definition, that reflects the progress that has been made in paleontology. The new definition needs to consider Seilacher's original idea, the development of the term Fossil-Lagerstätte since 1975, and provide actual metrics to follow. Additionally, it is important to define what is considered exceptional preservation, what is a high enough quantity of fossils to be considered a Konservat- and/or Konzentrat-Lagerstätte, what part of an outcrop/formation is a Lagerstätte, and what geological information needs to be provided when defining a new Lagerstätte.

Following these thoughts, we present a mineralogy-based classification of Konservat-Lagerstätten, building on Allison's (1988) and Muscente et al. (2017) ideas. This classification already underlies most of the site-based classification that is currently used, but will allow palaeontologists and non-paleontologists alike to understand and compare these highly important deposits in earth's history. We also suggest taking a step back and limiting the term Lagerstätte to the truly exceptional, as it was originally intended.

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The fidelity of microbial preservation in the Lower Devonian Rhynie cherts of Scotland

Michael Krings[1,2] and Hans Kerp[3]

[1] SNSB-Bayerische Staatssammlung für Paläontologie und Geologie, Richard-Wagner-Straße 10, 80333 Munich, Germany

[2] Department of Earth and Environmental Sciences, Palaeontology & Geobiology, Ludwig-Maximilians-Universität München, Richard-Wagner-Straße 10, 80333 Munich, Germany

[3] Forschungsstelle für Paläobotanik am Geologisch-Paläontologischen Institut, Universität Münster, Heisenbergstraße 2, 48149 Münster, Germany

Microorganisms are omnipresent and diverse in the bio- and geosphere today, and responsible for the sustainability of core ecosystem functions ranging from decomposition and bioerosion to the catalyzation of nutrient cycles (Madsen, 2011). With this recognition of the significance of microorganisms today, it is reasonable to presume a similar diversity and impact of microbial life in past ecosystems. However, microorganisms rather rarely lend themselves to preservation in recognizable form. Moreover, microbial life today is mostly classified based on molecular and genetic data, along with ultrastructural and life history features, that are difficult or even impossible to resolve with fossils. As a result, detailed comparisons between fossils and present-day forms that could be used to determine the affinities of the fossils and infer their ecological roles are rarely possible.

The success of finding microorganisms from the geologic past heavily relies on the way the fossils are preserved, even more so if their ecological roles are to be resolved, too. Cherts are the most important sources of evidence of fossil microorganisms because they provide a matrix in which even tenuous structures and fine details can be faithfully fossilized.

The Lower Devonian Rhynie cherts (including the Rhynie and Windyfield cherts), a silicified geothermal (hot spring) wetland ecosystem from Aberdeenshire, NE Scotland, has long been recognized as one of the most important rock deposits yielding structurally preserved (petrified) fossils of early terrestrial plants and animals (Trewin & Kerp, 2017). More recently the Rhynie cherts have also become attractive as a source of new information about the diversity and ecology of non-marine microorganisms some 407 Ma ago (Garwood et al., 2020). The fidelity of preservation in many cases allows the analysis of large sample sets of specimens and identification of sets of structural features that, albeit not necessarily diagnostic, are consistent among the specimens, and thus make it possible to recognize distinctiveness and assess diversity. The inventory of microbial life forms from the Rhynie cherts presently comprises bacteria (Fig. 1), coccoid and filamentous cyanobacteria (Figs 2–6), eukaryotic algae (Figs 7, 8), fungus-like organisms (Figs 10, 11), Fungi belonging to all major lineages except Basidiomycota (Figs 12, 13, 15–22), a putative testate amoeba (Fig. 9), a long-stalked microorganism of unknown affinity, and various remains of the enigmatic nematophytes (Fig. 14). In addition, the Rhynie cherts provide abundant direct evidence of interactions between different organisms because many fossils are preserved in situ within the context in which the organisms once lived; organismal relationships described to date include arbuscular mycorrhiza-like symbioses, a lichen-like consortium, various forms of parasitism, as well as saprotrophism and fungivory.

Fossils of fungi are very common in the Rhynie cherts (Krings et al., 2017). Filaments, hyphae (Fig. 15), mycelial cords, and different types of propagules and reproductive units (Figs 12, 13) are almost ubiquitous in the chert matrix, in litter accumulations, and in land plant parts. The most frequently encountered fungal interactions are spores of arbuscular mycorrhizal fungi (Glomeromycota) colonized by other, in most cases probably parasitic fungi or fungus-like organisms (Figs 16, 17). Inwardly directed pegs or papillae (termed callosities) that arise from the host spore wall and encase invading filaments or hyphae are a common host response (Fig. 18). Evidence of parasitism also occurs on the charophyte alga *Palaeonitella cranii* in the form of different types of fungal thalli growing out from the host (Fig. 22). The rhizoidal systems of the individual thalli usually advance into the host lumen without communicating with each other, but in some cases, show a meshwork-like pattern of interweaving (Fig. 21). Chytrids (Chytridiomycota) and chytrid-like organisms were generally the most common fungal colonizers of other organisms in the Rhynie paleoecosystem (Taylor et al., 1992). Apart from charophyte algae and fungi, they have been found on land plants and their spores (Fig. 19), putative crustacean resting eggs, unicellular algae, enigmatic propagule clusters in microbial mats (Fig. 20), and cyanobacteria (Fig. 5 [arrow]).

The fossils from the Rhynie cherts constitute the largest body of evidence of microbial interactions gathered to date from any ancient ecosystem. Other rocks that have been examined more systematically for fossil microorganisms include Mississippian and Pennsylvanian cherts from France, Pennsylvanian coal balls from Great Britain and North America, Permian and Triassic permineralized peat from Antarctica, Jurassic chert from Argentina, and the Eocene Princeton chert from Canada. While these deposits all have produced microbial fossils, including specimens yielding detailed information on interactions, none come close to the fidelity of preservation seen in the Rhynie chert.

Acknowledgments

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Figures

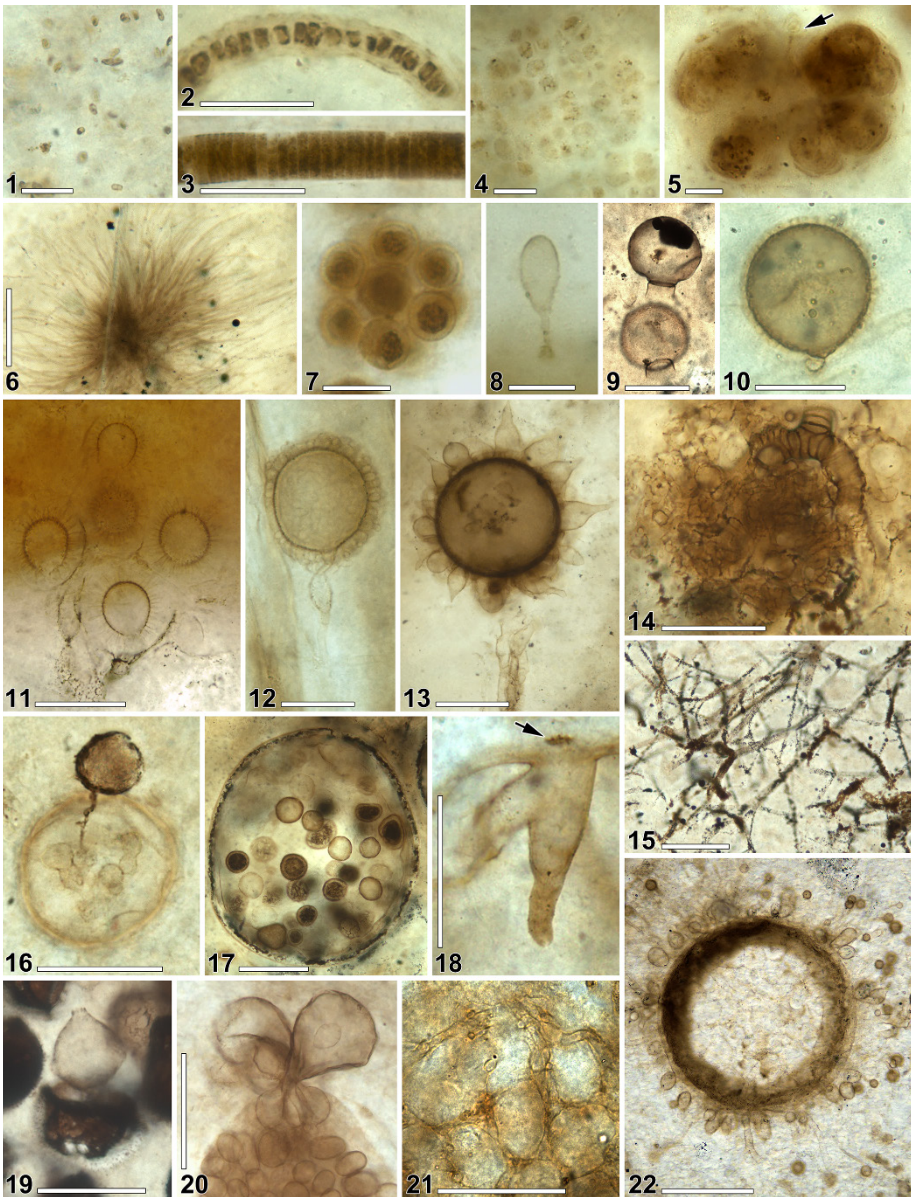

Fig. 1 (legend see next page)

Fig 1: Selected fossils of microorganisms and microbial interactions from the Lower Devonian Rhynie chert (specimen repositories: slides preceded by MS: Forschungsstelle für Paläobotanik am Geologisch-Paläontologischen Institut, Universität Münster, Münster, Germany; slides preceded by SNSB-BSPG: SNSB-Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany). **1.** Bacteria in chert matrix; slide SNSB-BSPG 2016 XII 6; bar = 20 µm. **2–6.** Cyanobacteria. 2. *Scytonema*-like filament; slide SNSB-BSPG 2016 XII 2; bar = 20 µm. 3. *Palaeolyngbya kerpii*, a large, *Lyngbya*-like filament; slide SNSB-BSPG 2015 XVIII 5; bar = 50 µm. 4. *Rhyniococcus uniformis*, a *Merismopedia*-like fossil forming unistratose, plate-like colonies; slide SNSB-BSPG 2016 VII 122; bar = 10 µm. 5. *Gloeocapsopsis*-like colony; slide SNSB-BSPG 2016 VII 76; bar = 10 µm. 6. *Croftalania venusta* forming hemispherical colonies on substrate surface; slide MS P2181; bar = 100 µm. **7,8.** Microscopic algae. 7. *Sphaerocystis*-like few-celled colony; slide SNSB-BSPG 2016 XII 7; bar = 10 µm. 8. *Characium*- or *Characiopsis*-like cell with stipe and basal attachment pad; slide SNSB-BSPG 2016 VII 1; bar = 10 µm. **9.** *Palaeoleptochlamys hassii*, a putative arcellinid amoebozoan test; slide SNSB-BSPG 1964 XX 24; bar = 50 µm. **10.** *Hassiella monospora* (Oomycetes), ornamented oosporangium; slide SNSB-BSPG 2013 XV 5; bar = 20 µm. **11.** *Triskelia scotlandica*, ornamented structures of unknown affinity growing in fungal hyphae; slide SNSB-BSPG 2008 XVI 6; bar = 50 µm. **12, 13.** Fungal reproductive units of unknown affinity (probably Mucoromycota). 12. *Zwergimyces vestitus*; slide SNSB-BSPG 2015 XIX 85; bar = 20 µm. 13. *Windipila spinifera*; slide MS P2; bar = 50 µm. **14.** Nematophyte branch knot; slide SNSB-BSPG 2015 XVII 19; bar = 50 µm. **15.** Fungal hyphae in chert matrix; slide SNSB-BSPG 2016 XI 3; bar = 200 µm. **16–20.** Chytridiomycota and chytrid-like organisms. 16. Zoosporangium on glomeromycotan spore; slide SNSB-BSPG 1965 I 336; bar = 50 µm. 17. Numerous (resting) spores in glomeromycotan spore; slide SNSB-BSPG 2013 XV 3; bar = 100 µm. 18. Callosity in fungal spore; arrow indicates site of parasite penetration; slide SNSB-BSPG 2017 XXXII 1; bar = 50 µm. 19. Sac-like zoosporangia on propagule cluster; slide SNSB-BSPG 2015 XIX 21; bar = 100 µm. 20. *Rhizophydites matryoshkae* zoosporangium on land plant spore; slide SNSB-BSPG 1964 XX 99; bar = 50 µm. **21, 22.** Colonizers of charophyte *Palaeonitella cranii*. 21. Meshwork-like interweaving of rhizoidal systems; slide SNSB-BSPG 2018 XXXV 10; bar = 50 µm. 22. Bulbil of *P. cranii* densely colonized by fungal thalli; slide SNSB-BSPG 2018 XXXV 1; bar = 200 µm.

Unlocking Vestiges of Microbial Life Hidden within Ediacaran Phosphorites of the Doushantuo Formation in South China

Liuyi Lu[a], Jan Schönig[b], Jan-Peter Duda[a], Joachim Reitner[a]

a. Department of Geobiology, Geosciences Centre of the University of Göttingen, Göttingen, Germany

b. Department of Sedimentology, Geosciences Centre of the University of Göttingen, Göttingen, Germany

Introduction

Phosphorites of the Doushantuo Formation at Weng'an (China) offer a unique glimpse into the evolution of the Ediacaran biosphere approximately 580 million years ago (Cunningham et al., 2017). Global attention has been drawn to this significant fossil lagerstätten, with particular emphasis on the Weng'an Biota in the upper phosphorite layers. Since 1998, researchers from around the world have been studying this remarkable deposit (Zhu et al., 2005), although certain aspects remain contentious. One of the ongoing debates centers around the interpretation of microfossils which are widely interpreted as animal embryos (Xiao et al., 2007). In order to better understand the nature of the Doushantuo phosphorites and, by extension, of the contained microfossils, we analyzed the relation between minerals and organic matter in the deposit with a variety of analytical imaging techniques (e.g., SEM-EDS, Raman spectroscopy, μXRF, EPMA).

Results and Discussion

We found that walls of individual ~500 μm sized microfossils are enriched in organic matter relative to calcium apatite at the surface. By contrast, the inner part of the walls is enriched in calcium apatite relative to organic matter. The interiors of the microfossils exhibit ~3 μm diameter sized organic matter aggregates interwoven with apatite. Relative enrichments of iron and sulfur show no direct relationship within the samples, indicating that these elements are not related to pyrite. The presence of abundant apatite within the deposit and distinct elemental sulfur enrichments associated with some of the microfossils support their interpretation as sulfur oxidizing (SOX) bacteria like *Thiomargarita* (Bailey et al., 2007). Thriving at the sediment-water interface below nutrient-rich, high-productive surface waters, SOX bacteria seem to have been ecologically and taphonomically significant in the Weng'an environment. Perhaps most importantly, SOX bacteria drove the local phosphorus cycle and promoted authigenic phosphate mineral formation, accounting for the excellent preservation of microfossils in the deposits. In addition, some of the microfossils show striking morphological similarities to modern microbial communities enclosed in spheres consisting of lectins (i.e., carbohydrate-binding proteins) related to exopolymeric substances (EPS). Today, such morphological spheres are for instance known from the Black Sea, where communities of anaerobic methanotrophic archaea (ANME-2) and sulfate reducing bacteria (SRB) are surrounded by a strong skin of EPS with high content of AAL–A568 lectin (Reitner et al., 2005; Reitner, 2010). Spheres containing microbial lectin-rich EPS have important ecological functions, for instance shielding the enclosed microorganisms against environmental stressors and detoxifying harmful metabolic substances produced by the enclosed microorganisms, and thus potentially provide useful information for geobiological reconstructions.

Conclusion

In the light of our findings, it is tempting to speculate that some of the Weng'an microfossils like *Megasphera* might be formed by strong EPS containing lectins that contained microbial communities, functionally (but not necessarily metabolically) similar to those known from the Black Sea. Regardless of the exact interpretation, our findings show that many of the studied microfossils in the Doushantuo phosphorites are remains of microorganisms, not animals. More detailed studies on fossils of the Weng'an biota are crucial to fully appreciate the geobiological significance of these iconic deposits.

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Unsettle the affinity *Vauxia*: a challenge from taphonomic studies

Cui Luo

State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, 39 East Beijing Road, Nanjing 210008, China.

As one of the most basic animal lineages (Schultz *et al.* 2023), sponges probably originated in the Neoproterozoic (Erwin 2020) but became readily recognizable in the fossil record only since the early Cambrian (Antcliffe *et al.* 2014; Chang *et al.* 2019; Luo & Reitner 2019; Reitner *et al.* 2022). The conspicuous gap between the expected emergence time of the Phylum Porifera and the first sponge spicule fossils was attributed to the lack of mineral skeletons in Precambrian sponges (e.g., Wood 2011; Luo & Reitner 2014). Studies of the morphology and biomineralization potential of non-spicular sponges are thus necessary and helpful to understand the earliest scenario of sponge evolution.

The Cambrian sponge fossil Family Vauxiidae is of particular interest in this issue because it has been regarded as the earliest representative of the main group non-spicular demosponges since Rigby (1986) (e.g., Luo & Reitner 2014; Botting & Muir 2018; Luo *et al.* 2020). These sponges possess a non-spicular skeleton, which is exclusively composed of anastomosing fibrous elements. Rigby (1986) assigned these sponges to the Order Verongiida, a living taxon with chitinous organic skeletons. This interpretation was rarely tested except for a single study announcing the discovery of chitin in the Burgess Shale fossil *Vauxia* (Ehrlich *et al.* 2013). However, recently described vauxiid fossils from different ages and localities of South China all exhibit silicified skeletal fibers, casting doubts on the previously believed verongiid affinity. In addition, the discovery of similar fibrous framework in some archaeocyaths (Luo *et al.* 2021, 2022) and in carbonates as old as 890 Ma (Turner 2021) is also appealing for a better understanding of the affinity and biomineralization of vauxiid sponges.

Taphonomic studies of the *Vauxia* specimens from the Burgess Shale are key to solve the crux of the mentioned questions. This study checked 45 specimens belonging to 5 *Vauxia* species deposited in the Smithsonian Natural History Museum (USNM) and Royal Ontario Museum (ROM). Based on optical microscopic observation, the preservation of their skeletal fibers can be classified into 5 types:

- fibers preserved in brownish color and with a positive relief;
- fibers in a positive relief and ultimately buried in a dark veneer that covers the whole fossil;

- fibers in a positive relief, transparent in color, and bounded by dark-colored materials;
- fibers completely flattened and preserved as a reflective veneer;
- fibers preserved as a flattened reflective veneer but exhibit a core in a positive relief.

Among them, preservation mode V was employed by Rigby (1986) as one of the main arguments for the verongiid affinity. However, analyses of elemental and mineral composition were only allowed for preservation types I, II, and III, due to the regulation of specimen management and limited accessibility to suitable facilities.

Specimens ROM56243b (preservation type III), ROM61237 (preservation type I), and RQ97377a (preservation types I and II) were selected for analyses using SEM, EDS, and Raman spectroscopy. Among them, ROM61237 was used for extracting chitin by Erlich et al. (2013). The results show that the transparent skeletal fibers in ROM56243b are now preserved with platy clay minerals, while the dark-colored material bounding the fibers is carbonaceous. In ROM97377a, all fossil specimens, whether in preservation type I or II (ROM61237 and part of RMO97377a) are covered by a veneer composed of amorphous organic carbon and enriched with calcium and phos-phorus relative to the host rock. In preservation type I, the brownish skeletal fibers are mainly composed of iron oxides, accompanied by a mixture of other minerals, including clay minerals, quartz, calcite, and dolomite. While in pre-servation type II (RQ97377a), the skeletons are exclusively composed of of iron-rich dolomite or ankerite.

These data indicate that none of the analyzed fossils should originally have had a chitinous fibrous skeleton as that of verongid demosponges. The organic skeleton of non-spicular demosponges is composed of chitin and spongin, which are more resistant to decay than other soft tissues (Gross *et al.* 1956; Junqua *et al.* 1974; Butterfield 1990). If chitinous skeletons were present in *Vauxia*, they should have been able to be preserved as carbonaceous compressions, like the carbonaceous film that covers the whole fossil. As these skeletons are now commonly replaced by multiple diagenetic minerals, it is reasonable to infer that they were primarily composed of a mineral that is unstable in diagenetic dissolution. Here, I suggest that calcium carbonate should be considered as a possible candidate. Among the analyzed specimens, iron-rich dolomites in the skeleton of RQ97377a (preservation type II) are least known as a diagenetic mineral in the Burgess Shale (Butterfield *et al.* 2007), and their occurrence in the skeleton is not accompanied by other common diagenetic minerals such as iron oxide and clay minerals. The rich magnesium element in the host rock could facilitate the transformation of calcium carbonate to dolomite in deep burial conditions. If this is correct, Vauxia may have a close relationship with some archaeocyaths, as hypothesized by Luo *et al.* (2021).

Nevertheless, this study only reveals the preservation of part of the *Vauxia* fossils from the Burgess Shale. Preservation types IV and V, and the silicified vauxiid fossils from South China still require further investigation.

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Micro- and nannofossil Lagerstätten – What can they contribute?

Mike Reich

Staatliches Naturhistorisches Museum Braunschweig, Gaußstr. 22, 38106 Braunschweig, e-mail: m.reich@3landesmuseen.de

Fossil Lagerstätten, such as conservation, stagnation, obrution, concentration or liberation deposits (Seilacher et al. 1985, Roden et al. 2020), often also hosts diverse and well-preserved fossil ecosystems consisting of microscopic, nanoscopic or mesoscopic fossils. Some authors have therefore used terms such as 'nannofossil lagerstätten' deposits (Bown 1993) or 'microfossil lagerstätten' (Wendler & Bown 2013, Schallreuter & Hinz-Schallreuter 2013, Haynes et al. 2016, Bown et al. 2017) for such deposits.

In addition, terms such as SSF ('Small shelly fossils') and SCF ('Small carbonaceous fossil') have long been used in connection with conservation deposits (Matthews & Missarzhevsky 1975, Butterfield & Harvey 2011).

In my presentation I will show that *in situ* investigations, for example by high-resolution scanning electron microscopy (e.g. Toarcian *Posidonia* Shale, Kimmeridgian/Tithonian Plattenkalk deposits), or special, modified micropalaeontological preparation/disintegration methods (Ordovician and Cretaceous partly silicified limestones) can provide essential contributions to the palaeontology and palaeobiology of fossil lagerstätten deposits.

The first provide exceptionally preserved nannofossil "graveyards" with completely preserved (or collapsed *in situ*) coccospheres, with just the very small coccoliths (smaller than 5 μm) present in greater numbers (Reich in Ansorge et al. subm.). Also ghost imprints on amorphous organic matter (AOM) provide diverse 'hidden' nannoplankton assemblages, as these also fill various gaps in the fossil record (e.g. Götz & Reich 2023). Secondly, early diagenetic fossilised partially silicified limestones of different ages (Sandbian/Katian, Schallreuter 1982; Turonian/Maastrichtian, Herrig 1993a) have long yielded exquisitely preserved microfossils, including ostracods (Schallreuter 1964, 1971; Herrig 1982, 1988, 1993b) and echinoderms (Reich 1995, 2021). These show uniquely preserved fossils in preservational windows that are either missing in limestones/chalk of the same age, or are only poorly/incompletely preserved there (see Fig. 1).

Combined micro- and macropalaeontological investigation and documentation methods often complement and enrich results (previously obtained only on macrofossils) in an ideal and unique way. These results validate that micro- and nannofossils, which have often received less attention so far, are powerful tools for analyzing fossil Lagerstätten and provide a strong control for the interpretation of various Phanerozoic, or older, fossil assemblages and biota.

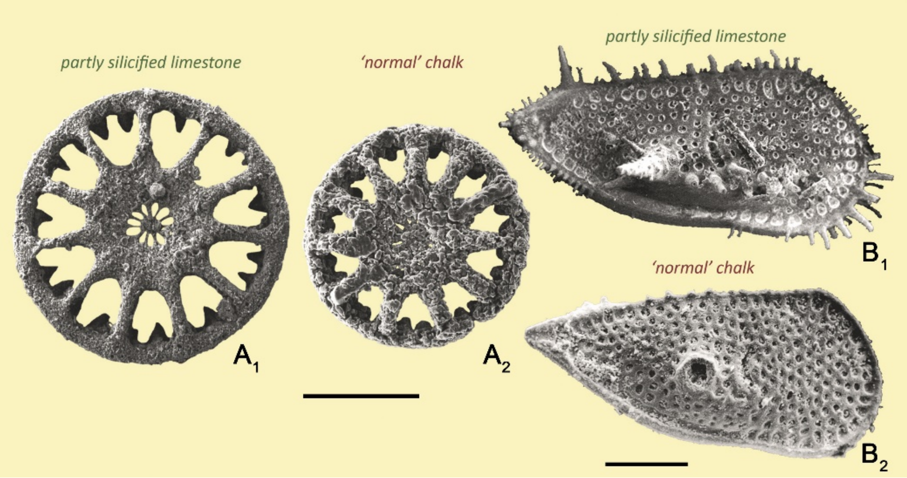

Fig. 1. Exceptional *versus* 'normal' preservation of various microfossils (holothurian ossicles and ostracods) from partially silicified limestones (concentration deposit) and white chalk (liberation lagerstätte) of the same age (Maastrichtian; southern Baltic Sea area). Please note the well-preserved coccoliths in A_1 as well as the preserved spines in B_1 (in contrast to the chalk specimens figured in A_2 and B_2). **A** *Myriotrochus (Oligotrochus) smirnovi* (Holothuroidea: Apodida: Myriotrochidae), **B** *Cuneoceratina pedata* (Ostracoda: Podocopida: Bythocytheridae). Scale bars 0.1 mm (A) and 0.2 mm (B). [from Reich 2014]

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The Late Jurassic Plattenkalk deposits (Kimmeridgian/Tithonian) of the 'Solnhofen Archipelago', Bavaria, Germany

Martin Röper[1], Mike Reich[2]

[1] Museum Solnhofen, Bahnhofstr. 8, 91807 Solnhofen, e-mail: m.roeper@solnhofen.de
[2] Staatliches Naturhistorisches Museum Braunschweig, Gaußstr. 22, 38106 Braunschweig, e-mail: m.reich@3landesmuseen.de

The Late Jurassic 'Solnhofen' Plattenkalk deposits of Bavaria are widely known as one of the most productive fossil Lagerstätten worldwide, having produced innumerable specimens of well-preserved marine protists, algae, invertebrates, and vertebrates, as well as a smaller number of terrestrial plants and vertebrates (e.g. Barthel 1978; Barthel et al. 1990; Röper et al. 1996, 1999, 2000, 2022; Röper 1998; Etter 2002; Selden & Nudds 2004; Reich et al. 2020; Kustatscher et al. 2023), including such iconic vertebrates as *Archaeopteryx*, *Compsognathus*, and *Juravenator* (Göhlich & Chiappe 2006; Wellnhofer 2008; Foth et al. 2014; Neumann et al. 2018; Reich & Wörheide 2018; Rauhut et al. 2018) (altogether >1,600 species; Kuhn 1961, Schultze 2015).

These Plattenkalk deposits in southern Germany were deposited during late Kimmeridgian/early Tithonian times in several sub-basins between coral-sponge reefs and sponge-microbialite mounds (e.g. Meyer & Schmidt-Kahler 1990; Röper 2005a, 2005b; Schmid et al. 2005; Fürsich et al. 2007a; Meyer 2015; Schweigert 2015).

Although the early Tithonian ('lithographic') Solnhofen beds *sensu stricto* (Altmühltal Formation, Niebuhr & Pürner 2014) is by far the most famous unit and has yielded most spectacular fossils so far, this mainly stems from the fact that these rocks have been exploited for commercial purposes for centuries, whereas other Plattenkalk deposits of overlying/underlying Formations and equivalents (e.g. Torleite, Tangrintel, Painten, Geisental, Mörnsheim, Usseltal) are as or even more fossiliferous, but have not been fully explored so far.

Detailed analyses are further complicated by the fact, known for more than 100 years (e.g. Walther 1904, Mayr 1967), that Plattenkalk fossils of different localities and stratigraphic ages have been repeatedly interchanged (especially Eichstätt↔Solnhofen) and given the more famous name 'Solnhofen'.

Only recently have attempts been made to distinguish the different faunas/floras in more detail and to see them in their stratigraphic, geographical and ecological/taphonomic framework (e.g. Röper 2005b, Fürsich et al. 2007b, Viohl & Zapp 2007, Röper & Reich 2018).

Indeed, the 'Solnhofen Archipelago' represents a unique and important window into a larger Mesozoic shallow marine environment, and undoubtedly was a global biodiversity hotspot of that time. However, focused and combined micro-

/macropalaeontological palaeoenvironmental analyses in connection with modern geobiological/biogeochemical investigations are still pending for the more than 30 Bavarian Plattenkalk sites, offering the opportunity for future research and discussions.

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The Nusplingen Plattenkalk – observations, assumptions and enigmas of a Late Jurassic fossil Konservat-Lagerstätte

Günter Schweigert

Staatliches Museum für Naturkunde, Rosenstein 1, 70191 Stuttgart, Germany
guenter.schweigert@smns-bw.de

The Nusplingen Plattenkalk or Nusplingen Formation is a Late Jurassic fossil Lagerstätte located in the southwestern part of the Swabian Alb, about 15 kilometres N of the Upper Danube Valley. The site was discovered in the first half of the 19th century and subsequently described by Friedrich August Quenstedt from Tübingen University and by Oscar Fraas from the Naturaliencabinet in Stuttgart, a forerunner institution of the present Natural History Museum. Several commercial and scientific excavations were executed since these early days; the last one by the Stuttgart Natural History Museum started in 1993 and is still going on. Remarkable fossils were found, unknown from elsewhere in Swabia, but similar to those from the celebrated Tithonian plattenkalks of Solnhofen and Eichstätt in Bavaria: prawns and lobsters, vampyromorph squids, coelacanths and other fish, thalattosuchian crocodiles and pterosaurs. The Nusplingen Plattenkalk is especially famous for well-preserved sharks, namely the iconic angel shark *Pseudorhina acanthoderma* (Fig. 1). Meanwhile, with over 400 recorded taxa the Nusplingen site is among the most diverse Jurassic localities worldwide. The Nusplingen Formation covers an area of less than 2.5 square kilometres. It is exposed in two small quarries exclusively dedicated to science, the Nusplingen Quarry and the Egesheim Quarry. These quarries are located in a distance of c. 250 metres from each other on top of the 'Westerberg' hill, W of the village of Nusplingen. A relict occurrence of Nusplingen Plattenkalk crops out at the 'Großer Kirchbühl' hill further to the south. The entire outcrop area of the Nusplingen Formation is protected as a national heritage site since the 1980ies. The Nusplingen Plattenkalk contains an ammonite assemblage that dates it into the late Kimmeridgian (Beckeri Zone, Ulmense Subzone), several hundred thousand years older than the 'classical' Solnhofen plattenkalks of Tithonian age. Jurassic deposits of Tithonian age as well as late Kimmeridgian beds coeval with the Nusplingen Plattenkalk are eroded in the closer area. More details and compilations of the geology of the Nusplingen site and its fossils can be found in Dietl & Schweigert (2004, 2011), Schweigert (2015) or Schweigert & Roth (2021).

What we know about environment and sedimentology

The Nusplingen Plattenkalk was deposited in a c. 80 to 100 metres deep lagoonal basin surrounded by slightly older siliceous sponge-microbial mounds. The total thickness of the Nusplingen Plattenkalk lies between 10 and 15 metres. It is overlain by breccias and olistoliths. The steep margins of the basin show dipping angles up to 45 degrees, whereas the seafloor of central parts of the lagoon was almost horizontal. Some of the surrounding mounds were tectonically uplifted above sea-level as small islands and underwent an early diagenesis leading to the formation of dedolomite. Terrestrial environments are indicated by abundant well-preserved terrestrial plants and a few terrestrial animals such as pterosaurs and insects. All beds of the Nusplingen Plattenkalk yield marine macrofossils such as ammonites (and their calcified lower beaks), belemnite rostra, fish scales and isolated shark teeth as well as marine planktic organisms (coccolithophorids, radiolarians, *Saccocoma*) and sponge spicules. The mouldic preservation of radiolarians is unique in the entire Upper Jurassic of Swabia (Zügel et al. 1998). Terrestrial plants are mainly represented by conifers and pteridosperms with anatomical adaptations to dry habitats. Charcoal of conifers indicates occasional wildfires (Uhl et al. 2012).

Although large portions of the section consist of finely laminated biodetritic limestones, only a few true sedimentary surfaces were observed. They show polygonal patterns characteristic for microbial mats (Fig. 2). The Nusplingen Plattenkalk is one of the type localities for "allodapic limestones" resulting from calcareous turbidites (tempestites?). These turbidites contain breccias with lithoclasts and fragmented fossils from neighbouring sponge-microbial mounds (Dietl et al. 1998; Bantel et al. 1999). Fossils that are common in the laminated limestones are almost completely absent in these turbidites (Schweigert 2020). On top of the thickest one of the turbidites there is a mass-occurrence of autochthonous echinoids with long spines (*Polycidaris nusplingensis*) that were adapted to firm grounds and low oxygenation and colonized the sea-floor for a short period of time (Grawe-Baumeister et al. 2000). This is one of the very few examples of mass mortality layers in the Nusplingen Plattenkalk. Mass mortality events of nektonic fossils have never been recorded. Occasionally, the laminated limestones are interrupted by a few millimetres-thick layers of micrite. It is the question whether these homogenous layers represent abiotic seasonal whitings or distal turbidites; in any case they were deposited as short-term events. In some parts of the section organic matter is still preserved as kerogen; in this respect the Nusplingen Plattenkalk is a black shale comparable to the Lower Jurassic Posidonia Shale. Like in the latter, phosphatisation plays an important role for the preservation of fossils (Briggs et al. 2005). Intervals with slumping and many other observations indicate extremely rapid early lithification (e.g., Schweigert & Dietl 2012a). The most prominent slump occurred close to the top of the section. It is covered by a decimetre-thick limestone bed that had probably formed immediately after the slumping event. Within the slumped interval we noticed a single chalky layer with roll marks of small ammonites and fish vertebrae that must originate from marginal parts of the basin (Schweigert & Dietl 2009). Besides the turbidites there is a single mudflow bed (Fig. 3) that yields a diverse assemblage of crabs and other small arthropods which are not recorded in the neighbouring Plattenkalk lithology. Apart from the short-term periods when the turbidites and slumps had formed the environmental conditions had been very calm. Fossils with long axes like the angel sharks show random orientation; there is no evidence for directed flows at the bottom of the Nusplingen basin. Isotopic data obtained both from belemnite rostra and shark teeth suggest water temperatures of c. 20° C for the depths where these animals had lived (Stevens et al. 2014; Hättig et al. 2019).

Taphonomical observations

Taphonomy is an important indicator for the reconstruction of palaeoenvironmental conditions, such as consistency of the substrate or the presence or absence of scavengers. Preservation of articulated vertebrate skeletons is a common feature of Solnhofen-type Lagerstätten. In the Nusplingen Plattenkalk, vertebrate remains are usually much better preserved at the bottom side whereas their top side often shows onset of decay or scavenging (Fig. 4). Many incompletely buried vertebrates and fragmented invertebrates must be interpreted as pabulites (lost prey accidentally brought in by predators) or regurgitalites. This is especially the case for a great number of incomplete benthic fossils (e.g., echinoids, asteroids, bivalves, erymid lobsters). Vice versa, occasionally *in situ* preserved stomach or crop contents allow the reconstruction of the food web. Clusters of oysters, sometimes associated with other fossils such as ammonites and/or belemnites are still a case of controversial discussion. In a single bed of the section of the Nusplingen Quarry such accumulations of small oysters and ammonites form clusters with diameters of half a meter and even more (Fig. 5). It is highly unlikely that these clusters had formed benthic islands, however, providing a generalized explanation for all these finds is impossible. Many observations such as vertical or oblique embedding of belemnites and ammonites or the three-dimensional embedding of multiple-branched conifer twigs point to remarkably high sedimentation rates (e.g., Schweigert 1999). In addition, there are some hints for the temporal existence of floating microbial mats that had separated two water-bodies and that developed not far away from the seafloor (Schweigert 2022).

Evidence from ichnology and other interactions between fossils and the seafloor

Only a few beds of the studied section show endobenthic ichnofossil communities, whereas others totally lack this kind of ichnofossils. The ichnocommonities are mostly dominated by a single opportunistic producer (*Parahaentzschelinia*) or a low-diverse assemblage with *Thalassinoides*, *Rhizocorallium*, *Chondrites* and a few others (Schweigert 1998). The producers of these burrows are never preserved. Bioturbation of the sediment normally destroys delicate fossil structures and organic matter. Thus, absence of bioturbation is the most important prerequisite for the formation of this conservation Lagerstätte. If bioturbation is incomplete, we note abrupt lateral changes between excellent preservation and total destruction of the fossils (Fig. 1).

Common ichnofossils of the non-bioturbated laminated limestones are phosphatic coprolites that may originate from various marine vertebrates (Schweigert & Dietl 2012b) and *Lumbricaria*, the faeces of aspidoceratid ammonites. The latter consists of very long densely coiled strings that exclusively consist of the calcitic ossicles of *Saccocoma*, a planktic crinoid. Regurgitalites are common as well. Together with many nektonic fossils, the coprolites and regurgitalites as well as the abovementioned pabulites indicate predation in and around the Nusplingen lagoon. In some beds we noted interactions between living animals and the seafloor, like swimming trails of vertebrates (e.g., *Undichna*, *Serpentichnoides*) and horseshoe crabs (*Kouphichnium*). Mortichnia of deadly injured crustaceans (common) and fishes (extremely rare) are recorded as well (Schweigert & Dietl 2002, 2005; Schweigert et al. 2016). The mortichnia show how the related animals tried to escape from the seafloor and left traces behind. These traces are not restricted to a single sedimentary plane but often affect a couple of limestone laminae. The only explanation for this observation is that these mortichnia had not formed on the surface of the seafloor but within the sediment, when thin layers had already started to become lithified but were still separated from each other by soupy layers, where the animals could move for a short distance. When such thin, still unconsolidated mud layers occurred on the surface of the seafloor, no interactions between organisms and the substrate are preserved. Then we either note the alleged absence of benthic fossils or the preservation of undertracks as in the case of the swimming trails. Touch marks of ammonites like those described from the Altmühltal Formation of Solnhofen and Langenaltheim are absent in the Nusplingen Plattenkalk, even when microbial mats were actually present.

Conclusions and some open questions

In the Nusplingen Plattenkalk, infaunal life as well as settling on the seafloor was obviously hampered not only by low oxygenation but equally by the hostile consistency of the substrate and a high sedimentation rate, as evidenced both from ichnofossils and taphonomy. These environmental conditions as well as very rapid early lithification favoured the exceptional preservation of otherwise unrecorded fossils. We still do not know about the reasons for some fluctuations in the abundance and/or composition of the fossil content and we do not know about the mechanisms of sedimentation in the laminated sections between the turbidite layers. Another unsolved question concerns the non-record of several groups of fossils well-known from other Solnhofen-type Lagerstätten, such as larvae and juvenile stages of arthropods, jellyfishes, or juvenile fishes and sharks.

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Figures

Fig. 1. An iconic fossil of the Nusplingen Plattenkalk: the angel shark *Pseudorhina acanthoderma* (O. Fraas). Here a female specimen (length c. 125 cm) preserved in a partly bioturbated bed (near basis of "bed N").

Fig. 2. Microbial mats showing polygonal patterns in the top part of "bed L" of the Nusplingen Formation.

Fig. 3. A c. 12-cm-thick coarse-grained mudflow deposit ("bed E") occurs locally in the section of the Nusplingen Quarry, concordantly overlain by finely laminated plattenkalks.

Fig. 4. A specimen of *Caturus* cf. *furcatus* Agassiz (length c. 38 cm) prepared from the bottom side. The bones and scales surrounding the specimen originate from the decaying upper side. The fish is preserved inside a plate and was only noticeable in cross-section.

Fig. 5. Extremely large clusters composed of the small oyster *Liostrea socialis* (Münster in Schlotheim) and a few ammonites (horizontal diameter c. 40 cm) are restricted to a single layer of "bed M". All photos: G. Schweigert.

Underestimated? Selected examples of the taphonomy of prehistoric sites in northern Germany

Thomas Terberger

Niedersächsisches Landesamt für Denkmalpflege, Scharnhorststrasse 1, 30175 Hannover
Seminar für Ur- und Frühgeschichte, Universität Göttingen, Nikolausberger Weg 15, 37154 Göttingen, thomas.terberger@phil.uni-goettingen.de

In recent years, the importance of taphonomic processes for the interpretation of Palaeolithic and Mesolithic sites has been increasingly recognized. In principle, the earlier a site is dated, the greater the chance of later effects on the preservation of the finds layers. However, favorable factors such as rapid embedding of the finds and/or a sediment trap can ensure high-quality preservation of Palaeolithic and Mesolithic sites. For the preservation of finds made of organic material, embedding in a wet soil environment and/or in limestone-rich sediments is particularly advantageous.

Northern Germany is characterized by a number of excellently preserved Middle Palaeolithic sites. In the case of Schöningen (district of Helmstedt), Lehringen (district of Verden) and Salzgitter-Lebenstedt, find layers were situated below the groundwater level, which even allowed the preservation of wooden artifacts. In these cases, discovery was due to deep soil interventions: In Salzgitter-Lebenstedt the finds were 4-6 m below ground level and in Schöningen over 10 m below ground level.

Even if riverbanks and lakeshores are preferred locations for sites, thick sediment deposits hardly allow the access of the find layers. For example in Lichtenberg, Lüchow-Dannenberg district we know of a Middle Palaeolithic site detected by a flint scatter on the surface. Better preserved finds have been located in deeper layers on the former lake shore by drillings, but access is very difficult. The importance of river valleys for the location of Neanderthal sites is demonstrated by many gravel pit finds from river Leine and Weser. A considerable number of hand axes were collected, but their context remains unclear.

The evaluation of taphonomic processes is particularly challenging for Middle Palaeolithic surface sites in northern Germany. Due to the ice sheet advance around 24,000 years ago no finds before the Late Glacial have survived from the young moraine area north of the Elbe or from north-eastern Germany. More recently the landscape-changing processes of the Saalian including ice lakes and flood outbursts have been discussed for north-western Germany. Where Middle Palaeolithic surface finds have been located, taphonomic processes play a major role in the artefact evaluation: it is not always easy to separate geofacts from Middle Palaeolithic artefacts. Sometimes even frost sherds were used as tool blanks and the surface preservation such as wind gloss plays an important role in the evaluation.

Find layers in caves and rock shelters require special source-critical consideration, as they can act as sediment traps and are often affected by erosion. In addition to a critical assessment of the taphonomy on the macro level, discussion on site level is necessary. For example the so-called spear horizon of site Schöningen 13 II-4 was initially interpreted as a single event, while later analysis suggests that the find layer resulted from repeated hunting visits at the lake shore site.

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Lower Jurassic concretions: a treasure trove for molecular fossils?

Volker Thiel

Georg-August-University Göttingen, Geoscience Centre, Geobiology, Goldschmidtstr. 3, 37077 Göttingen, Germany

Diagenetic concretions are widespread in the geological record and have been recognized as a source of exceptionally preserved fossils (e.g. Allison and Pye, 1994; Zaton and Marynowski, 2004). They commonly formed during shallow burial via localized lithification of soft sediment with calcite, dolomite, rhodochrosite, siderite, or apatite (Coleman, 1993; Wilson and Brett, 2013). However, putative modern counterparts are lacking and the underlying biological and geochemical processes are not fully understood. Organic matter (OM) degrading organisms probably play a key role in the precipitation process and it seems that particularly anaerobic microbial metabolisms control the geochemistry and isotopic composition of concretions (e.g. Raiswell, 1976; Coleman and Raiswell, 1981; Coleman, 1993; Marshall and Pirrie, 2013). Whereas the microbial respiration of OM would generally provide a supply of oxidized carbon, some of the metabolisms may shift alkalinity and pH, so inducing supersaturation required for carbonate or phosphate precipitation.

The idea that concretions may contain a better-preserved record of syndepositional and early diagenetic organic features has been put forward in a number of studies (Melendez et al., 2013; Plet et al., 2016; for a comprehensive compilation of biomarker studies on concretions and a summary of core results, see Plet et al., 2020). Earlier work on Jurassic carbonate concretions from the UK and Poland has, for instance, reported the unprecedented occurrence of unsaturated fatty acids (FA) along with the common saturated homologues, which still preserved the distinct even-over-odd predominance typical of biological OM (Wolff et al., 1992; Kiriakoulakis et al., 2000; Marynowski et al., 2007). Similar FA distributions and the preservation of mono- and diunsaturated FA were observed in concretions from Upper Jurassic (Kimmeridgian) strata on the Isle of Skye (Pearson et al., 2005), and in Cenozoic concretions from eastern Austria (Baumann et al., 2016).

It might thus be hypothesized that the inherent authigenic mineral precipitation can eventually ‘freeze’ the degradation process and preserve in the concretion at least some of the OM that initially fueled its formation, possibly along with biomarkers for the ancient biodegrading microorganisms. Some work has been performed in our lab over the last years to test this assumption. Lipid biomarkers were identified and quantified, *inter alia*, in Lower Jurassic concretions from Buttenheim (Bavaria, Lias δ, Pliensbachian; Thiel & Hoppert, 2018; Fig. 1, left) and Hondelage (Lower Saxony; Lias ε, Posidonia shale; Meyer, 2017; Fig. 1, right).

Particular attention was paid to whether the contained organic molecules actually differ qualitatively and/or quantitatively between concretions and the immediate host rocks – an important question that has rarely been investigated so far (Lengger et al., 2017; Plet et al., 2020).

A variety of molecular fossils, including *n*-alkanes, steranes, hopanes, carboxylic acids, aromatic hopanoids, isorenieratane and α-tocopherol, were preserved in the concretions studied. It was found that the Lower Jurassic materials preserve both, traits of the marine sediments in which they once formed, and individual diagenetic features related to the formation of the concretions.

The Hondelage concretions showed a depletion of C_{org} (mean of 5.4 wt.%, carbonate-free matter) compared to their host rocks (mean of 20.1 wt.%) suggesting a degradation of OM in the concretions through microbial activity. Similarly, depleted $\delta^{13}C_{carbonate}$ values (mean of -16.7 ‰) compared to the host rocks (mean of -7.4 ‰) point to intense bacterial sulfate reduction which is further indicated by higher pyrite contents in the concretions.

The Buttenheim samples indicate a background input from largely allochthonous (terrigenous) OM for all samples, and a very low thermal maturity. Some indicators, such as an increased abundance of ββ-hopanoic acids, suggest a lower maturity for the concretions as compared to their immediate clastic host rocks. This may be related to the lithology, but also to the input and rapid cementation of microbial OM that has been freshly produced during the formation of the concretions. Nonetheless, hydrocarbons (*n*-alkanes, hopanes etc.) represent a uniform background signal present in similar absolute amounts in the host rock and the concretions (see also Lengger et al., 2017). In contrast, fatty acids and α,ω-diacids are up to an order more abundant in the latter (Fig. 2). Such a difference is also observed in the concretions from Hondelage (see also Pearson et al., 2005).

It is suggested that these fatty acyl compounds derived from an alkyl-rich sedimentary OM where carboxylic acids released through lipids hydrolysis were intermittently precipitated as their Ca-salts (Hecht, 1935; Berner, 1968). During shallow burial, these substances may have provided (i) a steadily flowing energy source for sedimentary microbes, (ii) a source of carbonate ions, and (iii) a source of Ca-ions. All these factors may have promoted mineral precipitation that, probably in concert with other factors, eventually constituted the concretions. The tight association of carboxylic acids with carbonate-precipitating and, in particular, concretion-forming settings is obvious and should be tested by further studies and/or suitable experiments (see also Suess, 1970; Frye and Thomas, 1993).

Acknowledgments

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Figures

Fig. 1. left, concretion from Buttenheim (Lias δ, Pliensbachian); right, concretion from Hondelage *in situ* (Lias ε, Posidonia shale).

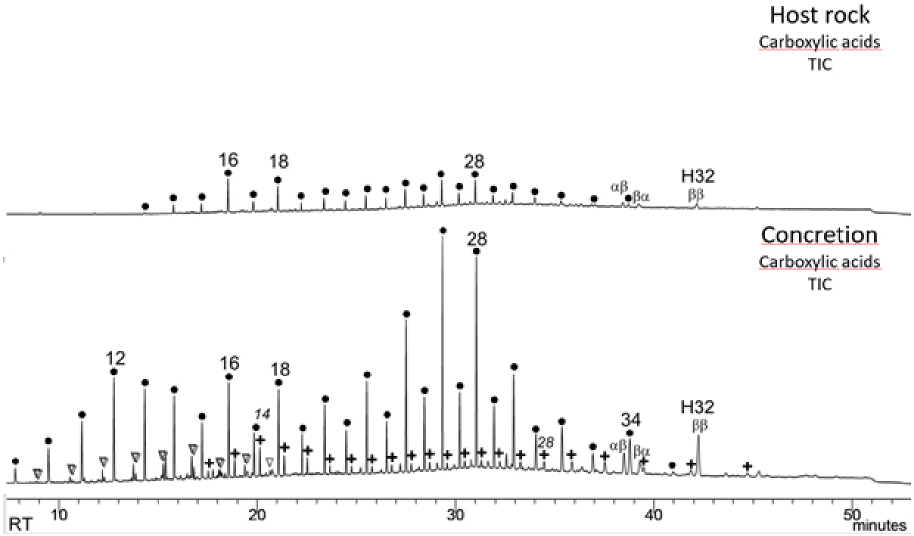

Fig. 2. GC–MS chromatograms (total ion currents, TIC) of carboxlic acid (FA) fractions (methyl ester derivatives) from a Buttenheim concretion (bottom) and their immediate clastic host rock (top). Chromatograms are approximately adjusted to compound abundances in the HCl-decarbonized residues. Filled circles = saturated *n*-fatty acids, numbers refer to carbon numbers; open triangles = *i*- and *ai*-fatty acids (bacterial source); crosses = a,ω-dicarboxylic acids (unknown source), numbers in italics refer to carbon numbers of a,ω-dicarboxylic acids; H32, αβ, βα, ββ = bishomohopanoic acid isomers (22*R*) with the respective 17(H),21(H)-stereochemistry (bacterial source). Data from Thiel and Hoppert (2018).

The UNESCO world heritage “Messel Pit Fossil Site” – taphonomical issues

Sonja Wedmann

Senckenberg Research Station Grube Messel, Senckenberg Research Institute and Natural History Museum Frankfurt/Main, Markstasse 35, 64409 Messel, Germany
e-mail: sonja.wedmann@senckenberg.de

The Fossillagerstätte „Messel Pit Fossil Site” is located in the state of Hesse (Germany) about 20 km southeast of Frankfurt am Main. Many extraordinarily well-preserved fossils have been found in this Konservat-Lagerstätte (e.g. Schaal & Ziegler 1992; Gruber & Micklich 2007; Smith et al. 2018), and since 1995 it is inscribed on the UNESCO world heritage list. The site is presently a large pit with a diameter of about 1 km X 0.7 km, and some 60 m deep. The fossiliferous sediments, called oil-shale, are finely laminated claystone sediments rich in organic substance. These oil-shale sediments were deposited in a former meromictic lake whose water column was permanently stratified into the upper mixolimnion and lower monimolimnion; the lake existed for about one million years (Goth 1990). A drilling project conducted in the year 2001 showed that the former Lake Messel was a maar lake (Schulz et al. 2002, Felder & Harms 2004) which was created by phreatomagmatic eruptions about 48.06 million years ago (Mertz & Renne 2005; Lenz et al. 2015, Kaboth-Bahr et al. in revision 2023). The original diameter of the former maar lake was bigger than the present outcrop. Felder & Harms (2004) estimated an amount of post-Eocene erosion of 50–100 m, Büchel & Schaal (2018) estimated a more extensive amount of post-Eocene erosion of approximately 300 m. This implies that the shore areas of the former lake are lost, because the “oil-shale”-sediments formed exclusively in the lake’s deep, anoxic region, the monimolimnion (Goth 1990).

The Messel oil-shale contains a burial community (taphocoenosis) of plants and animals which inhabited either the former maar lake itself, or lived in the former shore area, or in habitats surrounding the lake (e. g. Wuttke et al. 2018). All organisms which typically live in the littoral zone had to get somehow transported into the monimolimnion to be preserved as fossils. All terrestrial organisms had first to get into the lake, before they could be transferred into the monimolimnion of former Lake Messel to become preserved as fossils.

The excavations of Senckenberg in Messel in the year 2022 yielded the distribution of fossils as recorded in the excavation log as shown in Fig. 1. Especially the proportions of plants and insects may vary. Among the vertebrates, fishes are by far the most common fossils; in 2022 they made up 97 % of the vertebrate fossils, which is to be expected in a former lake. Except for fishes, 13 other vertebrate fossils were found in 2022, among them dominated fossils of birds (including several isolated feathers).

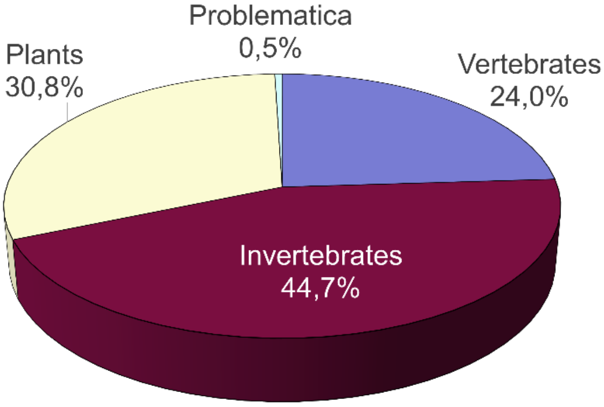

Fig. 1: Distribution of fossils recorded in the excavation log of the Senckenberg excavation activity in the Messel Pit in the year 2022, conducted at digging site F9, in the layers 185 to 230 cm above local marker horizon alpha. Problematica are vertebrate remains which could not be determined to a certain vertebrate taxon in the field. N= 1831.

In Messel the fossils of birds and of bats are found relatively often (Harms 1999), especially in comparison to other fossil sites (Franzen et al. 1982). Among mammals, bats are by far the most often found group in Messel (Harms 1999). More than 700 bat fossils are known from Messel and most of their skeletons are rather complete (Wuttke et al. 2018). How and why the bats, and essentially all terrestrial vertebrates died and became preserved in former Lake Messel is still under discussion. Maybe simply the extremely low rate of sedimentation (between 0.1 and 0.2 mm per year in the oil-shale after Goth (1990), around 0.2 mm per year after Kaboth-Bahr et al. (in revision 2023)) leads to the false impression of special abundance (Wuttke et al. 2018). For the arboreal lizard *Geiseltaliellus* it is suggested that the found specimens did not die near the shore, but drowned near the middle of the lake (Smith & Wuttke 2012). Or there might be other causes of death, like toxic gases or carbon dioxide (Franzen et al. 1982; Franzen & Köster 1994; Habersetzer et al. 1994) or the drinking of water poisoned by toxic cyano-bacteria (Koenigswald et al. 2004).

Concerning body fossils of insects, the most numerous finds are terrestrial beetles (Coleoptera), among them especially weevils. This is reflected in the composition of insects in the collections, e.g. in the Senckenberg Messel insect collection where beetles comprise around 60% of the inventoried specimens (Lutz 1990, Wedmann 2018). Second to beetles are cases of aquatic caddisfly larvae (Trichoptera) (Wedmann 2018). Field studies in selected years between 2008 to 2015 regarding the frequencies of discovery of insects (including also insect remains which cannot be identified further) revealed that cases of caddisfly larvae in some sites can amount to 20%, in one site up to 30% of all insect remains. In Fig. 2 two results from field studies in the years 2011 (Fig. 2A) and 2012 (Fig. 2B) are presented exemplarily. During each study period, all fossils from an excavation site that could be identified as possible insect remains were recorded and identified in the field as far as possible. The excavation team investigated representative samples of more than 1000 fossils from different excavation sites in different years, to enable an as unaffected comparison as possible between different excavation sites. Especially for the abundance of cases of caddisflies a pattern seems to emerge. Caddisfly-cases are consistently rare in excavation sites located in the center of the Messel Pit, in digging site I 14 (Fig. 2A), and are considerably more often found in excavation sites located more towards the margin of the Messel pit, in the digging sites E 8/9, G 8/9 or G 8 (G 8 shown in Fig. 2B). Digging site L 12/13 yielded 15% caddisfly cases. A possible explanation for these different frequencies might be the different distance from the shore, because caddisfly larvae are shore-dwellers and their cases cannot be transported easily. Concerning beetle remains (Coleoptera), the proportion of remains identifiable as beetles is larger in the center and less high at the margin. But it should be kept in mind that also a time-factor might influence the different frequencies. In all digging-sites nearer to the margin only layers around marker horizon alpha could be investigated, while at digging site I 14, near the center, only the much younger layers around marker horizon M could be investigated, because only the exposed uppermost layers are accessible for excavation.

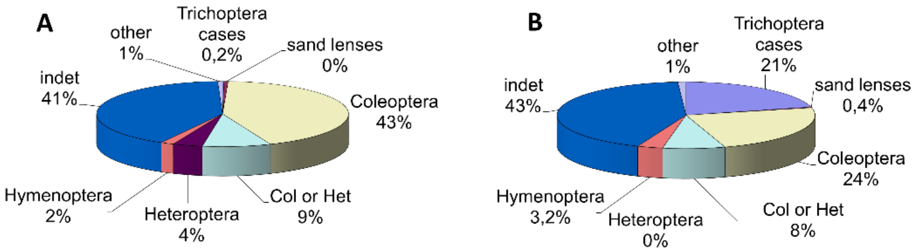

Fig. 2: Results of field studies in the Messel Pit investigating the frequencies of different groups among samples of roughly 1000 insect remains. **A:** Composition of insect remains from excavation site I 14 (located near the lake center), layer 135-220 cm above local marker horizon M, N = 1130 fossils, year of data acquisition: 2011. **B:** Composition of insect remains from excavation site G 8 (located nearer the lake margin), layer 10 cm below to 70 cm above above local marker horizon alpha, N = 1068 fossils, year of data acquisition: 2012.

Already Franzen et al. (1982) noted that apparently size-sorting processes have an impact on the composition of sizes not only of the found vertebrates, but also of the plants. Neither large terrestrial vertebrates nor trunks of trees have been found in Messel (e. g. Franzen et al. 1982). The presence of larger inflows which influenced the currents in the former lake has been proposed mainly on the base of alignment of the longitudinal axis of fish fossils with directions of the flow changing through time from northeast to northwest (e. g. Franzen et al. 1982). An inflow from northeastern direction was also supported by Lutz (1990) who investigated the insect taphocoenosis. But in my opinion the currently available, much larger collection of fossil insects does not include many reliably allochthonous taxa which would support the assumption of a large inflow (own observation SW 2023). One strong argument by Lutz (1990) in favor of an inflow was the presence of a certain aquatic beetle group, the Eubrianacinae (Coleoptera, Psephenidae). But Wedmann et al. (2011) argued that these beetles should be rather considered an autochthonous element of former Lake Messel because of their (for aquatic taxa) high numbers and relative wide occurrence. Based on the ecology of extant lake-dwelling eubrianacine larvae, this would imply that probably former Lake Messel had a beach area where some rocks or stones were present, and it would support the assumption that former Lake Messel was quite large (Wedmann et al. 2011). Almost none of the other aquatic insect groups found in Messel can be considered reliably allochthonous. Considering the insects, in my opinion there are no convincing arguments to favor big stable inlets into former Lake Messel. Based on extensive study of the fish fauna, Micklich (2012) concludes that Lake Messel was not steadily isolated from external water bodies, and that water exchange occurred probably during occasional periods of high water level, and not necessarily via fixed inlets and outlets.

A very different taphonomic issue which has been investigated only rarely is the presence of spiculites in the Messel Pit, which distributions were studied by Richter & Baszio (2009). They demonstrate that spiculites (sediments containing many sponge spicules) occur with a relative wide distribution in the eastern part of the Messel pit, and they are present also in certain layers in different drilling cores, including the research drilling FB 2001. Due to the scarcity of data it is very difficult to draw ecological inferences.

The local marker horizons found in the Messel Pit are of utmost importance for the correlation of different fossil sites, and they are used as references for the relative stratigraphic positions of fossils. Franzen et al. (1982) described marker horizons alpha, beta and gamma, some years later Schaal et al. (1987) added marker horizon M. There are many open questions concerning the origin of the different local marker horizons. Some new research is being done in this regard (e.g. Liesegang & Wuttke 2022; Kaboth-Bahr et al. in revision), but it goes beyond the scope of this paper to discuss this in more detail.

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Adaptive evolution of hexactinellid sponges from the Cambrian black shale Lagerstätten of China

Hao Yun[1, *], Cui Luo[2], Dorte Janussen[3], Xingliang Zhang[1], Joachim Reitner[4]

[1] State Key Laboratory of Continental Dynamics and Shaanxi Key Laboratory of Early Life and Environments, Department of Geology, Northwest University, Xi'an 710069, China

[2] State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology & Center for Excellence in Life and Paleoenvironment, Chinese Academy of Sciences, Nanjing 210008, China

[3] Senckenberg Research Institute and Nature Museum, Frankfurt am Main 60325, Germany

[4] Göttingen Academy of Sciences and Humanities in Lower Saxony, Göttingen 37073 and Department of Geobiology, Centre of Geosciences, University of Göttingen, Göttingen 37077, Germany

[*] Corresponding author: yunhao@nwu.edu.cn

Black shales are mostly deposited in dysoxic to anoxic marine environments that inhospitable to most benthic animals (Zhou and Jiang, 2009; Oschmann, 2011; Jin et al., 2016). However, sponge communities dominated by diverse hexactinellids (more than 17 genera) were discovered from the Cambrian black shale Lagerstätten (Niutitang, Shuijingtuo, Hetang, and Huangboling formations; Stages 2 to 4 of Cambrian) in southern China (Steiner et al., 1993; Yuan et al., 2002; Wu et al., 2005; Yang et al., 2010; Luo et al., 2021). It is generally believed that sponges (especially hexactinellids) have a strong tolerance to deep sea and low oxygen environments (Tabachnick, 1991); related biological experiments have also shown that living sponges can survive in low oxygen conditions at 0.5-4% of present atmospheric level (Mills et al., 2014; Micaroni et al., 2022). Nevertheless, these sponges are struggling within low-oxygen conditions and often rely on adaptive specializations and/or coexisted anaerobic microorganisms to maintain metabolism (Hoffmann et al., 2005; Schonberg, 2021; Micaroni et al., 2022; Yun et al., 2022, 2023). Therefore, the flourishing sponge community in Cambrian black shales reflect an intriguing adaptive evolution of sponges.

The adaptive specialization of black shale sponges is well revealed by two articulated fossil species: *Sanshapentella tentoriformis* Yun et al., 2022 and *Hyalosinica archaica* Mehl and Reitner in Steiner *et al.*, 1993 from the Cambrian Stage 3 Shuijingtuo and Niutitang formations (*ca.* 518 Ma), respectively (Fig. 1). The *S. tentoriformis* has a unique dendriform body that composed of a columnar trunk and multiple conical high projections; each projection is framed by a quadripod-shaped dermal pentactine spicules. This body shape likely reflects a consequence of adaptation that help enlarging the surface area-volume ratio and then maintaining an effective using of oxygen and a low energy cost in the hypoxic condition. The *H. archaica* possesses an ovoid main body and an impressive long, ropelike stalk, representing the oldest extinct taxon that took advantage of a long root tuft/stalk to elevate the main body above the sediment surface. The long root tuft links *Hyalosinica* to a series of fossil and recent sponge taxa (e.g., Reid, 1968; Mehl and Hauschke, 1995; Janussen, 2014) and indicates a parallel evolution within the Hexactinellida in response to two types of special environmental pressures: 1) frequent currents from different directions and 2) dysoxia.

Different morphological groups of the sponge bodies are discerned from 15 hexactinellid genera that preserved in the Cambrian black shales (Fig. 2). The common sponge bodies, including ovoid and cylindrical shapes, are characterized with a relatively smooth wall and mostly a conspicuous osculum at the top (represented by *Diagoniella*, *Protospongia*, and *Triticispongia*). Some cylindrical bodies have an uneven body wall that characterized by numerous small, circular parietal gaps (represented by *Hintzespongia*) and/or a serrated oscular margin (represented by *Lantianospongia*). The above-mentioned dendriform (and tent-like) *S. tentoriformis* and long stalk-bearing *H. archaica* represent the most uncommon body shapes within the Cambrian sponge communities. Generally, the ovoid and cylindrical bodies were adapted to a large spectrum of environments and thus are 'one size fits all' in the adaptive evolution. However, the uncommon bodies, such as *Lantianospongia*, *Hyalosinica*, and *Sanshapentella*, are restricted to black shales, indicating that they are adaptive morphological specializations in response to the inhospitable, oxygen-deficient environments.

In conclusion, the Cambrian black shale Lagerstätten of China preserved diverse sponge (mostly hexactinellid) skeletons and bodies that have shed light on the morphology, ecology, and adaptive evolution of the Porifera.

Acknowledgments

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Figures

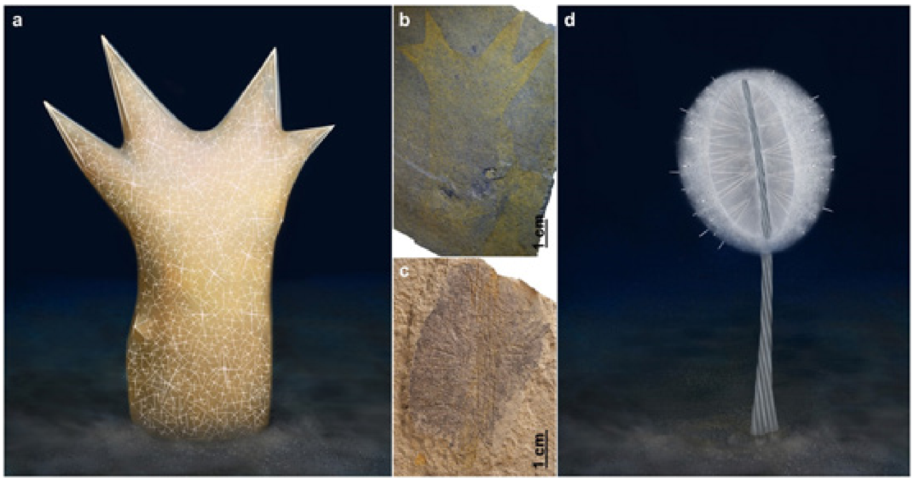

Fig. 1 Articulated sponge fossils from the early Cambrian black shales. (a, b) *Sanshapentella tentoriformis* Yun et al., 2022 from the Shuijingtuo Formation (Cambrian Stage 3; Qingjiang biota) in Hubei Province, China; (c, d) *Hyalosinica archaica* Mehl and Reitner in Steiner et al., 1993 from the Niutitang Formation (Cambrian Stage 3) in Hunan Province, China.

(Fig 2 see next page)

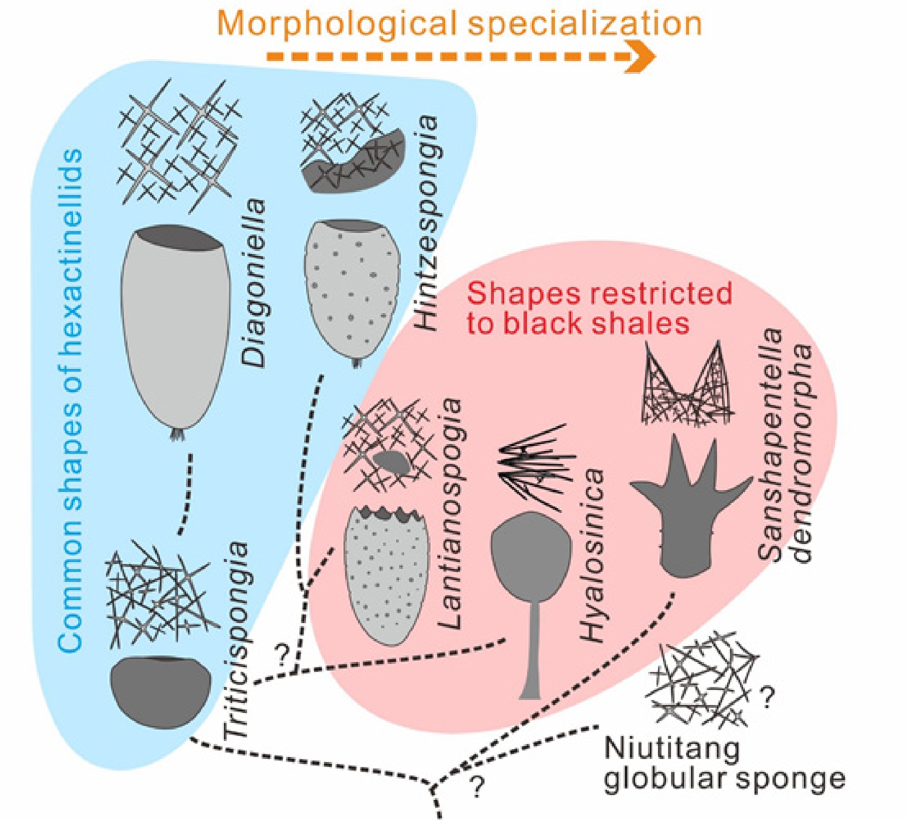

Fig. 2 Morphological specialization and phylogenetic relationship (dashed lines) of representative hexactinellids from the Cambrian black shale Lagerstätten of China.

Thermal maturity of Cambrian Burgess Shale-Type Lagerstätten

Xingliang Zhang and Yuheng Qiao

State Key Laboratory of Continental Dynamics, Shaanxi Key laboratory of Early Life and Environments, Department of Geology, Northwest University, Xi'an 710069, China

Burgess Shale-type (BST) Lagerstätten, in which soft-bodied fossils were preserved as organic carbon films in black shales (Gaines et al., 2008), provide a wealth of information on the early evolution of animals for yielding diverse faunas preserved with soft-tissues (Fig. 1). Geological evidence that are central to understanding the exceptional preservation of these biotas and the paleoenvironments they inhabited may be obscured by the post-depositional alteration due to metamorphism at depth and weathering near the Earth's surface. Over 50 BST Lagerstätten have so far been reported in Cambrian strata worldwide (Gaines, 2014; Muscente et al., 2017), including a high density of such deposits in Cambrian of South China (Zhang et al., 2001, 2008; Fu et al., 2019; Zhu et al., 2019). Paleontological investigations have produced a wealth of knowledge on Cambrian biotas, and geochemical, sedimentary, and taphonomic studies have begun to reveal details of the environments they inhabited and the nature and significance of their exceptional preservation (Zheng et al., 2022). However, geothermal history of BST Lagerstätten has been limitedly investigated. Important progress recently been made using Raman spectroscopy of carbonaceous BST fossils. The maximum metamorphic temperatures of the Spence Shale (Marshall et al., 2012), Burgess Shale and the Sirius Passet Lagerstätten (Topper et al., 2018) were determined using the Beyssac Raman geothermometer (Beyssac et al., 2002, 2003) on carbonaceous material (CM) comprising fossils. All three of these previously investigated deposits occur in Laurentia, whereas the burial depth and metamorphic temperatures of BST Lagerstätten from South China and other continents have not yet been explored. Here we use the Kouketsu Raman geothermometer (Kouketsu et al., 2014) to estimate the peak metamorphic temperatures experienced by fossils from the two Lagerstätten in their type areas, and tested the results by reconstructs burial history of the two Lagerstätten through basin modeling (Basinmod).

Raman geothermometer analyses of fossil carbonaceous material demonstrate that peak temperatures varied across localities with different burial depth (Fig. 2). Chengjiang fossils from the two productive localities (Sanjiezi and Tanglipo) were thermally altered at a peak temperature of 308 ± 50 °C and 301 ± 50 °C, respectively. Specimens collected from the Hongjunshao locality, ~100 km northeast of Kunming City, are much less weathered and have more intense and smoother Raman spectra that generate peak temperatures with a narrow range, averages being 236 ± 21°C. The temperatures calculated from the two Qingjiang fossil localities (fresh samples) are somewhat different, the average being 238 ± 21 °C for the Jinyangkou samples and 271 ± 15 °C for the Tianzhushan samples, collected ~30 km west of the Jinyangkou section. Basin modeling demonstrate that the most fossiliferous sections of the Chengjiang have experienced a similar burial history and were buried at a maximum depth of ~8500 m in the early Triassic, corresponding to ~300°C, while the type locality of the Qingjiang biota was buried at a maximum depth of ~8700 m in the early Jurassic, corresponding to ~240°C (Fig. 3). In the Tianzhushan section, ~30 km west of the type locality of the Qingjiang biota, the black shales of the Shuijingtuo Formation that yield Qingjiang fossils experienced a parallel burial history. However, its maximum burial depth reached ~9700 m during the early Jurassic, over 1000 m deeper than the Jinyangkou section, and hence its peak metamorphic temperature reached ~270 °C. It is evident that the results of Raman geothermometer calculations are in good agreement with the peak metamorphic temperatures estimated by basin modeling where data are available.

Integrated burial history and Raman spectroscopic analyses indicate that the peak metamorphic temperatures experienced by the Chengjiang and Qingjiang biotas varied among localities for differences in burial history and maximum depth: temperatures calculated from three localities of the Chengjiang biota are 308 ± 50 °C, 301 ± 50 °C, and 236 ± 21 °C, while those calculated for two localities of the Qingjiang biota are 271 ± 15 °C and 238 ± 22 °C (Fig. 2). In comparison with other BST biotas, the Chengjiang deposit is less thermally mature, but outcrops at the most productive localities are strongly weathered. By contrast, the type locality of the Qingjiang biota (Jinyangkou) is the least mature of BST deposits yet studied. Along with the Chengjiang and the Burgess Shale, the Qingjiang biota lies in an elite tier of BST Lagerstätten representing the highest diversity and fidelity of preservation of labile tissues. Not only has the Qingjiang experienced significantly lower peak burial temperatures than other BST deposits, but its fossils have not suffered compositional alteration by weathering (Fig. 1). Therefore, the Qingjiang biota appears to hold the most promise for resolving longstanding questions surrounding the preservation of exceptional Cambrian biotas and the environments in which they flourished.

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Figures

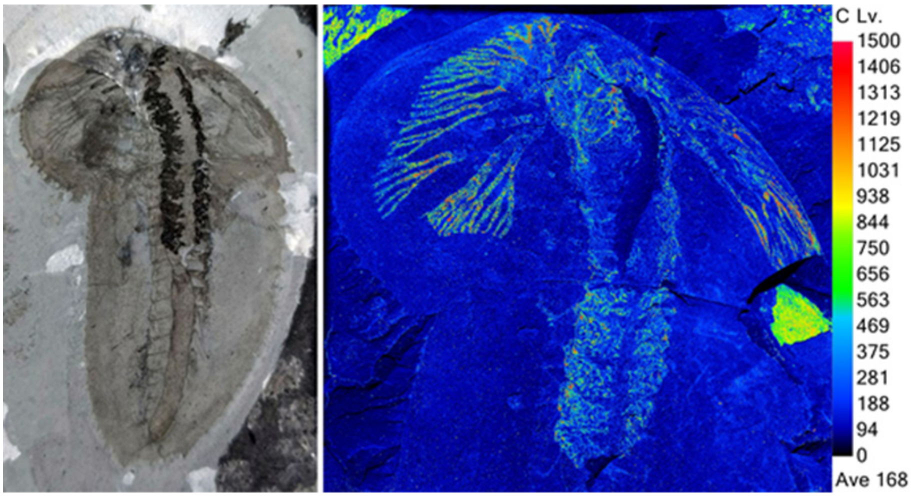

Fig. 1. left, arthropod fossil *Naraoia spinosa* from the Jingyangkou section of the Qingjiang biota (ca 518 Ma), showing ramification pattern of gut diverticular system in head region. Right, EPMA carbon map of anterior part of left, showing that soft tissues were preserved as carbon film and carbon gradient in different tissues.

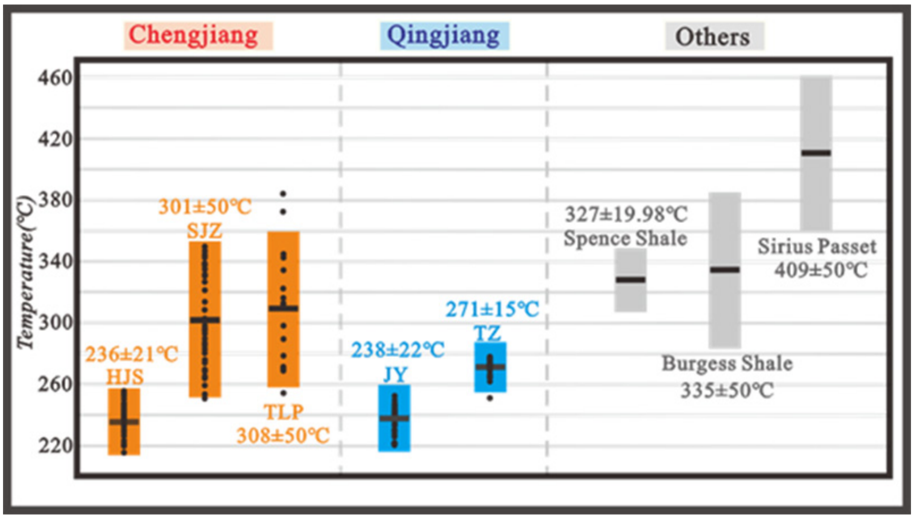

Fig. 2. Peak metamorphic temperatures of Cambrian BST Lagerstätten calculated using Raman geothermometry.

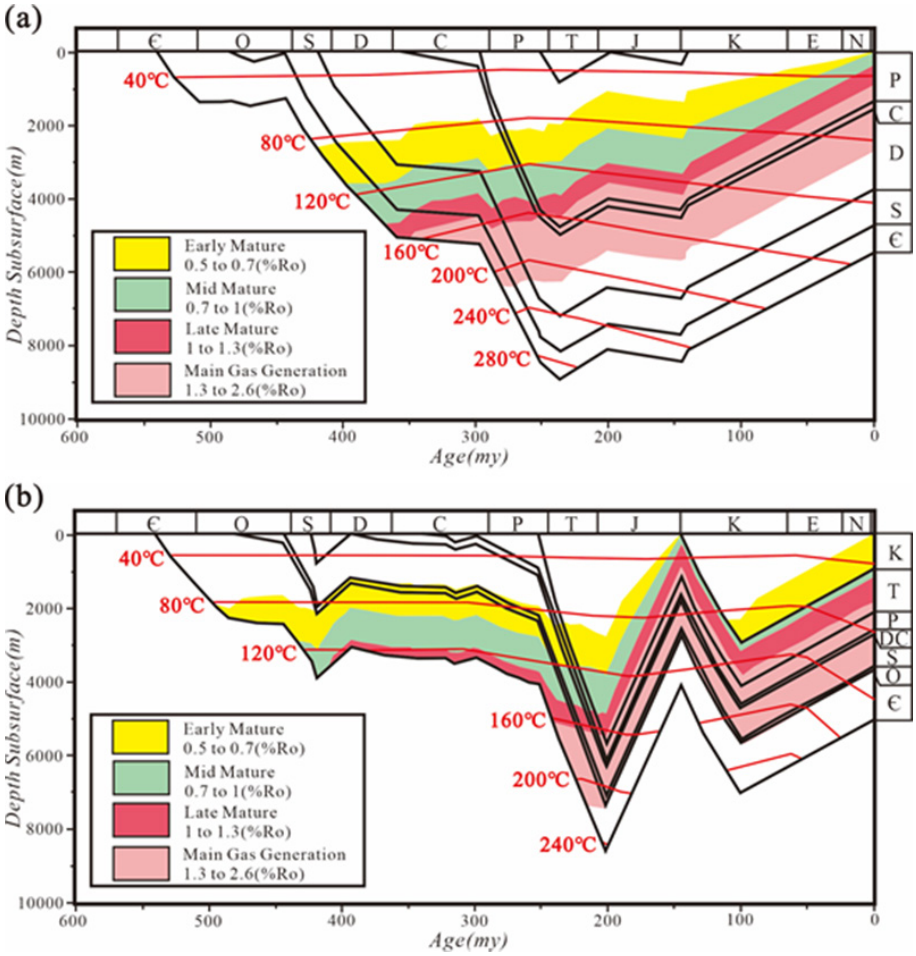

Fig. 3. Burial and thermal history of strata that yield Chengjiang and Qingjiang fossils. Colored strata represent thermal maturity listed in the lower left of each diagram. The lowest line demonstrates burial history of each fossil-bearing formation with the metamorphic temperature labeled in red. (a) The Yu'anshan Formation of the Sanjiezi section reached a maximum burial depth of ~8500 m and a peak burial temperature of nearly 300°C in the early Triassic. (b) The Shuijingtuo Formation at Jinyangkou reached a maximum burial depth of ~8700 m and a maximum burial temperature of ~240 °C during the early Jurassic.