SHEDDING NEW LIGHT ON THE TRIASSIC–JURASSIC TRANSITION IN THE GERMANIC BASIN

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Novel insights from the Bonenburg section & palynotaxonomy and nomenclature of plant microfossils

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Julia Gravendyck

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Selbstständigkeitserklärung

Hiermit bestätige ich, dass ich die vorliegende Arbeit selbstständig und nur unter Zuhilfenahme der angegebenen Literatur angefertigt habe.

This work was carried out between 2017 and 2020 under joined supervision of Prof Dr. Julien B. Bachelier at the Institute of Biology at Freie Universität Berlin in the framework of the Dahlem Research School´s graduate program „Biodiversity, Ecology and Evolution“.

1st reviewer:	Prof. Dr. Julien Bachelier
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> “
> Geologists have a saying – rocks remember.
>
> Neil Armstrong

To all those who have nurtured my thirst for knowledge

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Foreword

This is a cumulative dissertation based on published and unpublished manuscripts.

The references cited in unpublished parts throughout this dissertation are listed together in alphabetical order after chapter 9.

A publication list including contribution statements for each manuscript is provided after the references.

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Summary

The overarching aim of this thesis was to integrate the Bonenburg section and its extremely well-preserved palynoflora within the existing framework of end-Triassic records, and describe and compare its paleoenvironmental changes and vegetation history during the end-Triassic mass extinction.

In 2017, the outcrop of ‘Bonenburg’ in Western Germany came into the spotlight of paleontological studies after the discovery of a new species of reptile potentially representing the oldest fossil of plesiosaurian found worldwide to date. Unfortunately, the lack of age diagnostic macrofossils in the Triletes Beds complicate correlations of this end-Triassic record and the only available fossils for such purposes are organic walled microfossils, i.e. palynomorphs. A part of this thesis was thus to confirm the interpretation of a Rhaetian age (~208–201 Ma) using paylnological data. Additionally, a stratigraphic framework was needed to correlate the locality of these new prominent reptile remains with other contemporaneous sections.

The excellent preservation of palynomorphs in the new Bonenburg section provides informative insights for stratigraphic, taxonomic and paleoecological purposes. Amongst paleoecologists studying the end-Triassic biotic crisis, it is still disputed whether animals and plants were affected alike. It is also disputed whether plants show similarly raised values of extinction as animals do, and whether they indicate severe terrestrial changes that might also have affected marine life, fostering faunal extinction.

To achieve the overarching aim, the thesis pursues three main objectives. (1) To confirm the Rhaetian age of the plesiosaur and to characterise and correlate the new section palynostratigraphically with other European sections. Special focus lies on the potential correlation of the similarly reddish Triletes Beds in the Germanic Basin and Schattwald Beds in the Eiberg Basin. (2) To provide an environmental reconstruction and record of the vegetation history to determine whether and how terrestrial systems were affected by a changing environment. To support palynological applications in the first two objectives as well as future studies, the thesis also attempts to (3) review and revise relevant palynotaxonomy and palynological practices.

To meet the first objective, we used an interdisciplinary approach combining lithology, carbon isotope signatures, and macro- and microfossils of the Bonenburg section. Palynologically, we confirmed the Rhaetian age of the plesiosaur and a major result of our work was the

integration of the qualitative palynostratigraphy. This enabled us to correlate this new locality with other contemporaneous European sections, and also supported correlation of the reddish Triletes Beds from the shallow epicontinental shelf of the Central European Basin, with the Schattwald Beds from the Eiberg Basin, i.e. the western Tethys shelf area.

To address the second objective, we used a detailed quantitative palynological analysis. A palynofacies-zonation was established and compared with the respective palyno-assemblages. These showed similar patterns overall, however, minor differences indicated that palynological assemblages were not exclusively driven by facies change. A novel approach for a Triassic–Jurassic boundary section was applied investigating biodiversity patterns beyond taxonomic richness, which provided new insights into how severely the primary producers were affected by environmental changes. Two intervals of increased environmental stress were indicated, but these preceded the marine extinction. Preliminary results indicated an increased darkening of palynomorph walls at the transition from the Triletes to the Contorta beds, coinciding with the marine extinction event. However, further work is necessary to better understand the underlying causal mechanisms for the palynological ‘dark zone’. An important side observation of this study is the documentation of malformed pollen and spores, and tetrads, which opens an important new perspective for future study of this section.

To approach the third objective, we consulted relevant type-material of Rhaetian key taxa of well-known German and Austrian palynologists (e.g., Potonié, Thiergarth, Schulz, Mädler, and Klaus). The challenges we encountered lead to the revision of existing palynotaxonomic practices as well as the proposal of new practices to aid future taxonomic works. These revised and new practices were then employed to revise several Rhaetian key taxa, which lead to the most extensive and up-to date catalogue of Rhaetian taxonomy of the Germanic Triassic. We also proposed emendation of the *Code of Nomenclature for algae, fungi, and plants*, to rectify a current problem that prevents designation of neotypes. The discussed palynotaxonomy in this thesis therefore not only revised Rhaetian paleopalynology in detail, but made a crucial contribution to paleobotany at large.

Zusammenfassung

Das übergeordnete Ziel dieser Arbeit bestand darin, das neue Bonenburg Profil und seine hervorragend erhaltene Palynoflora in das Rahmenwerk bestehender Korrellationsschemen von spät-Triassischen Archiven zu integrieren und die Paläoumweltveränderungen und Vegetationsgeschichte während des End-Trias-Massenaussterbens zu beschreiben und zu vergleichen.

2017 rückte der Aufschluss „Bonenburg“ in Westdeutschland in das Licht der Öffentlichkeit durch den Fund des weltweit bisher ältesten Plesiosaurier-Fossils. Palynologie (dieser Arbeit) wurde konsultiert, um die Einschätzung eines Rhätischen Alters (~208-201 Ma) zu bestätigen. Darüber hinaus bedurfte es eines stratigraphischen Kontextes, um diese neue Reptilienfundstelle mit anderen zeitgleich abgelagerten Profilen zu korrelieren. Die einzigen verfügbaren Fossilien, die zu Korrelationszwecken genutzt werden können, sind Mikrofossilien mit extrem erhaltungsfähigen Sporopolleninhüllen, die sogenannten Palynomorphen.

Die exzellente Erhaltung der Palynomorphen aus Bonenburg bietet informative Einblicke für stratigraphische, taxonomische und paläoökolologische Zwecke. Unter Paläoökologen, die sich mit dem end-triassische Massenaussterben befassen, ist es immer noch umstritten, ob Tiere und Pflanzen gleichermaßen betroffen waren. Es ist auch umstritten, ob Pflanzen ähnlich erhöhte Werte des Artensterbens wie Tiere zeigen und ob Veränderungen der Landvegetation möglicherweise einen Einfluss auf das marine Faunensterben hatten.

Um das übergeordnete Ziel zu erreichen, verfolgt die Arbeit drei Hauptziele. (1) Bestätigung des Rhätischen Alter des Plesiosauriers, sowie palynostratigraphische Charakterisierung des Bonenburg Profils, um es mit anderen europäischen Profilen zu korrelieren. Besonderer Fokus liegt auf der möglichen Korrelation der gleichsam rot gefärbten Triletes Schichten des Germanischen Beckens und den Schattwald Schichten des Eiberg Beckens. (2) Rekonstruktion der Umweltbedingungen und Vegetationsgeschichte, um zu ermitteln, ob und wie stark terrestrische Systeme von den sich verändernden Umweltbedingungen betroffen waren. Um palynologische Anwendungen relevant für die ersten beiden Ziele sowie zukünftigen Studien zu unterstützen, bemüht sich diese Arbeit außerdem (3) die relevante Palynotaxonomie zu überarbeiten.

Um das erste Ziel zu erfüllen, verfolgten wir einen interdisziplinären Ansatz, für den wir die Lithologie, Kohlenstoff-Isotope, Makro- sowie Mikrofossilien des Bonenburg Profils

untersuchten. Mithilfe der Palynologie bestätigten wir das angenommene Rhätische Alter des Plesiosaurier-Fossils**.** Der wesentliche Beitrag dieser Arbeit liegt in der Integration der qualitativen Palynostratigraphie, die es uns ermöglichte, das neue Profil mit anderen zeitgleich abgelagerten Profilen zu korrelieren. Dies unterstützte auch die Korrelation der Triletes Schichten (Epikontinental-Schelf des mitteleuropäischen Beckens) mit den Schattwald Schichten (westliches Tethys-Schelf des Eiberg-Beckens).

Zur Verfolgung des zweiten Ziels nutzten wir eine detaillierte quantitative palynologische Analyse. Eine Palynafazies-Zonierung wurde etabliert und mit Palynomorphen-Vergesellschaftungen verglichen. Diese Zonierungen zeigten ähnliche Muster, kleinere Unterschiede suggerieren jedoch, dass Palynomorphen-Gesellschaften nicht ausschließlich von Faziesänderungen beeinflusst werden. Ein für die Untersuchung des Trias-Jura-Grenzabschnitt neuartiger Ansatz wurde verwendet, um nicht nur die Biodiversitätsveränderung der Artenzahl allein, sondern mit anderen Biodiversitäts-Indizes zu untersuchen. Unsere neuen Erkenntnisse legen nahe, dass es zwei Intervalle erhöhten Umweltstress gab, die dem marinen Artensterben vorausgingen. Vorläufige Ergebnisse zeigten ein erhöhtes Aufkommen besonders dunkler Palynomorphen. Am Übergang der Contorta Schichten zu den Triletes Schichten, was mit dem marinen Artensterben zusammenfällt. Eine wichtige Nebenbeobachtung dieser Arbeit war die Dokumentation missgebildeter Pollen, Sporen und Tetraden, die eine wichtige neue Perspektive für zukünftige Studien der Umweltveränderungen dieses Zeitabschnitts eröffnen.

Zur Erreichung des dritten Ziels konsultierten wir ein das Typenmaterial Rhätischer Schlüsselformen von prominenten deutschen und österreichischen Palynologen (Potonié, Thiergart, Schulz, Mädler, Klaus). Die Herausforderungen, mit denen wir bei deren Bearbeitung konfrontiert wurden, legte die Überarbeitung bestehender palynotaxonomischer Praktiken nahe. Zusätzlich entwickelten für neue Herangehensweisen, die zukunftige taxonomische Arbeiten erleichtern sollen. Diese überarbeiteten und neuen Praktiken wurden dann eingesetzt, um mehrere Rhätische Schlüsselformen zu revidieren, was in dem bisher umfangreichsten und zeitgemäßen Katalog der Rhät-Palynomorphen der germanischen Trias mündete. Außerdem haben wir eine Änderung des *Code of Nomenclature for algae, fungi, and plants* vorgeschlagen, um eine ein aktuelles Problem zu lösen, welches momentan die Beschreibung von Neotypen für fossile Taxa verhindert. Die von uns diskutierte Palynotaxonomie hat damit nicht nur einen wesentlichen Beitrag für die Paläopalynologie geliefert, sondern auch einen entscheidenden Beitrag für Paläobotanik als großes Ganzes geleistet.

Chapter 1

General Introduction

While many geological ages are described from other countries, the Triassic was first described from Germany by Friedrich von Alberti (1795-1878). He recognised the triad of this time-interval, consisting of the lithologically very distinct 'Buntsandstein', 'Muschelkalk' and 'Keuper, and leading to its subsequent name 'Triassic' from Greek τριάς = three (Meschede 2015). Later, many of the key taxa of the Triassic, especially the Rhaetian and 'Rhaetoliassic', were described from the Germanic Triassic (GT) by R. Potonié and coworkers, Mädler, Schulz, and many others. Today, the GT is one of the prime foci when studying climate change-induced mass extinctions at the Triassic–Jurassic transition.

In 2017, the find of the so far oldest plesiosaurian remains put 'Bonenburg', an outcrop from Northrine-Westfalia, and the GT, once more in the focus of paleontological studies (Sander et al. 2016; Wintrich et al. 2017). Palynology, together with other disciplines, was consulted to support the interpretation of a Rhaetian age of the newly described *Rhaeticosaurus mertensii*. However, a stratigraphic framework was needed to correlate the new locality and its prominent reptile remains with other sections. However, a crucial difficulty in this matter is the lack of fossils, except for palynomorphs, in the so called Triletes Beds in the Germanic Basin. Especially molluscs have their last appearance just before the bottom of the Triletes Beds. Subsequently, it is also still disputed whether the Triletes Beds are an interval of mainly faunal extinction, and whether plants experience severe disturbance like animals. This question is particularly relevant as severe terrestrial changes might also have affected marine life and foster massive faunal extinction.

Due to the excellent preservation of the palynological record in Bonenburg and the exceptionally extensive record of the extinction interval, especially a well recorded transition from the pre-extinction to the extinction interval, this new section also provides a prime spot to investigate the question of mass-extinction during the end-Triassic biotic crisis. It is particularly relevant as palynology can add to the results and insights provided by other disciplines, focusing on vertebrates as well as invertebrates, and tie them together with lithology and geochemistry to better understand this climate-induced crisis. The overarching aim of this thesis is therefore to integrate the Bonenburg section within the existing framework of end-Triassic records, and describe and compare its paleoenvironmental changes and vegetation history during the end-Triassic mass extinction.

In order to provide a solid palynostratigraphic framework and environmental reconstruction, palynotaxonomy is key to all palynological analyses. In comparison to aquatic palynology, palynotaxonomy of terrestrial taxa is lacking unified indexes. Working on the Bonenburg section has shown a patchwork of potentially synonymous and ambiguous taxa. Clear and unambiguous name of taxa and circumscriptions are essential for correlating and comparing results in between different sections. Especially the circumscription of the marker fossil for the base of the Jurassic, *Cerebropollenites thiergartii*, and its distinction from other associated taxa are difficult. Consultation of Rhaetian type material and the coinciding scientific inheritance of Dr. Schulz, an important worker in the Germanic Triassic, revealed further challenges, especially the need for revision of several key taxa, as well as some palynotaxonomic practices. This was needed to make use of the full potential of the Bonenburg section and its excellent palynomorph preservation and to improve the backbone of future palynological studies that are used to evaluate this extinction event.

To achieve the overarching aim, the thesis pursues three main objectives. (1) Characterise the new section palynostratigraphically and correlate it with other European sections, especially the similarly red-stained Schattwald Beds in the Eiberg Basin including the important Global Boundary Stratotype Section and Point (GSSP) Kuhjoch (**Chapter 2**). (2) Provide an environmental reconstruction and evaluation of the vegetation history in order to see whether and how terrestrial systems were affected by a changing environment (**Chapter 3**). (3) Review and revise relevant palynotaxonomy by consulting type material, and comparing it with new insights from the Bonenburg section. Pursuing this goal revealed several challenges inherent to palynology (**Chapter 4**), and for which we proposed new palynotaxonomic practices (**Chapter 4-6**) in order to arrive at an updated palynotaxonomic framework (**Chapter 7**). The revision of the key taxon *Cerebropollenites thiergartii* and related taxa was of particular palynotaxonomic interest (**Chapter 8**).

In view of the above given objectives, the content of this thesis is distributed amongst the chapters as follows:

Chapter 2 establishes a **stratigraphic framework** for the Bonenburg section. With an interdisciplinary approach, the Bonenburg section is studied for its lithology, isotope signatures as well as its macro- and microfossils. This collaborative work presents the qualitative and mainly stratigraphic results of the palynological analysis and ties them together with lithostratigraphy and other biostratigraphies. While especially the latest Rhaetian is barren of any other fossils but palynomorphs, the work provides important information that, together with isotopes, allows the correlation of the Triletes Beds from the shallow epicontinental shelf of the Central European Basin with the Schattwald Beds from the Eiberg Basin, i.e. the western Thetis shelf area.

Chapter 3 depicts the quantitative results of the Bonenburg section by discussing the **macroecological patterns of the terrestrial vegetation history during the end-Triassic biotic crisis in the Central European Basin.** It shows a refined stratigraphic framework comparing palynofacies-zonation with revised palyno-assemblage zonation and discusses the terrestrial vegetation history as suggested by palynology. Comparing biodiversity patterns for the first time beyond taxonomic loss it sheds new light on how severely the primary producers were affected by environmental changes. A key discovery of this study is the observation of aberrant, i.e. malformed pollen and spores, as well as uneven tetrad formations. Through comparison with other sections, the study allows inferences about supra-regional tendencies of change and their implications for other studies focusing on mass extinction.

Chapter 4 provides a **summary of nomenclatural practices** a **discussion of current challenges** when attempting to work with type material, necessary for potential revisions, **and proposes new best practices** on how to conduct and present palynotaxonomy, which is then applied in the next chapters.

Chapter 5 presents the background for a quantitative approach, i.e. **taxon user statistics**, to evaluate them as resources for evaluation of the frequency of names use for taxonomic studies. It **compares two important databases**, the hand-written John Williams Index and Palynodata complemented by Google Scholar, to discuss their suitability for taxonomic studies, and advantages and disadvantages in regard to the study question.

Chapter 6 introduces the new **Citation Share (CS)**, **Citation Rate (CR)** and **Establishment Index (EI)** as three simple metrics representing how (relative) frequently a name is used and how established it is. Analysing quantitative data derived from databases can help evaluate how well a certain name was adopted by the scientific community. This can then inform subsequent taxonomic and nomenclatural practices. For competing names, the EI provides a tool to argue in favour of formal proposal for conservation, protection or rejection of (a) name(s) that are threatened by other names, to ensure taxonomic and nomenclatural stability.

Chapter 7 presents the **systematic palynotaxonomy** of taxa relevant to the Triassic–Jurassic transition in the Germanic Triassic. It applies the new palynotaxonomic practices suggested in chapters 4 to 6, and revisits and summarises important original descriptions, including many first

English translations to facilitate easy reference for future work. It also re-evaluates the type material of Thiergart (1949), Klaus (1960), Mädler (1964), and Schulz (1967), compares it with the Bonenburg material, and discusses problems and the need for revisions where applicable. This also led to the revision of *Cerebropollenites thiergartii* presented in the next chapter (see below). Additionally, this chapter attempts to **solve** a **paradox** encountered **in the *Code of Nomenclature for algae, fungi, and plants*** during the study of holotype material. Especially in Germany many holotypes dating back before the second world war have to be considered lost and even if the material is still available, this thesis has shown that many of them are in such a degraded state, that they are deprived of any informative value. When attempting to escape the situation by designating new types a coded paradox was encountered. In order to rectify the situation a proposal to amend the code of nomenclature made, which is presented in this chapter.

Chapter 8 revises the stratigraphically crucial ***Cerebropollenites thiergartii* and associated taxa** using the theory and methods laid out in the previous chapters. The discrimination of this and associated taxa is important for stratigraphy, especially the definition of the Triassic–Jurassic transition. Former misidentifications and a series of misunderstandings makes unambiguous classification difficult and complicates correlations schemes. The availability of this crucial type from the Schulz inheritance has led to the revision of this taxon and associated taxa as presented in this chapter.

Chapter 9 summarises the key results of this thesis and their significance and novelties palynology and beyond, and closes with important side observations of this study, such as the occurrence of aberrant palynomorphs before and after major crises, and their potential for future studies to re-evaluate the concept of mass extinctions.

Chapter 2

Stratigraphic Framework of the Bonenburg Section – General Palynostratigraphy and Correlation with other Triassic–Jurassic Sections

Martin Schobben*, **Julia Gravendyck**, Franziska Mangels, Ulrich Struck, Robert Bussert, Wolfram M. Kürschner, Dieter Korn, Martin Sander, Martin Aberhan.

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A comparative study of total organic carbon-δ^{13}C signatures in the Triassic–Jurassic transitional beds of the Central European Basin and western Tethys shelf seas

Martin Schobben[1, 2]*, Julia Gravendyck[3], Franziska Mangels[1], Ulrich Struck[1, 4], Robert Bussert[5], Wolfram M. Kürschner[6], Dieter Korn[1], P. Martin Sander[7] and Martin Aberhan[1]

With 8 figures and 1 table

Abstract. Stratigraphic studies are an integral component in understanding the chronology of events that led to the end-Triassic mass extinction, by resolving causal relationships between environmental upheavals and biotic response. Successful correlation of Triassic–Jurassic (Tr–J) successions is complicated by the disappearance of macro-fossils that are otherwise central components in stratigraphic studies. This problem is exacerbated in multiple Tr–J sections situated in Europe, where the so-called "Event Beds" – assumed to demarcate the extinction interval – are virtually devoid of fossils. An alternative stratigraphic approach entails the reconstruction of carbon isotope records, where stratigraphic fluctuations in carbon isotope composition are considered to track changes in the global biogeochemical carbon cycle. The predominance of carbonate-lean sections has prompted the reconstruction of total organic carbon (TOC)-based carbon isotope records. However, bulk rock derived TOC is the diagenetically stabilized remnant of organic components that accumulated on the sea floor, and which can originate from multiple sources. In this study, we assess long-term TOC-based carbon isotope trends at two sites: Bonenburg (Central European Basin) and Kuhjoch (the Tr–J Global Stratotype Section and Point; western Tethys shelf seas). We focus on the TOC ^{13}C-enrichment of the Event Beds with the aim of deciphering stratigraphic fluctuations in relation to their main driver (the exogenic carbon pool versus organic matter source changes). By studying the systematic co-variance of several sedimentary parameters (TOC, total nitrogen [TN], and the palynomorph composition), we infer that the TOC composition is possibly characterized by insignificant organic matter source changes in terms of the marine and terrestrial organic carbon contributions. By contrast, a clay mineralogical shift to more K-depleted minerals as well as the elevated occurrence of wood fragments in the Event Beds suggest a terrestrial organic matter source shift from immature substrates to substrates predominated by "pre-aged" or "fossil organic matter" under a changing continental weathering regime. This outcome urges for reservations when

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Authors' addresses:
[1] Museum für Naturkunde Berlin, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Invalidenstr. 43, 10115 Berlin, Germany
[2] Utrecht University, Department of Earth Sciences, Princetonlaan 8A, 3584 CB Utrecht, The Netherlands
[3] Freie Universität Berlin, Institut für Biologie, Altensteinstr. 6, 14195 Berlin, Germany
[4] Freie Universität Berlin, Institut für Geologische Wissenschaften, Malteserstr. 74–100, 12249 Berlin, Germany
[5] Technische Universität Berlin, Institut für Angewandte Geowissenschaften, Ackerstr. 76, 13355 Berlin, Germany
[6] University of Oslo, Departments of Geosciences, P. O. Box 1047 Blindern 0316 Oslo, Norway
[7] University of Bonn, Steinmann Institute, Division of Paleontology, Nussallee 8, 53115 Bonn, Germany
* Corresponding author: m. a. n.schobben@uu.nl

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interpreting TOC-based carbon isotope records in terms of global C-cycle perturbations, especially when coinciding with lithological and mineralogical changes. On a more positive note, the shift towards positive carbon isotope values appears to be a recurring feature, possibly testifying to a globally significant climate-controlled weathering regime shift.

Key words. carbon cycle, palynostratigraphy, chemostratigraphy, mass extinction, weathering

1. Introduction

The Late Triassic interval is signified by dramatic faunal and floral turnovers on a backdrop of environmental and climatic change (McElwain et al. 1999, Whiteside et al. 2007, Whiteside et al. 2010, van de Schootbrugge et al. 2009, Ruhl et al. 2011, Blumenberg et al. 2016). Contemporaneous intense magmatic activity, known as the Central Atlantic Magmatic Province, has been identified as a potential trigger for these perturbations (e. g., Marzoli et al. 2018). Although being one of the "Big Five" mass extinctions (Raup & Sepkoski 1982), the severity and abruptness of the biodiversity depletion is contested by some authors (e. g., Tanner et al. 2004). Nevertheless, there is evidence of globally elevated latest Triassic extinction rates of benthic organisms (Kiessling et al. 2007), severely disturbed reef ecosystems (Dunhill et al. 2018), selective extinction among hypercalcifying organisms (Hönisch et al. 2012), and a turnover of phytoplankton, marine reptiles, and temnospondyl amphibians (van de Schootbrugge et al. 2007, Wintrich et al. 2017, Konietzko-Meier et al. 2018). These factors altogether rank the event as a pivotal moment in Earth history, which defined the course of evolution and helped shape present-day ecosystems.

Robust stratigraphic frameworks are a necessity to resolve the complex interplay of these environmental changes and consequential biotic responses. Ammonite biozones are used as the official definition for the base of the Jurassic system (von Hillebrandt et al. 2013). Palynostratigraphy is an alternative correlative tool, which has been successfully applied in certain basins (Kuerschner et al. 2007, Bonis et al. 2009). Over the last decades, carbon isotope chemostratigraphy has increasingly gained in importance as the basis for global correlative schemes that link individual Tr–J boundary sections (Palfy et al. 2001, Hesselbo et al. 2002, Guex et al. 2004, Galli et al. 2005, Kuerschner et al. 2007, Ruhl et al. 2009, Bachan et al. 2012, Dal Corso et al. 2014, Yager et al. 2017).

Many studies have focused on pronounced negative shifts in the carbon isotope composition of organic matter, postulating a sudden marine productivity collapse, climate-driven methane hydrate dissociation and volcanism-derived CO_2 as possible triggers for these isotopic signatures (Ward et al. 2001, Palfy et al. 2001, Hesselbo et al. 2002, Whiteside et al. 2010, Ruhl et al. 2011, Dal Corso et al. 2014, Yager et al. 2017). Some authors have also focused on positive carbon isotope excursions observed in sedimentary total organic carbon (TOC) and carbonate rock (Bachan et al. 2012, Yager et al. 2017). The signal-to-noise ratio is low, however, and although compound-specific C isotope analyses confirm a perturbation of the atmosphere–ocean system (Whiteside et al. 2010, Ruhl et al. 2011), noisy records might preclude the faithful recognition of a globally contemporaneous signal (Lindström et al. 2017b). For instance, organic matter source changes might significantly contribute to stratigraphic fluctuations in TOC-based carbon isotope curves and obscure the recognition of signals forced by the exogenic carbon reservoir (Arthur et al. 1985, Popp et al. 1989, van de Schootbrugge et al. 2008). Moreover, high-amplitude sea level fluctuations are a prominent feature of this time interval, which might have caused condensation and sedimentation breaks (Hallam 1981, Hallam & Wignall 1999, Hesselbo et al. 2004), but could also lead to extensive reworking of land-derived sedimentary organic material (Bachan et al. 2012).

A disproportional number of well-studied Tr–J transitional beds are located in Europe (e. g., Jüngst 1928, Morbey 1975, Lund 1977, Karle 1984, Kuerschner et al. 2007, Bonis et al. 2009; 2010, Heunisch et al. 2010, Lindström et al. 2017b, Barth et al. 2018), hence these sites form an excellent basis to test the ubiquity of C isotope signals based on TOC. In addition, correlative schemes based on lithology, macro-fossils and palynomorph assemblages provide an independent stratigraphic framework (von Hillebrandt et al. 2013, Lindström et al. 2017b, Barth et al. 2018).

Many of the European sites exhibit marked lithological changes, with a progradational unit just before the ammonite-defined system boundary that recurs at many localities (Hallam 1981, Hallam & Wignall 1999, Lindström et al. 2017b). Total organic carbon of this lithological unit is accompanied by pronounced higher carbon isotope values in comparison to the bracketing strata. We deem it necessary to better resolve the organic matter sources of the transitional beds by improving our understanding of the sedimentological and mineralogical characteristics of these lithological units. By not only studying the so-called “Event Beds” (Lindström et al. 2017b) but also the bracketing intervals, placed within a wider geographic context, we try to identify general patterns in the stratigraphic record of the TOC-based C isotopes and to separate the effects of variations in local organic matter sources and global contributions of the exogenic carbon pool.

2. Geological setting

2.1. Palaeogeography of the Central European Basin and the western Tethys shelf seas

During the Late Triassic the area that comprises the modern contours of Europe was situated at temperate latitudes (between 30° N and 50° N) and was largely covered by shallow epicontinental seas from which few scattered continental blocks, such as the Rhenish Massif, and Bohemian Massif and the Fennoscandian High emerged (Fig. 1). Important depocenters of these shallow seas were located in the Central European Basin (CEB) and the western Tethyan shelf seas, which appear to have been structurally connected (Bachmann et al. 2008, Barth et al. 2018). Well-studied Tr–J sections of the western Tethyan shelf are mainly known from the intracratonic Kössen and Eiberg basins. One of these sites, the Kuhjoch section, has been assigned as the Global Stratotype Section and Point (GSSP) for the base of the Jurassic System (von Hillebrandt et al. 2013). In NW Europe, relatively larger parts of the Tr–J boundary succession are likely missing or highly condensed (van de Schootbrugge et al. 2008, Lindström et al. 2017b).

2.2. General lithology of the Central European Basin and the western Tethys shelf seas

A Rhaetian transgression induced deposition of shales and deltaic sandstones of the Contorta Beds along the

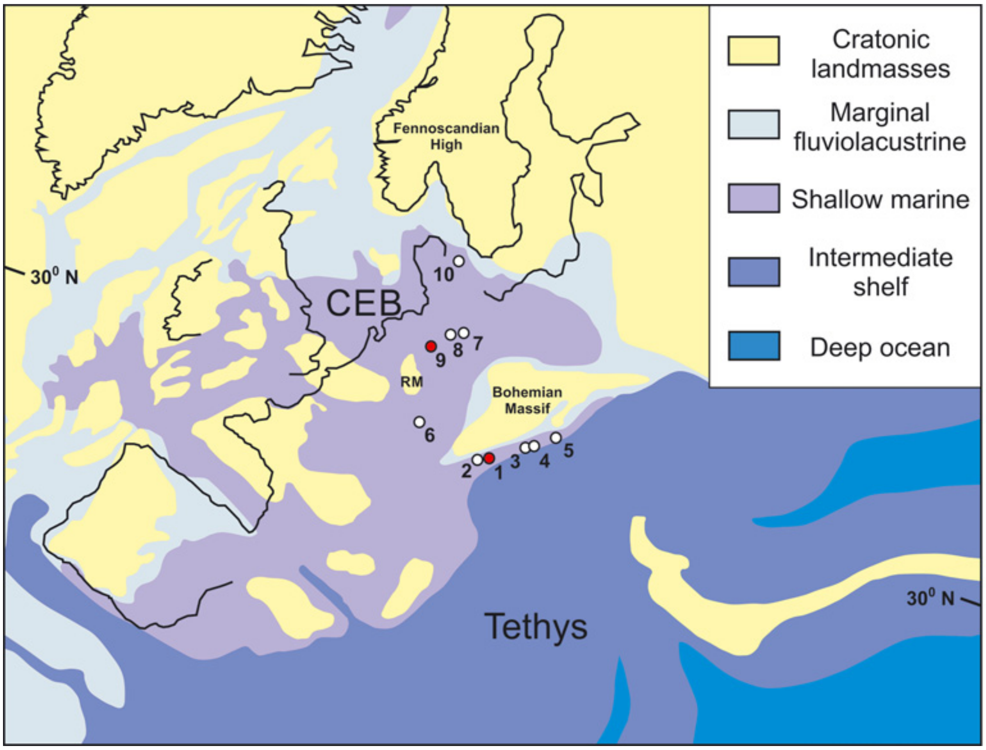

Fig. 1. Geographic reconstruction of the Central European Basin and western Tethys shelf seas in the Late Triassic. 1 – Kuhjoch, 2 – Hochalplgraben, 3 – Kendlbachgraben, 4 – Tiefengraben, 5 – Restentalgraben, 6 – Mingolsheim, 7 – Mariental, 8 – Schandelah, 9 – Bonenburg and 10 – Stenlille (RM = Rhenisch Massif) (modified after: van de Schootbrugge et al. 2009).

north-western half of the CEB, replacing terrestrial lithologies. The Fennoscandian High and the Bohemian Massif are considered the main contributors of detrital sediment input (Nielsen 2003, Bachmann et al. 2008, Fischer et al. 2012, Barth et al. 2018). During the same interval, the western margin of the Tethys Ocean experienced increased siliciclastic sedimentation which reduced the areal extent of previous extensive carbonate platforms (Hauptdolomit Formation/Dachstein Formation) (Hallam 1981, Krystyn et al. 2005, von Hillebrandt et al. 2013). Mixed carbonate and siliciclastic sedimentation (Kössen Formation) continued in intracratonic depressions, such as the Kössen and the Eiberg Basins, which were bordered by reefs at the northern boundary and the southern seaward shelf edge (Oberrhät Limestone). Peak occurrences of marine palynomorphs indicate a Late Triassic sea level highstand in the CEB (Hallam & Wignall 1999, Lindström & Erlström 2007, Barth et al. 2018). In the Eiberg Basin, this interval marks a lithological change, with a distinct dark and bituminous layer, the so-called “T-Bed” (Krystyn et al. 2005, Ruhl et al. 2010).

A subsequent global sea level fall exposed many marine sections around the world (Hallam 1981). However, sedimentation seems uninterrupted in deeper parts of the depocenters, and continued deposition might have been aided by concomitant subsidence (Nielsen 2003, Krystyn et al. 2005, Barth et al. 2018). This change is documented as grey marly deposits of the Tiefengraben Member (Kendlbach Formation) in the Northern Calcareous Alps. In the CEB this drop in sea level has been connected with the formation of a progradational unit of organic matter-poor silt and sandstone, known as the Triletes Beds in Germany and time-equivalent units in Denmark (Lindström et al. 2017b). Another conspicuous and widespread unit in the Eiberg Basin is a bright red clayey marl unit, known as the Schattwald Beds (Lindström et al. 2017b). The similarities of these lithological units of the CEB and western Tethys shelf seas led the previous authors to propose a shared name for these units: the “Event Beds”.

A subsequent transgression has been linked with severe condensation and the lack of several earliest Jurassic ammonite biozones in many sections of the CEB (van de Schootbrugge et al. 2008, Lindström et al. 2017b). By contrast, the sections of western Tethys shelf seas document a return to grey marls of the Tiefengraben Member, which contain the oldest known psiloceratid ammonite (*Psiloceras spelae tirolicus*). Eventually, the ongoing transgression resulted in the formation of limestones of the Breitenberg Member (Kendlbach Formation) (von Hillebrandt et al. 2013). Earliest Jurassic sediments of the CEB are generally of an open marine origin with ammonites belonging to the *Planorbis* biozone (Psilonotenton Formation) (e. g., Wetzel 1929, Blind 1963, Bloos 1999, van de Schootbrugge et al. 2009, Lindström et al. 2017b).

3. Materials and Methods

3.1. Materials

The Tr–J transitional beds of the Bonenburg and Kuhjoch sections are studied for their sedimentological, palaeontological, and bulk geochemical characteristics as representatives for the CEB and the western Tethys shelf seas, respectively. The Bonenburg site (51.5631° N; 9.0401° E) is an active brick quarry situated 1 km NW of the village of Bonenburg (City of Warburg, Germany). Samples were taken over a 40 m interval with an approximate resolution of 50 cm. The Kuhjoch GSSP site (47.4839° N; 11.5306° E) is located in the western part of the Northern Calcareous Alps (NCA), 25 km NNE of Innsbruck and 5 km ENE of the village of Hinterriss (Austria). This section (~24 m) was sampled over an interval of 9 m at 20 cm intervals (Bonis et al. 2010, von Hillebrandt et al. 2013). In the lab, the surface of the rock samples was removed to prevent contamination with modern organic material, after which the material was ground manually with agate mortar and pestle, except for a few limestones which were ground with a mechanic agate mill.

3.2. Bulk rock biogeochemical analysis

In order to remove the carbonate content, the samples were treated with 2M HCl and left over night to react at room temperature. This procedure was repeated until no further reaction was observed. The residues were repeatedly washed with MilliQ water^{TM} and dried at 40 °C. The de-carbonated samples were analyzed for total organic carbon content and associated carbon isotopic composition with a THERMOFlash AS 11121 elemental analyzer linked to a THERMO/Finnigan conflo interface (at the Museum für Naturkunde, Berlin). A separate analysis on untreated sample material was carried out to obtain total nitrogen (TN) composition. The analytical precision was monitored by a lab-internal standard (peptone) and yielded relative standard deviations (RSDs) of 3 % for the C and N concentration and 0.05‰ (2SD) for C isotope composition. All carbon isotope measurements are reported in standard delta notation relative to VPDB. Obtained TOC values of de-carbonated substrates were corrected for weight-loss during acid digestion. These analyses were complemented with published carbon isotope data of the Mingolsheim core (Quan et al. 2008), Stenlille core (Lindström et al. 2015), Mariental core (van de Schootbrugge et al. 2013), Schandelah core (van de Schootbrugge et al. 2019) and several outcrops of the NCA (Kuhjoch, Restentalgraben, Kendlbachgraben, Hochalplgraben, and Tiefengraben) (Kuerschner et al. 2007, Ruhl et al. 2009). In addition, TOC, TN and percent carbonate mineral data for Kuhjoch were taken from Ruhl et al. (2010).

Whole rock element analyses have been performed at the Museum für Naturkunde Berlin with a Bruker AXS S8 TIGER on fused samples for major elements. The production of the fused pellets required 0.6 g of ground sample, which had been dried at 105 °C, mixed with 3.6 g of di-lithiumtetraborate together with 0.5 to 20 g of ammoniumnitrate (where the amount depends on the oxidation grade). Subsequently, fusion of sample pellets was performed with an OXIFLUX burner chain in Pt/AU crucibles. Precision of elemental analysis was monitored by analyzing a range of international standards, and repeated measurement of standard element concentrations yielded RSDs that are better than 5 %. Element data of the Kuhjoch section are taken from Tanner et al. (2016).

3.3. Microfloral analysis

Forty-four samples were collected from the Bonenburg section, 19 from the Contorta Beds and 13 from the Triletes Beds of the Exter Formation, and 12 from the Psilonotenton Formation. Palynological processing was performed according to standard laboratory protocols at the palynological laboratory of the department of Geoscience, University of Oslo, Norway. Between 5 and 15 g dry sediment from each sample were crushed and a Lycopodium tablet (containing 12 542 spores on average) was added. Alternate treatments with HCl and HF were conducted to remove carbonate and silicate minerals, respectively. The residue was washed with water until pH was neutral and sieved with a 15 µm mesh, treated with heavy liquid solution ($ZnCl_2$) to remove the remaining inorganic residue (e. g., pyrite), and sieved again with a 15 µm mesh. The organic residue was mounted on four slides per sample with Entellan®Neu. The slides are stored in the collections of the department of Geosciences at the University of Oslo. About 300 organic particles and 300 terrestrial palynomorphs were counted per sample for palynofacies and quantitative palynological analyses, respectively. The rest of each slide plus an additional slide were screened for rare species separately from the palynomorph count for qualitative analysis. Palynomorphs were classified mainly based on Nilsson (1958), Klaus (1960), Schulz (1962, 1967), Morbey (1975), Schuurman (1976), Lund (1977), and Pedersen & Lund (1980). A list of all identified morphotaxa is given in the supplement. First (FO) and last (LO) occurrences of stratigraphically important taxa were identified. This dataset was extended with data from previous palynological studies on the Kuhjoch section (Bonis et al. 2009, Schobben 2011).

3.4. Data processing, statistics and visualization

Data processing, statistical data treatment and visualization were performed on the open-source platform R (R Core Team 2018), and were aided by the R packages: ggplot2 (Wickham 2009), gridExtra (Auguie 2017), ggtern (Hamilton 2017) and broman (Broman & Broman 2017). The palynomorph assemblage zones, as suggested by qualitative analysis, were verified quantitatively by constrained clustering analysis using the CONISS-function in Tilia (Grimm 2011). The manuscript was written as a R Markdown document, and was aided by the R packages: knitr (Xie 2014, Xie 2015, Xie 2018) and kfigr (Koohafkan 2015). The R Markdown file as well as the biogeochemical and microfloral data are available as an online supplement.

4. Chemical weathering indices

The emphasis of this study lies on the contributions of changing organic matter sources and their control on $\delta^{13}C_{TOC}$ fluctuations. Hence, tracing changes in the terrigenous organic carbon (OC) flux over time is a prime objective, and can be forced by changes in the parent material or differential weathering intensities. The same processes would also steer stratigraphic changes in clay mineral assemblages, as thermodynamic and kinetic constraints determine the chemical composition of clay minerals formed by the weathering of crystalline rocks at Earth's surface (Nesbitt & Young 1984). In essence, the fundamentals of clay chemical composition can, at least in part, be traced back to the parent material, in which some minerals are susceptible to weathering, such as potash feldspar and plagioclase, whereas others are more resistant to weathering, such as quartz and Ti-bearing oxides. These differences can be traced by the selective removal of soluble elements from the parent material with a classical study of the ratios of elements that are presumed to be soluble and mobile against immobile elements. Immobile elements form hydrolyzates and have a large ionic radius, increasing their tendency to be adsorbed on clay minerals (Buggle et al. 2011). Although processes like authigenic clay mineral formation (potentially aided by bacteria), cation adsorption and sorting effects (Konhauser et al. 2002, Michalopoulos & Aller 2004) can skew these generalized assumptions, first-order trends in these element distributions might still be entrained in the chemistry of marine sedimentary rock. For instance, authigenic clay minerals only compose a small percentage of the total sediment mass in deltaic sediments of the Amazon River (Michalopoulos & Aller 2004). Hence, bulk chemistry of the produced material will primarily be controlled by the sediment source and the weathering intensity. By presenting the molar proportions of Na_2O, K_2O and Al_2O_3 on a ternary coordinate system, we attempt to evaluate changes in the terrestrial clay mineral flux for the Tr–J boundary beds of Kuhjoch and Bonenburg.

5. Results

5.1. Litho- and biostratigraphy Bonenburg

The lithological subdivision and palynological zonation can be used to reconstruct an independent stratigraphic framework, enabling a comparative analysis of the supra-regional significance on facies-dependent $\delta^{13}C_{TOC}$ fluctuations. Biostratigraphic information is derived from macroinvertebrates (ammonites, bivalves, conchostracans) and palynomorphs (Fig. 2). Particularly terrestrial palynomorphs, which make up at least 40 and up to 90 % of the palynomorph samples (Fig. 3), exhibit distinct changes in their relative abundances across the Rhaetian and the Tr–J boundary interval at Bonenburg. In this paper, we only present the palynostratigraphically relevant data and five informal assemblage zones of terrestrial palynomorphs that can be recognised (Fig. 2).

Contorta Beds: Thin-bedded to massive mudstones dominate the Contorta Beds. In the basal part of the unit, mudstones and very fine to fine-grained sandstones form coarsening-upward successions. Beds of heterolithic mudstone and sandstone with trace fossils occur sporadically in the middle and upper part of the unit. Shell pavements of marine bivalves and inarticulate brachiopods, bonebeds, and carbonate concretions are intercalated at irregular intervals (Fig. 2). The mudstones contain pyrite and gypsum throughout, whereas dolomite is largely restricted to the middle and upper part. A shift from dark grey to reddish and brownish sediment colours indicates the contact of the Contorta Beds to the Triletes Beds. Biostratigraphically relevant macroinvertebrates of the Contorta Beds include common occurrences of the Rhaetian bivalve *Rhaetavicula contorta* which is the only macrofossil that can be utilized to correlate the Contorta Beds of the CEB with sequences from the western Tethys (Golebiowski 1990). Two other bivalves, *Protocardia rhaetica* and *Pteromya langportensis*, are shared with coeval Rhaetian deposits of the Penarth Group of Great Britain (Ivimey-Cook et al. 1999, Mander et al. 2008) while *P. rhaetica* is also known from Rhaetian deposits of Winterswijk in the Netherlands (Klompmaker et al. 2010).

The Contorta Beds harbor three bonebeds (Fig. 2), labelled bonebed 1 to 3 (Sander et al. 2016, Wintrich et al. 2017). Bonebed 2, the main bonebed, which is subdivided into two layers, bonebed 2 a and bonebed 2 b, contains a typically Rhaetian vertebrate fauna composed of taxa also known from the Bristol Channel area of SW England (Storrs 1994, Korneisel et al. 2015, Mears et al. 2016, Sander et al. 2016, Wintrich et al. 2017). Stratigraphically informative are the chondrichthyan teeth *Hybodus cloacinus*, *Lissodus minimus*, and *Rhomphaiodon minor* as well as the reptile *Pachystropheus rhaeticus* (Sander et al. 2016, Wintrich et al. 2017). In addition, bonebed 2 has produced numerous isolated plesiosaur vertebrae (Sander et al. 2016, Wintrich et al. 2017) and very large shastasaurid ichthyosaur vertebrae typical of the Rhaetian (Fischer et al. 2014, Lomax et al. 2018). Finally, temnospondyl amphibian remains, including the youngest well-dated non-brachiopoid remains, have been found, suggesting a strong influence of the end-Triassic extinction event on temnospondyl amphibians (Konietzko-Meier et al. 2018). Three metres below bonebed 2, the only known

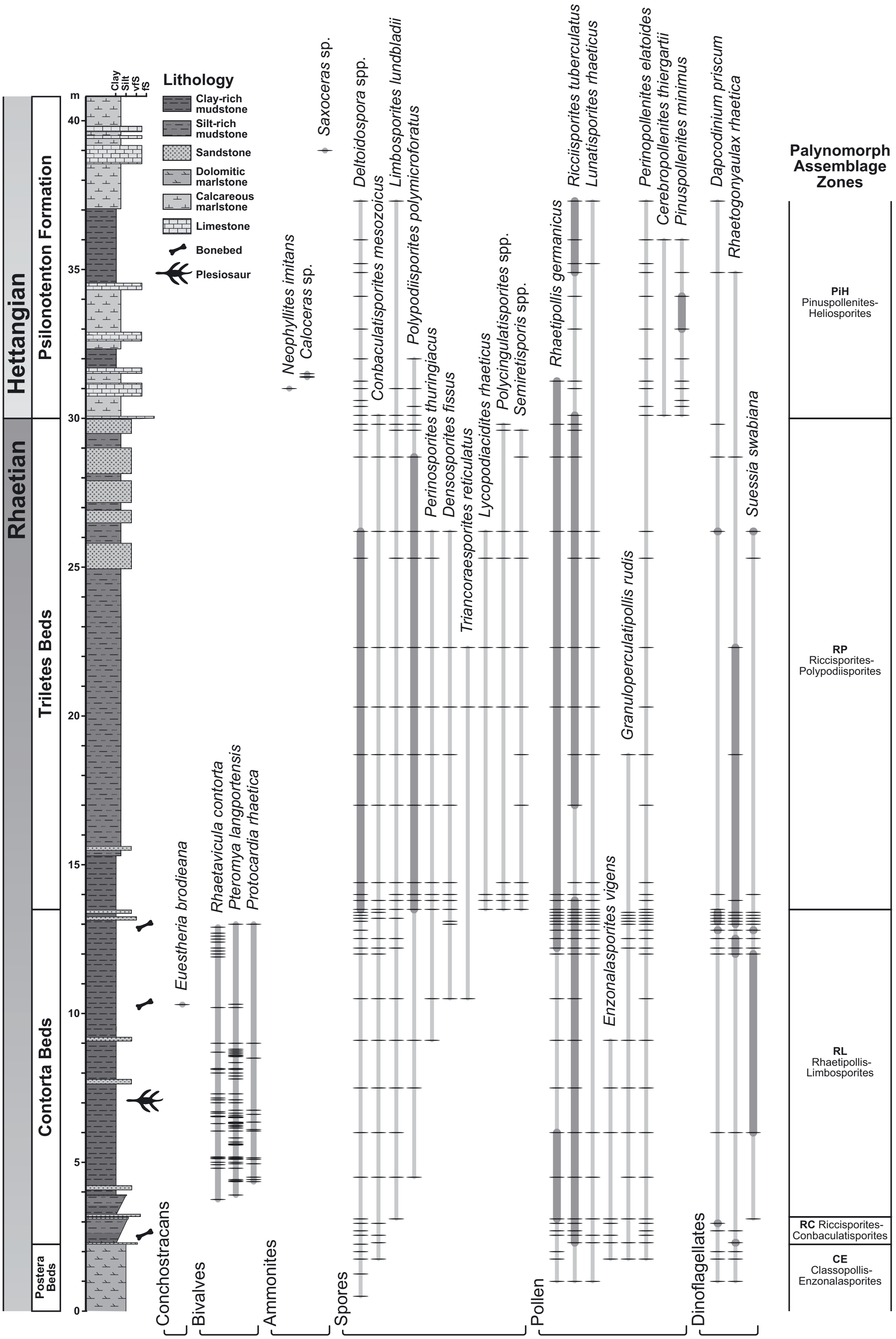

Fig. 2. Lithological column and stratigraphic ranges of key fossils from the Triassic–Jurassic transition at Bonenburg. Horizontal marks indicate the presence of a taxon in a sample. In palynomorph taxon ranges, dark grey segments indicate that the relative abundance of a taxon is higher than 5 % of the terrestrial assemblage (pollen and spores) or the aquatic assemblage (dinoflagellates) respectively. Note variable spacing of analysed samples for invertebrates and palynomorphs.

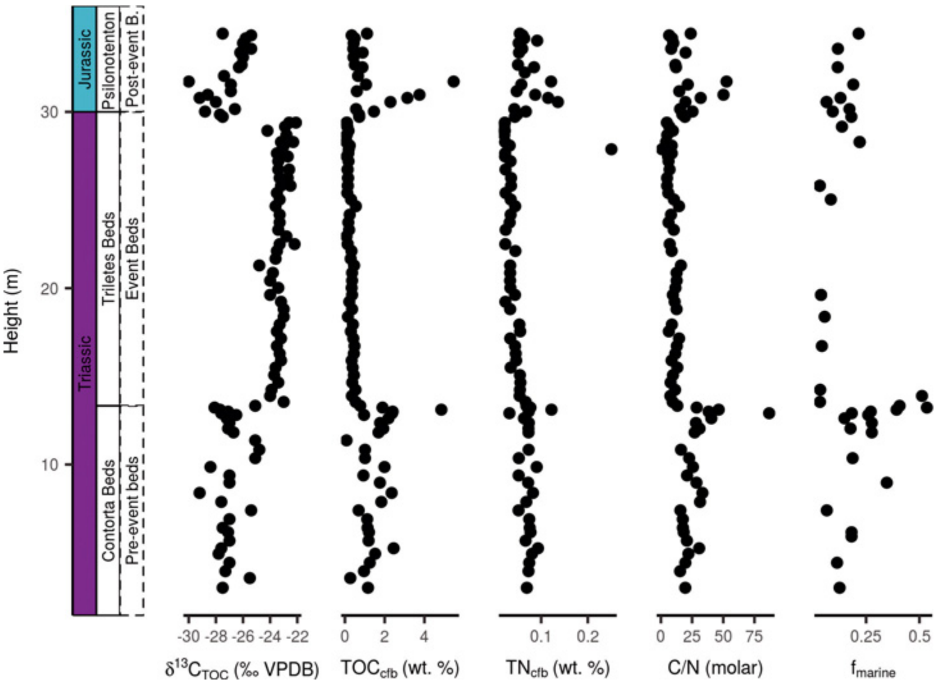

Fig. 3. Stratigraphic plots of total organic carbon-based carbon isotopes, total organic carbon and bulk nitrogen content (cfb stands for carbonate-free basis), molar C to N ratios and the fraction of marine palynomorphs (marine palynomorphs/[marine + terrestrial palynomorphs]) of the Bonenburg section.

Triassic plesiosaur skeleton that unequivocally proves that several lineages of plesiosaurs crossed the Tr–J boundary was recovered (Wintrich et al. 2017).

Immediately below bonebed 2, the chonchostracan *Euestheria brodieana* occurs in several tightly spaced monospecific layers, indicative of the upper Rhaetian *Euestheria brodieana* Zone (Kozur & Weems 2010). Palynologically, the lowermost part of the Contorta Beds (2.2–2.9 m) represents the *Ricciisporites–Conbaculatisporites* Assemblage Zone (RC-Zone; Fig. 2), with the eponymous taxa accompanied by *Classopollis* spp., *Rhaetipollis germanicus* and *Ovalipollis* spp. with the latter three dominating the assemblage. The remainder of the Contorta Beds (2.9–13.5 m) is assigned to the *Rhaetipollis–Limbosporites* Assemblage Zone (RL-Zone; Fig. 2) which is dominated by the eponymous taxa and other pollen such as *Ovalipollis* spp. and *Classopollis* spp. Within the RL-Zone morphotaxa richness increases to 74 taxa because a number of spores – especially the stratigraphically important *Densosporites fissus*, *Perinosporites thuringiacus*, and *Triancoraesporites reticulatus* – have their FOs. Reversely pollen taxa richness decreases and *Granuloperculatisporites rudis* is virtually absent from 9 m up-section with its highest, but only singular, occurrence at 19 m. Of particular stratigraphic importance is the FO of *Limbosporites lundbladii* at the base of this zone.

Triletes Beds (Event Beds): The lower part of the Triletes Beds consists of massive or wavy bedded mudstones and thin sandstones. In the upper part, very fine to fine-grained wavy bedded, ripple cross-bedded and occasionally small-scale cross-bedded sandstones become dominant. Dolomite is present in the lower part of the unit whereas the middle and upper part is calcareous. The biostratigraphic classification of the Triletes Beds is exclusively based on palynomorphs, since macrofossils are absent, except for very few unidentifiable plant remains. The Triletes Beds (13.5–30.0 m) represent the *Ricciisporites–Polypodiisporites* Assemblage Zone (RP-Zone; Fig. 2). With 110 identified taxa, this assemblage zone contains the greatest taxonomic richness and the best preserved palynomorphs within the section. The zone is dominated by spores and characterized by abundant occurrences of *Polypodiisporites polymicroforatus* and *Ricciisporites tuberculatus*. The latter continuously makes up 10–40 % of the terrestrial assemblage while all other pollen, except *Lunatispor-*

ites rhaeticus and *Perinopollenites elatoides*, occur sporadically only. The spore *P. polymicroforatus* makes up 5–20 % of the zone and is joined by a diverse spore assemblage. At the beginning of the last quarter of the Triletes Beds (around 26 m) many palynomorphs have their LOs (e. g., *Densosporites fissus*, *Triancoraesporites reticulatus*, *Perinosporites thuringiacus* and *Lycopodiacidites rhaeticus*), or decline in abundance (*Deltoidospora* spp. and *Concavisporites* spp.). Of biostratigraphic importance is the FO of *Semiretisporis* spp. and *Polycingulatisporites* spp. at the base and their LO at the top of the RP-Zone as well as the LOs of *Densosporites fissus*, *Triancoraesporites reticulatus*, *Perinosporites thuringiacus*, *Lycopodiacidites rhaeticus* at 26 m. Furthermore, palynofacies analyses show a distinct increase in the fraction of wood fragments in this unit.

Psilonotenton Formation: The Triletes Beds are unconformably overlain by an oyster-rich coquinoid limestone bed that belongs to the Psilonotenton Formation. The Tr–J boundary is placed at the base of this erosive oyster shell bed at 30 m, based on ammonoid biostratigraphy and palynoflora (see below). The Psilonotenton Formation consists predominantly of wavy to horizontally bedded marl- and mudstones with only minor limestones and contains marine bivalves and ammonites. The latter allow for a biostratigraphical subdivision of the succession (see discussion for ammonoid zonation and correlations; Section 6.1). Three ammonoid-bearing levels are identified: (1) A single specimen of *Neophyllites imitatum* from the limestone bed at 31 m suggests an attribution of the bed to the second biohorizon of the British standard zonation (Page 2002), indicating the lower part of the *Planorbis* Chronozone. (2) Crushed specimens of *Caloceras* sp. from the limestone bed at 31.5 m indicate a higher position in the *Planorbis* Chronozone (*Johnstoni* Subchronozone). (3) A single specimen of *Saxoceras* sp. from the limestone bed at 39 m allows attribution to the upper part of the *Liassicus* Chronozone (*Laqueus* Subchronozone). This Hettangian part of the section is further characterized palynologically by a dominance of pollen, overall low taxonomic richness and generally poor preservation. *Heliosporites reissingeri* and *Deltoidospora*/*Concavisporites* spp. are the most common spores in this interval. This part of the section is assigned to the *Pinuspollenites-Heliosporites* Assemblage Zone (PiH-Zone; Fig. 2). The previously abundant *Ricciisporites tuberculatus* is substituted by *Classopollis* spp. which markedly increased in abundance from 0–1 % to 36–70 % in the Hettangian part of the section. The lowest part of the PiH-Zone still contains typical elements from the previous zone such as the sporadically occurring *Limbosporites lundbladii* and *Polypodiisporites polymicroforatus*. *Ricciisporites tuberculatus* is still common in the lowermost quantitative Hettangian samples, but strongly decreases in abundance thereafter. The uppermost part of the palynologically studied section is distinguished by the abundant reoccurrence of *Ricciisporites tuberculatus* and scattered occurrences of spores and pollen that were common in the RP Assemblage Zone. Of stratigraphic importance is the FO of *Cerebropollenites thiergartii* and *Pinuspollenites minimus* at the base of the Psilonotenton Formation.

5.2. Litho- and biostratigraphy Kuhjoch

The lithostratigraphy and palynostratigraphy of the Kuhjoch Tr–J GSSP has been intensively studied (e. g., Bonis et al. 2009, von Hillebrandt 2013), and we limit our discussion to the most salient points required to enable a correlation. This correlative scheme differs from the official stratigraphic definitions (Section 2.2 and Fig. 4) in order to test the facies-dependence of the TOC-carbon isotope composition in the Event Beds. The studied interval comprises a ~24 m succession of marine limestone and marl with varying proportions of siliciclastic and carbonate material, and can be decomposed into the following units. 1) **Pre-event Beds**: the topmost 2 m of the Kössen Formation (Eiberg Member), overlain by a dark bituminous layer, with abundant bivalve and fish remains (the so-called "T-Bed"; Krystyn et al. 2005, Ruhl et al. 2010), followed by grey and yellowish-grey marls containing the last occurrences of the ammonoid *Choristoceras marshi* (von Hillebrandt et al. 2013). 2) **Schattwald Beds (Event Beds)**: the lithology changes to a conspicuous bright red-coloured fossil-poor lithology, distinctive for the occurrences of *Polypodiisporites polymicroforatus*, *Ricciisporites tuberculates* and *Deltoidospora* spp. Local tectonics resulted in a minor fault at the top part (2.16 m above the base of this unit), thereby creating a small hiatus. A second outcrop towards the east (Kuhjoch East) of the main site (Kuhjoch West) was excavated, yielding a more gradual transition into the overlying unit. 3) **Post-event Beds**: transition from red to grey marls with thin silt- and sandstone layers more common up-section. At 6.3 m above the top of the Kössen Formation, the

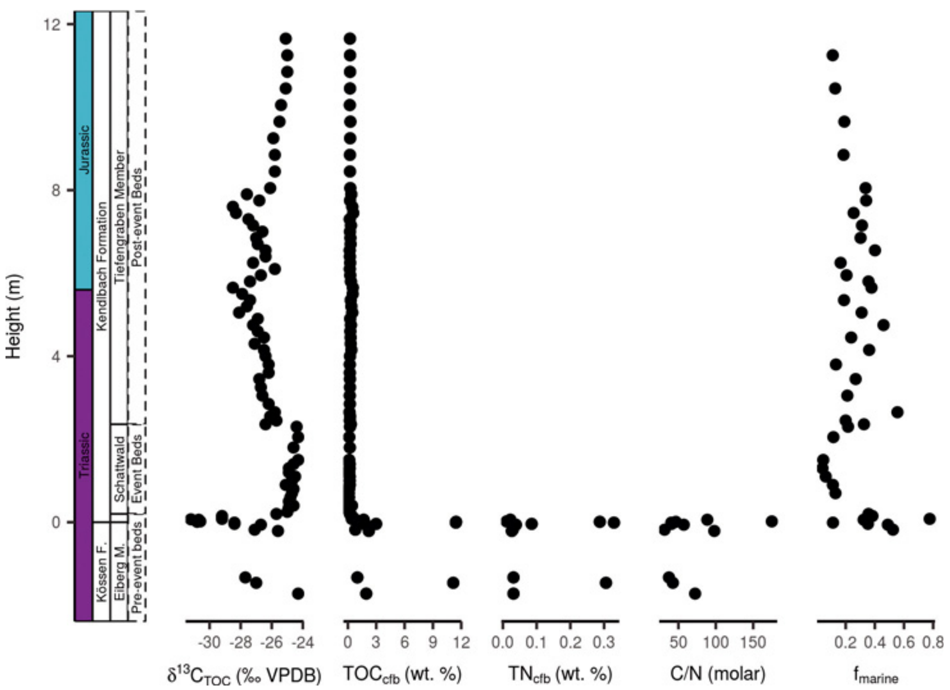

Fig. 4. Stratigraphic plots of total organic carbon-based carbon isotopes, total organic carbon and bulk nitrogen content (cfb stands for carbonate-free basis), molar C to N ratios and the fraction of marine palynomorphs (marine palynomorphs/[marine + terrestrial palynomorphs]) of the Kuhjoch section.

ammonite *Psiloceras spelae tirolicum* appears. The first occurrences of *Cerebropollenites thiergartii* and *Ischyosporites variegatus* are used as informal stratigraphic markers for the Tr–J boundary (von Hillebrandt et al. 2013).

5.3. Comparative mineralogy of the Tr–J transition beds

The Kuhjoch material is relatively more depleted in Na_2O and K_2O content when compared with the Bonenburg sediments, thereby alluding to a different source or local weathering regime (Fig. 5). A shared characteristic of Kuhjoch and Bonenburg is a clear differentiation between the chemical composition of the major lithological units, with the Schattwald and Triletes Beds being the most depleted in K_2O and Na_2O, indicating a higher predominance of K-depleted minerals (e. g., kaolinite) in the mineral assemblage. By contrast, the Hettangian samples of both sites have relatively enriched values of K_2O and Na_2O, indicative of less intense weathering in the source area or a different source of clay mineral production. Most immature are the sediments of the Pre-event Beds of Kuhjoch and the Contorta Beds of Bonenburg. Powder X-ray diffraction of the Bonenburg sediments supplemented by X-ray analyses of <2 µm fractions of selected samples show that the clay mineral assemblage of the Contorta Beds consists of illite (muscovite), chlorite, illite-smectite mixed layers, and kaolinite. In contrast, the Triletes Beds are significantly enriched in kaolinite, whereas in the Psilonotenton Formation the kaolinite content decreases again.

5.4. Bulk rock biogeochemical properties of the Tr–J transition beds

The $\delta^{13}C_{TOC}$ of the oldest beds of the Bonenburg section (Contorta Beds) fluctuates between –29.2 and –24.8‰ (Fig. 3). Above 13.5 m, at the transition of the Contorta Beds to the Triletes Beds, a sharp shift to 3.7‰ higher $\delta^{13}C_{TOC}$ values can be discerned. The up-section interval between 13.5 to 30 m records consistently stable $\delta^{13}C_{TOC}$ of around –23.3‰. A sharp shift to about 3.8‰ lower $\delta^{13}C_{TOC}$ marks the transition to more carbonate-rich strata of the Psilonotenton Formation. The succeeding up-section interval documents ^{13}C-depleted TOC, ranging between –30.0 and –25.4‰. Stratigraphic variations in $\delta^{13}C_{TOC}$ of the Kuhjoch section are signified by a pronounced negative shift to –31.2‰ at the height

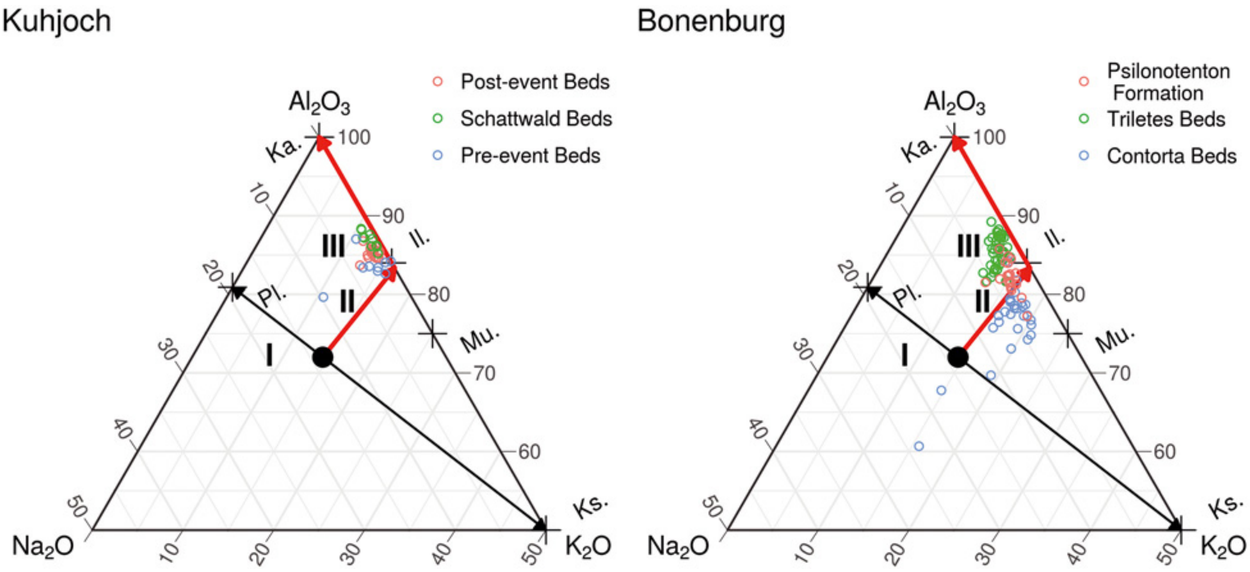

Fig. 5. Modified A–CN–K ternary diagram (cf. Nesbitt & Young 1984), plotting the molar proportions of Al_2O_3, Na_2O and K_2O. The characteristic upper continental crust composition is demarcated by a large black dot. Together with the minerals plagioclase (Pl.), K-feldspar (Ks.), muscovite (Mu.), illite (Il.) and kaolinite (Ka.), these values provide anchor points for evaluating the geochemical trends at Bonenburg and Kuhjoch. Trendlines are drawn for the initial source rock plagioclase to K-feldspar ratio (I), and for plagioclase weathering (II) which is considered to be the initial phase of weathering, based on the observation that K-feldspar is less susceptible to leaching. This is followed by intense weathering and subsequent loss of potassium, forming K-depleted clay minerals (III). Both the Schattwald Beds and Triletes Beds seem to have been sourced from the most intensely weathered substrates compared with the bracketing strata, which are marked by relatively higher concentrations of potassium and sodium.

of the T-Bed (data taken from Ruhl et al. 2009; Fig. 4). A return towards more positive values is followed by generally high and invariable values in the Schattwald Beds ($\delta^{13}C_{TOC}$: –25.1‰). After this, a second negative shift demarcates the transition to the Post-event Beds (Tiefengraben Member), followed by ^{13}C-depleted TOC values ($\delta^{13}C_{TOC}$: –28.5‰) until approximately 8 m above the T-Bed.

We present TOC and TN values on a carbonate-free basis (cfb) to mitigate variable dilution of the element concentrations by changing sediment carbonate content. In the Contorta Beds, TOC_{cfb} and TN_{cfb} average at 1.54 % and 0.07 %, respectively, and are highly variable, with pronounced peaks in TOC_{cfb} and TN_{cfb} in the upper part of the Contorta Beds (Fig. 3). By contrast, the Triletes Beds are depleted in TOC_{cfb} (0.26 %) and TN_{cfb} (0.04 %) and further stand out for their absence of significant variations. The lithological boundary of the Triletes Beds to the Psilonotenton Formation is again associated with pronounced peaks in TOC_{cfb} and TN_{cfb}, followed up-section by continued enrichment (TOC_{cfb}: 1.30 % and TN_{cfb}: 0.07 %) and variability. Stratigraphic variations in molar C/N (TOC/TN) and the marine palynomorph fraction follow to some extent TOC_{cfb} and TN_{cfb} modulations. Although published data on TN_{cfb} and C/N (data taken from Ruhl et al. 2010) are rather incomplete for large portions of the Kuhjoch section (Fig. 4), it is still noteworthy to mention that maxima in TOC_{cfb}, TN_{cfb} and C/N coincide within the T-Bed. More than half of the palynomorph assemblage consists of marine constituents in samples from the uppermost Pre-event Beds and the Post-event Beds of Kuhjoch, but this fraction (f_{marine} = marine palynomorphs/[marine + terrestrial palynomorphs]) is markedly depleted within the Schattwald Beds to values lower than 0.2. By contrast, f_{marine} values of 0.17±0.13 (mean and SD) are encountered in the Bonenburg material, with only minimal variation throughout the investigated sequence. In addition, palynomorphs make-up only 0.12±0.09 (mean and SD) of all counted organic particles ($f_{palynomorph}$ = palynomorphs/total organic particles), whereas wood particles account for 0.58±0.23 (mean and SD) of the organic debris in the Bonenburg material (f_{wood} = woods fragments/total organic particles).

6. Discussion

6.1. A correlative framework for the Central European Basin and the western Tethys shelf seas

Ammonite zonation: Hettangian ammonite biostratigraphy is well established for several regions in Central and Western Europe such as south-western England (e. g., Page & Bloos 1998, Bloos & Page 2000, Page 2002), northern Germany (e. g., Lange 1941), south-western Germany (e. g., Wetzel 1929, Blind 1963, Bloos 1999) and the NCA (e. g., Wähner 1886, Lange 1952, Blind 1963, Bloos 2004, von Hillebrandt & Krystyn 2009). Correlation of these regions showed that the Alpine successions are more complete than those of the other regions. Earliest Jurassic ammonite assemblages are characterized by *Psiloceras planorbis* (*Planorbis* Subchronozone; Trueman 1922) and in Great Britain can be subdivided into six biohorizons (Page & Bloos 1998, Page 2002). Less complete successions are known from northern Germany, where the "Psiloceras-Stufe" was subdivided into six zones with *Psiloceras psilonotum*, *Ps. plicatulum* and various species of *Neophyllites* characterizing the oldest zone (*Psiloceras psilonotum* Zone). In south-western Germany, Wetzel (1929, 1932), and Bloos (1999) identified three fossil assemblages beginning with (1) *Neophyllites imitans* and *N. antecedens*, (2) *Psiloceras psilonotum*, rare *Neophyllites becki* and *Ps. plicatulum*, and (3) *Caloceras franconicum* and *Curviceras subangulare*. In the NCA, Jurassic ammonite assemblages older than the *Planorbis* Chronozone were first recognized by von Hillebrandt & Krystyn (2009). In this respect, the Alpine sections more closely resemble successions in Nevada (Guex et al. 1998, 2004) and Chile (von Hillebrandt 2000) where assemblages are characterized by *Psiloceras spelae* and *Psiloceras tilmanni*.

Terrestrial palynomorph assemblages: Our palynological zonation mainly follows Lund (1977) with respect to the RL- and RP-assemblage zones. Minor differences are related to the Tr–J transition. Barth et al. (2018) suggested the new *Deltoidospora–Concavisporites* Zone (DC-Zone) to cross the Tr–J transition incorporating Lund's topmost upper Rhaetian and the lowermost part of the *Pinuspollenites–Trachysporites* Zone (PT-Zone). Although in Bonenburg a transitional phase, characterized by elements of both the RP- and the PiH-Zone is indicated in the uppermost part of the Triletes Beds, it does not show a continuous high abundance of *Deltoidospora* spp. and *Concavisporites* spp. typical for the new DC-Zone, nor a "transitional spore peak interval" as generally recorded in the CEB (Lund 1977, Barth et al. 2018), Sweden (Larsson 2009) and the Danish Basin (Lindström et al. 2017a). The increased dominance of pollen over spores can obscure changes in the spore assemblage. However, when examining changes only within the spore assemblage, it becomes apparent that the Bonenburg section depicts an increase in 'spores indet' along the transition from the RP- to the PiH-Zone. Considering the occurrence of aberrant *Deltoidospora* spp. and *Concavivsporites* spp. in the basal Hettangian, as documented in Barth et al. (2018), we cannot exclude that a number of aberrant *Deltoidospora* spp. and *Concavivsporites* spp. is included in 'spores indet' in our count that could have been included in these taxa as aberrant forms. Nevertheless, when comparing changes in the overall terrestrial assemblage, i. e. comparing pollen and spores (also incorporating spores indet) the Bonenburg section does not show the "spore peak" with the same amplitude as recorded by other authors (Lund 1977, Heunisch 2010, Lindström 2016, Barth et al. 2018).

The palynological zonation of the NCA (Kuerschner et al. 2007, Bonis et al. 2009, von Hillebrandt et al. 2013) correlates well with the zonation of the CEB (Barth et al. 2018), and this also holds for Bonenburg with minor differences. Comparison of Bonenburg with the zonation of Morbey (1975) for the Kendelbach section shows that the base of Morbey's TK Zone (i. e. the Me-subzone) is characterized by the appearance of *Perinosporites thuringiacus*, which in Bonenburg, after two singular occurrences in the RL-Zone, occurs continuously from the base of the RP-Zone. Compared to the NCA, *Trachysporites* spp. generally occurs in low abundances in Bonenburg. Low abundances of this genus were also reported from southern Sweden (Larsson 2009), and the respective zone is accordingly called *Pinuspollenites-Heliosporites* Zone, differing from the otherwise commonly used PT/TPi-Zone (Lund 1977, Kuerschner et al. 2007, Bonis et al. 2009, Heunisch et al. 2010, von Hillebrandt et al. 2013, Barth et al. 2018). Lund (1977) reported similarly scattered and rare occurrences of *Trachysporites* spp. in the Rhaetian and Hettangian of Eitzendorf close to Bonenburg. There seems to be a general tendency that in the CEB and in the British Rhaetian-Hettangian succession *Trachysporites* spp. is comparatively rare while *Deltoidospora* spp. is more abundant (Lund 1977, Larsson 2009, Heunisch et al. 2010, Bonis et al. 2010, Barth et al. 2018), as opposed to the western Tethys shelf sections where *Trachysporites* spp. dominates over *Deltoidospora* spp. Another notable difference concerns the subdivision of the interval corresponding to the RP-Zone in the CEB. Kuerschner et al. (2007), Bonis et al. (2009) and von Hillebrandt et al. (2013) describe two zones for this interval: the *Rhaetipollis–Porcellispora* (RPo) Zone and *Trachysporites–Porcellispora* (TPo) Zone (see correlation schemes in Bonis et al. 2009, Lindström et al. 2017b, Barth et al. 2018). Like other CEB sections, Bonenburg does not show such changes in spore composition and apart from the described differences, the Bonenburg section correlates well with the western Tethys shelf sea sections.

Besides quantitative changes in whole terrestrial pollen assemblages, a few notable FOs and LOs of individual taxa characterize the Tr–J transition. These first and last occurrences can be used for correlations with the Alpine realm and beyond. Typical Triassic palynomorphs (e. g., *Lunatisporites rhaeticus*, *Triancoraesporites* spp.) are still present in the Kössen Formation and the Schattwald Beds. The records of these taxa show that they disappear at the top of the RPo-Zone. In St Audrie's Bay (UK), the LOs of these taxa are towards the top of the Cotham Member of the Lilstock Formation, although they do not disappear exactly synchronously at this level (Warrington et al. 1994, Hounslow et al. 2004, Warrington 2005, Bonis et al. 2010). In Bonenburg, the mentioned palynomorphs occur until the upper quarter of the Triletes Beds, which allows correlating the Schattwald Beds with the lower three quarters of the Triletes Beds.

These findings can be used for a provisional correlation of the CEB and the western Tethys shelf seas deposits and support previous correlations by Lindström et al. 2017b and Korte et al. (2019). This stratigraphic framework, primarily based on lithology, but supported by biostratigraphy, enables testing the facies-dependence of the TOC-carbon isotope composition in the Event Beds. Accordingly, in this framework, we suggest a synchronous deposition of the Contorta Beds and Pre-event Beds (of the NCA) and of the Triletes Beds and Schattwald Beds, respectively. However, the Tr–J transitional beds of Bonenburg, and many sites of the CEB, are incomplete around the transition from the Triletes Beds to the Psilonotenton Formation. Hence it remains unknown how the Psilonotenton Formation and the Post-event Beds of the NCA relate within this stratigraphic framework.

6.2. Organic matter sources and preservation

An evaluation of organic matter sources and preservation is required in order to determine the potential of stratigraphic δ^{13}C$_{TOC}$ variations to faithfully represent temporal changes in the isotope composition of the Late Triassic to Early Jurassic atmosphere/ocean system. By establishing that the sections show distinct changes in lithology, floral and faunal composition and mineralogy, we highlight the necessity to evaluate the organic matter composition. A clay mineralogical shift to more K-depleted minerals in the Event Beds invokes a changing weathering regime that, in turn, could have been accompanied by an organic matter source shift, where, for instance, marine and terrestrial OC end-members are usually characterized by different C isotope compositions (Arthur et al. 1985, Hayes et al. 1999, Strauss and Peters-Kottig 2003, Poole et al. 2004). Moreover, during greenhouse conditions the C isotope fractionation associated with metabolism of C3 land-plants is diminished, forming ^{13}C-enriched OC (Arthur et al. 1985, Strauss and Peters-Kottig 2003). Hence, an enhanced influx of terrestrial sourced organic compounds in a Tr–J greenhouse world could explain the ^{13}C-enriched Events Beds, and an assessment of the organic matter composition is therefore desirable.

The sediments' TOC and TN are frequently used parameters to assess the fidelity of δ^{13}C$_{TOC}$, as they can allude to the primary OC sources (e. g., Ruhl et al. 2010). Especially the ratio of sedimentary C to N is often considered as a property to distinguish between the relative proportions of terrestrial and marine end-members contributing to the total pool of organic matter, where marine organic matter is more-enriched in N-bearing compounds ($C/N = 5–7$) relative to terrestrial organics ($C/N > 20$) (De Lange 1992, Meyers 1994, Schubert & Calvert 2001). In a similar fashion, the palynological count data, in terms of the absolute or relative proportions of marine versus terrestrial elements, is considered to reflect the major contributing OC sources (e. g., Bonis et al. 2010). These parameters do, however, have inherent limitations, and an evaluation of their specific fidelity is required to assess their effectiveness in tracking source-induced stratigraphic δ^{13}C$_{TOC}$ variations.

Crossplots of palynofacies, palynomorph, elemental and isotope data reveal distinct correlative trends, where δ^{13}C$_{TOC}$ displays a pronounced negative correlation with TOC$_{cfb}$, reproducible for both localities

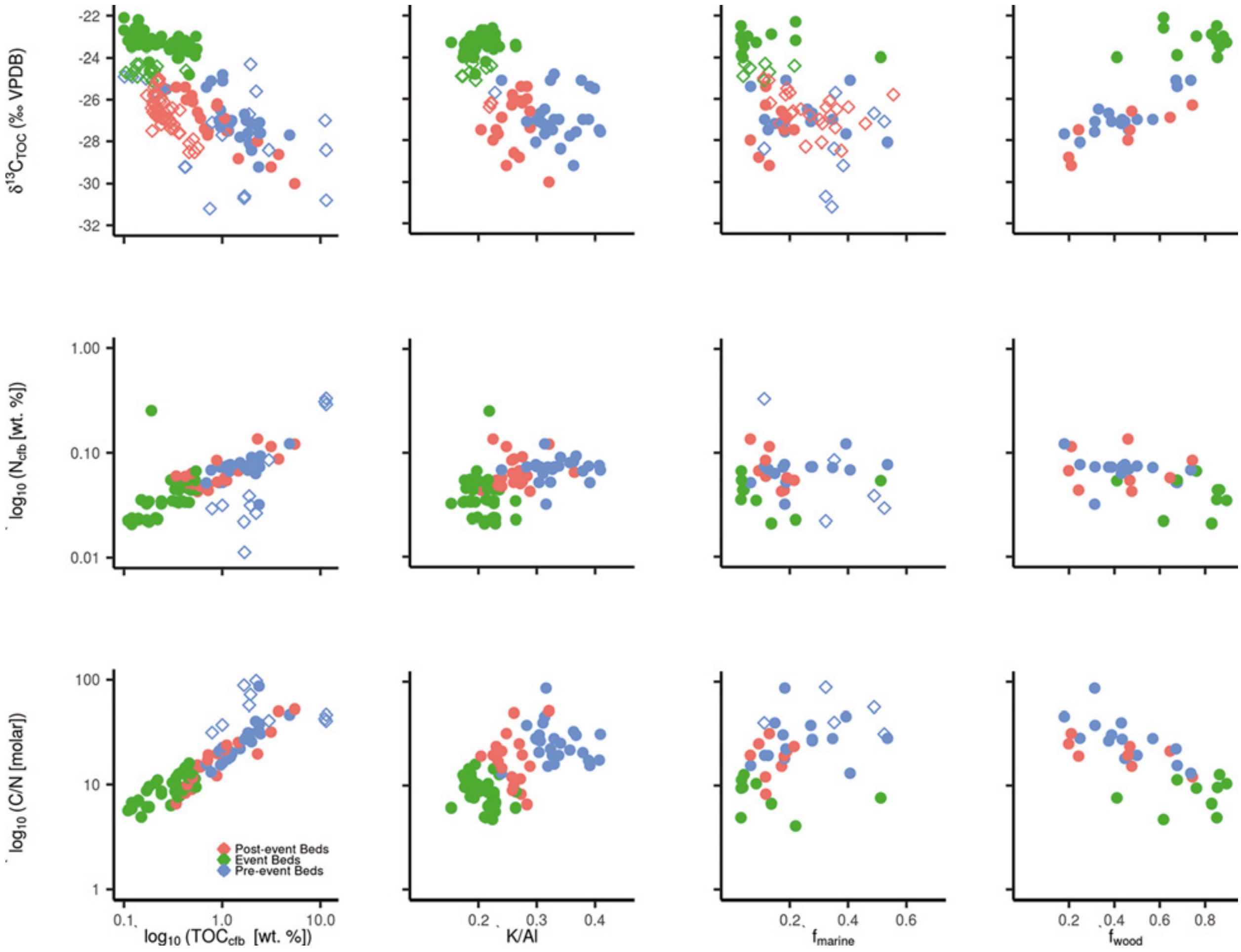

Fig. 6. Crossplots of $\delta^{13}C_{TOC}$, TN and C/N versus TOC, fraction of marine palynomorphs (marine palynomorphs/[marine + terrestrial palynomorphs]), fraction of wood fragments (woods fragments/total organic particles) and K/Al for Kuhjoch (diamonds) and Bonenburg (dots).

(Fig. 6 and Table 1). In addition, there is clear differentiation in the co-variance of $\delta^{13}C_{TOC}$ with TOC_{cfb} according to lithological units, where the Schattwald Beds and Triletes Beds plot in a distinctive area of the Cartesian coordinate system. These relationships suggest a control of the organic substrate on the C isotope composition. Significant positive linear trends can be observed between $\log_{10}(TOC_{cfb})$ and $\log_{10}(TN_{cfb})$ (Table 1) suggesting that these bio-essential elements have a common source, and an ad hoc interpretation would regard this feature to be representative for a lack of significant changes in the organic matter source. These simplistic views on C/N are complicated by the $\log_{10}(C/N)$, which also positively correlates with $\log_{10}(TOC_{cfb})$ (Fig. 6 and Table 1). The linear relationships on a log-log plot for these parameters might approach a power law, and hence describe proportional changes across orders of magnitude. This suggests that stratigraphic trends towards elevated TOC and C/N are of a larger amplitude when compared with constituent TN variations which are relatively dampened. As such, the linear relationships on the log-log plots for TN–TOC and C/N–TOC can be explained by an increased input of organic matter that predispositions subsequent degradation of accumulated organic substrates towards more labile N-bearing organic matter compounds (Twichell et al. 2002, Arndt et al. 2013). Nevertheless, many factors determine the long-term diagenetic stabilization of sedimentary organic matter. For example, sedimentation rates, mineral surfaces, and sorption to minerals are potential factors that can control organic matter preservation (Hedges & Keil 1995).

Further complexities are evident in the co-variance of K/Al and $\log_{10}(TN_{cfb})$, which reveal a strong correlation and a clear separation of the sample space

Table 1 Results of linear model fitting.

Section	x	y	Intercept	Coefficient	r^2	p
Bonenburg	$\log_{10}(\mathrm{TOC_{cfb}}[\mathrm{wt.\%}])$	$\delta^{13}\mathrm{C_{TOC}}$	–26.35	–3.96	0.78	< 0.05
	$\log_{10}(\mathrm{TOC_{cfb}}[\mathrm{wt.\%}])$	$\log_{10}(\mathrm{TN_{cfb}}[\mathrm{wt.\%}])$	–1.21	0.38	0.60	< 0.05
	$\log_{10}(\mathrm{TOC_{cfb}}[\mathrm{wt.\%}])$	$\log_{10}(\mathrm{C/N}\ [\mathrm{molar}])$	1.28	0.62	0.80	< 0.05
	K/Al [atomic]	$\delta^{13}\mathrm{C_{TOC}}$	–19.79	–21.29	0.46	< 0.05
	K/Al [atomic]	$\log_{10}(\mathrm{TN_{cfb}}[\mathrm{wt.\%}])$	–1.72	1.66	0.24	< 0.05
	K/Al [atomic]	$\log_{10}(\mathrm{C/N}\ [\mathrm{molar}])$	0.47	2.63	0.31	< 0.05
	f_{marine}	$\delta^{13}\mathrm{C_{TOC}}$	–24.94	–4.72	0.09	0.07
	f_{marine}	$\log_{10}(\mathrm{TN_{cfb}}[\mathrm{wt.\%}])$	–1.29	0.30	0.05	0.23
	f_{marine}	$\log_{10}(\mathrm{C/N}\ [\mathrm{molar}])$	16.41	28.91	0.06	0.17
	f_{wood}	$\delta^{13}\mathrm{C_{TOC}}$	–29.78	7.24	0.67	< 0.05
	f_{wood}	$\log_{10}(\mathrm{TN_{cfb}}[\mathrm{wt.\ \%}])$	–1.00	–0.44	0.28	< 0.05
	f_{wood}	$\log_{10}(\mathrm{C/N}\ [\mathrm{molar}])$	45.54	–43.88	0.41	< 0.05
Kuhjoch	$\log_{10}(\mathrm{TOC_{cfb}}[\mathrm{wt.\%}])$	$\delta^{13}\mathrm{C_{TOC}}$	–27.53	–2.18	0.35	< 0.05
	$\log_{10}(\mathrm{TOC_{cfb}}[\mathrm{wt.\%}])$	$\log_{10}(\mathrm{TN_{cfb}}[\mathrm{wt.\%}])$	–1.74	1.11	0.82	< 0.05
	$\log_{10}(\mathrm{TOC_{cfb}}[\mathrm{wt.\%}])$	$\log_{10}(\mathrm{C/N}\ [\mathrm{molar}])$	1.81	–0.11	0.04	0.55
	K/Al [atomic]	$\delta^{13}\mathrm{C_{TOC}}$	–21.25	–19.45	0.28	0.09
	f_{marine}	$\delta^{13}\mathrm{C_{TOC}}$	–25.18	–5.55	0.27	< 0.05
	f_{marine}	$\log_{10}(\mathrm{TN_{cfb}}[\mathrm{wt.\%}])$	–0.40	–2.30	0.63	0.11
	f_{marine}	$\log_{10}(\mathrm{C/N}\ [\mathrm{molar}])$	1.72	–0.11	0.01	0.87

according to the major lithological units (Fig. 6 and Table 1). Similar correlations have been related to the ability of ammonium to substitute for potassium in clay minerals, as the ionic radius of both cations is about the same (De Lange 1992). This non-exchangeable ammonium (or clay-bound NH_4^+) is most common in illite and rare in kaolinite. Comparably strong correlations between K/Al and nitrogen have been observed for modern marine sediments and have been explained by the illite content of these substrates. These patterns suggest that reduced illite content (relative to kaolinite) in the Triletes Beds could explain the depleted TN content. If correct, we can deduce that TN reflects the contribution of clay-bound ammonium, and the strong relation of TN with TOC has other underlying mechanisms than commonly inferred for non-fixed N sources. Weathering and sediment transport-related effects might be responsible for the diminished clay-bound N content of the Triletes Beds. With increased continental weathering (Zajzon et al. 2012), elevated siliciclastic input could have diluted the organic matter flux, thereby explaining the low TOC content of the Event Beds. Dilution of organic matter by siliciclastic material is a phenomenon observed in modern deltaic environments (Hedges & Keil 1995).

Relative contributions of marine versus terrestrial palynomorphs correlate poorly with $\delta^{13}C_{TOC}$ (Table 1), and variation of f_{marine} stays in a relatively narrow range (0.17±0.13 [mean and SD] of the total palynomorph pool, and $f_{\mathrm{palynomorphs}}$ account for 0.12 ±0.09 [mean and SD] for Bonenburg, Fig. 3). Combined, these observations suggest that commonly made inferences, based on TOC, TN and the relative contribution of marine palynomorphs, are either inconclusive in identifying potential sedimentary OC source shifts, or invoke insignificant changes in the relative contribution of marine versus terrestrial OC, at least, within the framework of this study. This exercise therefore shows that TOC, TN, and the fraction of marine palynomorphs are less than perfect parameters to elucidate the source and diagenetic pathways of sedimentary organic carbon for this setting. Notable is the connection of clay mineralogy with TN and C/N, and the associated assertion that clay-bound NH_4^+ is an important source of N. This complicates inferences on the major source of organic matter, notably the relative contributions of marine versus terrestrial end-members. It, therefore, leaves open the question whether the precursor organic carbon pool was dominated by marine or terrestrial OC constituents.

The strong correlation of $\delta^{13}C_{TOC}$ and the fraction of wood fragments (Fig. 6 and Table 1), the abundance and relatively large range of f_{wood} (0.58±0.23 [mean and SD]), support a terrestrial-dominated OC pool for the Bonenburg section, or, at least, that a change in the composition of land-derived organic matter forced the stratigraphic variations in $\delta^{13}C_{TOC}$. Furthermore, a

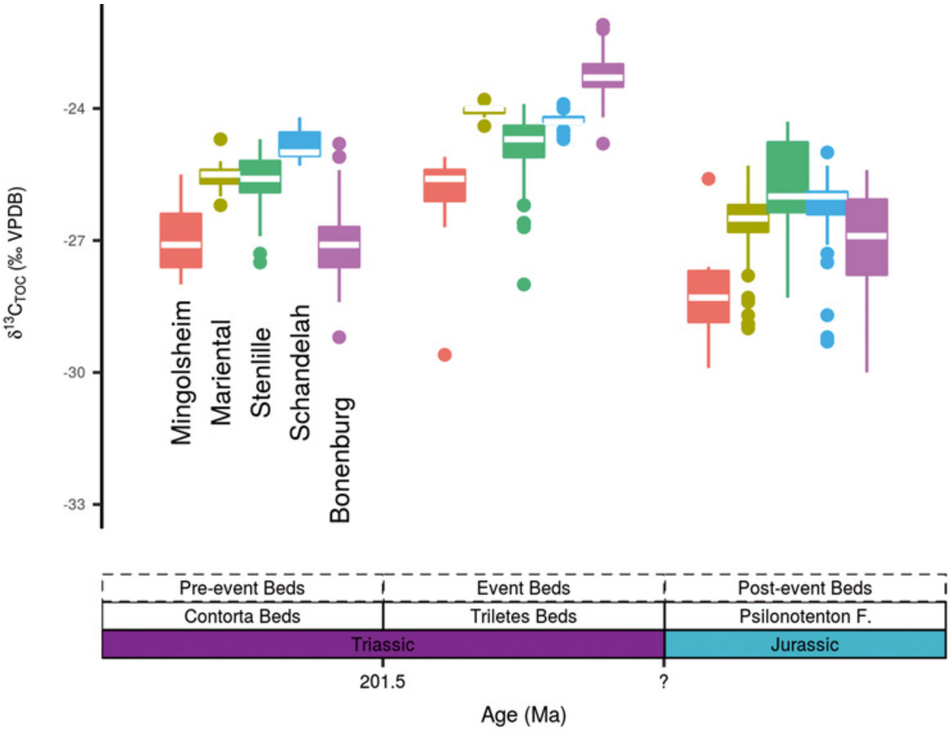

Fig. 7. Boxplots of $\delta^{13}C_{TOC}$ of the combined sites in the CEB binned for three stratigraphically distinct units (Section 5.1), compiling data from the Mingolsheim core (Quan et al. 2008), the Stenlille core (Lindström et al. 2012), the Mariental core (van de Schootbrugge et al. 2013), the Schandelah core (van de Schootbrugge et al. 2019) and the Bonenburg section (this study). Age of the lower boundary of the Triletes Beds is after Lindström et al. (2017 b) and Korte et al. (2019); the Tr–J is comprised by a hiatus in the CEB.

common pattern in the crossplots of $\delta^{13}C_{TOC}$ with K/Al is that the values of the Schattwald and the Triletes beds cluster in a distinct domain of the plot with relatively little scatter. This pattern suggests uniformity in the source of organic matter and clay minerals. By contrast the younger and older parts of the succession show more overlap and contain a more variable signal. This uniformity extends beyond Kuhjoch and Bonenburg to sections where similar trends in the clay mineral assemblages with an increase or predominance of kaolinite in the topmost Rhaetian beds occur in the NCA (Pálfy & Zajzon 2012, Zajzon et al. 2012) and in several other regions in Europe (Simms & Ruffell 1989, Ahlberg et al. 2003, Michalik et al. 2010, van de Schootbrugge et al. 2009, Bránski 2014, Nystuen et al. 2014). These similarities in first-order trends hint at a common temporal evolution of clay mineral formation and/or similar climate-driven weathering regime shift for these geographically distinct sites. In addition, compilations of $\delta^{13}C_{TOC}$ for the CEB (the Mingolsheim, Stenlille, Mariental and Schandelah cores; Fig. 7) and western Tethys shelf seas (the Restentalgraben, Tiefengraben, Kendlbachgraben and Hochalplgraben sections; Fig. 8) suggest that ^{13}C-enriched TOC with low variability is a shared characteristic for the Events Beds (Triletes and Schattwald beds). This is further corroborated by Kruskal-Wallis rank sum tests and Pairwise Wilcoxon rank sum tests, which show that the median $\delta^{13}C_{TOC}$ of the stratigraphic units are significantly different, except for the Contorta Beds and Psilonotenton Formation of Stenlille and Bonenburg which cannot be distinguished (Fig. 7). This observation fits within the chemostratigraphic correlation scheme of the Tr–J boundary interval which was recently reviewed by Korte et al. (2019).

6.3. Perspectives on TOC-carbon isotope based stratigraphic schemes

Transient negative excursions in $\delta^{13}C_{TOC}$ of the Tr–J boundary intervals have been linked to pronounced perturbations of the global carbon cycle, based on compound-specific C isotope analysis (Ruhl et al.

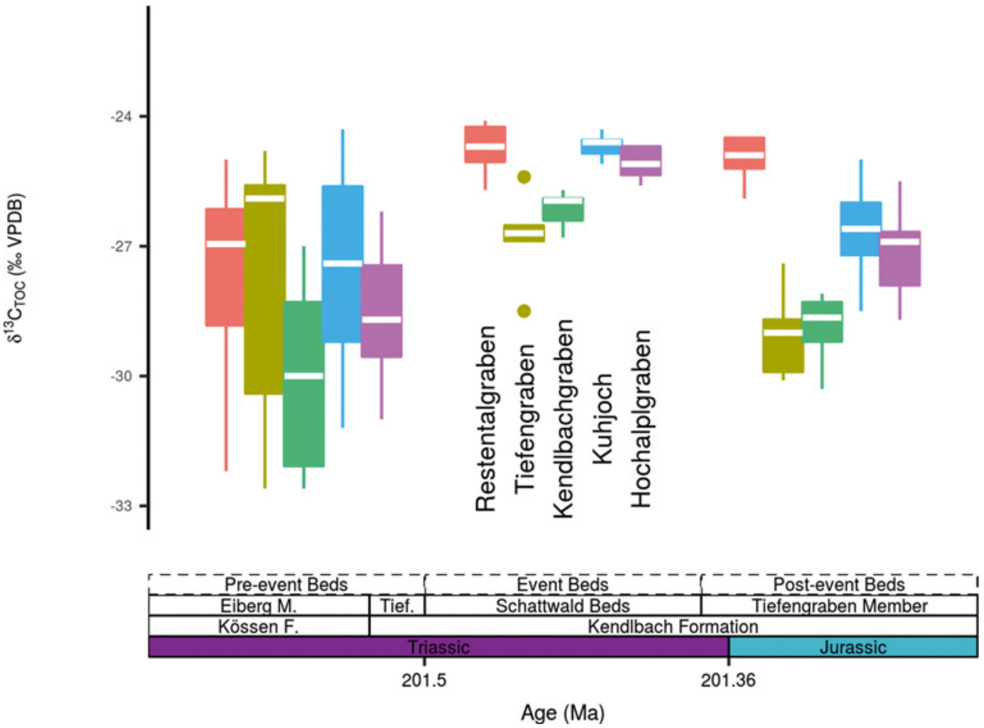

Fig. 8. Boxplots of $\delta^{13}C_{TOC}$ of the combined sites in the NCA binned for three stratigraphically distinct units (Section 5.2), compiling data from the Restentalgraben, Tiefengraben, Kendlbachgraben, Kuhjoch and Hochalplgraben sections (Kuerschner et al. 2007, Ruhl et al. 2009). The Kendlbachgraben and Tiefengraben lithological subdivision is based on clay mineralogy analysis by Zajzon et al. (2012) and a change to a more silty lithology (Kuerschner et al. 2007), respectively. Age of the lower Schattwald Beds is after Lindström et al. (2017 b) and Korte et al. (2019); the age of the Tr–J boundary is after Wotzlaw et al. (2014). (Tief. = Tiefengraben Member).

2011). By contrast, long-term $\delta^{13}C_{TOC}$ trends over the Tr–J transitional beds, and, in particular, the positive $\delta^{13}C_{TOC}$ signature of the Event Beds, have not undergone equivalent rigorous testing (see discussion in Bachan et al. 2012, Yager et al. 2017 for potential explanations for TOC ^{13}C-enrichment in the Event Beds).

The supra-regional TOC ^{13}C-enrichment in the Event Beds (Fig. 7 and Fig. 8) suggests a primary isotope signature, which traces the isotope composition of the exogenic carbon reservoir, which in turn is dictated by the fluxes in (volcanism and metamorphism-derived C) and out (burial of C) of the system. Furthermore, considering a 10^5 y duration of the Event Beds (Fig. 8 and Lindström et al. 2017b), the $\delta^{13}C_{TOC}$ should have originated from a well-mixed reservoir, as the residence time of carbon in the ocean-atmosphere system (10^5 y) is larger than the ocean mixing time (10^3 y) (Kump 1989, Dickens et al. 1995). It thus follows that the magnitude of the inflection to positive values should have been uniform across the whole ocean. However, this observation seems to be at odds with the variable magnitude of the observed C isotope shift (Fig. 7 and Fig. 8), and alternative explanations need to be explored.

Local $\delta^{13}C$ departures from the global C isotope signal could result from restricted seawater exchange of the basin with the open ocean (Holmden et al. 1998, Saltzman 2001, Bachan et al. 2012). Alternatively, spatial variations in the plankton community composition, and changes in the contributions of marine versus terrestrial components, can drive locally distinct sedimentary organic matter $\delta^{13}C$ signatures, which are produced by differences in C isotope fractionation associated with photosynthate production (Arthur et al. 1985, Farquhar et al. 1989, Meyers 1994, Kump & Arthur 1999). As marine palynomorph counts are potentially a poor reflection of the total sedimentary organic matter (where they represent only a small fraction of the organic particle pool, based on palynofacies analysis), a change in predominantly marine to terrestrial organic components can not entirely be discounted as the underlying cause for the ^{13}C-enriched values of the Event Beds. Nevertheless, a most parsimonious scenario should also consider evidence of redox changes, and connected elevated levels of marine primary productivity, during the latest Rhaetian (Kasprak et al. 2015). These oceanic changes might relate to the collapse of terrestrial vegetation and elevated nutrient fluxes from the continents (Meyer et al. 2008, van de Schootbrugge et al. 2009, Algeo & Twitchett 2010, Kasprak et al. 2015). The synergistic effect of enhanced continental weathering and nutrient flux to the shelf environment favors a scenario of a change in the terrigenous OC flux over changes in the marine versus terrestrial end-member contribution. Combined with the ubiquity and highly variable occurrence of wood fragments in the Bonenburg section, these indices point towards a significant control of terrestrial-derived organic material on the $\delta^{13}C_{TOC}$ of the Tr–J transition beds. This interpretation is in accordance with previous studies of sections in the CEB and western Tethys shelf seas that employed kerogen characterization and compound specific C isotope analysis (van de Schootbrugge et al. 2009, Ruhl et al. 2010, Ruhl et al. 2011). In this case, $\delta^{13}C_{TOC}$ might reflect the isotope composition of atmospheric CO_2 (Strauss and Peters-Kottig 2003). However, small local deviations could arise from differences in the original organic matter transported from the continent to the seafloor (the organic debris of C_3 plants can range over several per mill in $\delta^{13}C$; O'Leary 1988, Cloern et al. 2002, Poole et al. 2004) and from differential trajectories of early diagenetic stabilization (Benner et al. 1987, Lehmann et al. 2002). Consistent with this reasoning, the co-variance of K/Al, and, in particular, the fraction wood fragments with $\delta^{13}C_{TOC}$, suggests that temporal $\delta^{13}C_{TOC}$ variations could equally be forced by source changes within the terrestrial OC flux.

The close correspondence of a clay mineralogy change, wood fragment abundance, and a shift to more ^{13}C-enriched TOC in the Event Beds therefore invokes a causal relationship. A change in the weathering regime might introduce more refractory terrestrial organic material ("pre-aged" or "fossil organic material" Meyers 1994) through increased physical erosion on land and an elevated riverine influx. A vegetation die-back and an enhanced hydrological cycle would be potential consequences of large-scale ecosystem destruction and greenhouse warming (van de Schootbrugge et al. 2009, Bonis et al. 2010, Ruhl et al. 2011), exposing and mobilizing previously untouched and mature organic matter sources. Additionally, a climatic shift to warmer and more humid conditions would have elevated chemical weathering rates, where episodic inundation could have catalyzed oxidative degradation of organic substrates (Hedges et al. 1999), leading to proportionally more refractory organic material transport to the depocenters. Such recalcitrant tissues (e. g., woody components) are known to harbor more positive C isotope signatures (O'Leary 1988, Jahren 2004, Cernusak et al. 2009, Schneebeli-Hermann et al. 2013). Hence, elevated contributions of recalcitrant organic material would be a viable pathway to drive $\delta^{13}C_{TOC}$ to higher values, a mechanism which should be explored in future studies on the Tr–J transitional beds. Factors such as the amount, source, and degradability of the original terrestrial organic compounds could be additional factors, which determine the ultimate TOC composition and could account for variations in the magnitude of the observed positive $\delta^{13}C_{TOC}$ shift. Intriguingly, the signal to more positive $\delta^{13}C_{TOC}$ is reproducible for different sites and even basins (e. g., Bachan et al. 2012, Blumenberg et al. 2016, Yager et al. 2017), potentially pointing toward a globally extensive event, which might still serve as a (regional) stratigraphic marker.

6.4. Statigraphic and environmental relevance of the Events Beds

The Event Beds have been a prime subject in recent studies (van de Schootbrugge et al. 2009, Pálfy & Zajzon 2012, Zajzon et al. 2012, Lindström et al. 2017b), which do not necessarily regard this unit to be the expression of sediment progradation forced by a sea level rise (Hallam & Wignall 1999). Instead the former mentioned studies infer an increased supply of siliciclastic sediments into the basin, possibly associated with more intense weathering under hot and humid greenhouse conditions. A fairly consistent positive $\delta^{13}C_{TOC}$ signature and the K-depleted clay mineral assemblage of the Event Beds further enforce this notion of a supra-regional event, where either climate-driven weathering intensification or a sudden terrigenous source change underlies the lithological transition. This sedimentary regime shift clearly differentiates the Event Beds from younger and older deposits.

The relevance of this sedimentary regime shift for palaeoenvironmental studies is twofold. First, increased sediment supply may result in dilution of micro- and macro-fossil assemblages and lead to the erroneous inference of a biological collapse. Facies-dependent controls on fossil assemblages, and obtained quantitative estimates of stratigraphic ranges and diversity patterns, are a general concern in palaeontological studies (e. g., Patzkowsky & Holland 2012, Wang et al. 2014). Similarly, variable contributions of land-derived material, linked with elevated sediment rates, pose a problem for geochemical studies, as shown here for the stratigraphic potential of $\delta^{13}C_{TOC}$ and also for the interpretation of trace element enrichment patterns (e. g., Quan et al. 2008, Tanner et al. 2016). Second, elevated sediment fluxes are suggested to be a prime driver of the environmental perturbation at the Tr–J transition and other extinction events (e. g., the end-Permian mass extinction) by increasing water column turbidity and siltation which affected benthic filter-feeders on the shelf (Algeo & Twitchett 2010, Lindström et al. 2012), and by stimulating marine anoxia through elevated nutrient supply and increased levels of productivity (Meyer et al. 2008, Algeo & Twitchett 2010, Kasprak et al. 2015).

7. Conclusions

A robust stratigraphic framework is a prime prerequisite to understand the biotic and environmental changes at the Triassic–Jurassic boundary interval. Although carbon isotope records are a promising tool for global correlations by recording perturbations of the exogenic carbon reservoir as stratigraphic δ^{13}C fluctuations, multiple factors can bias this archive. Our study focused on stratigraphic TOC-based carbon isotope fluctuations in terms of their predominant contributors (i. e. organic matter sources versus the exogenic C pool) for key Tr–J sections. Lithology, macro-fossils and palynomorphs of the Bonenburg and Kuhjoch Tr–J transitional beds form a good basis to correlate these sites within their respective sedimentary basins, but also enable a tentative correlation between sections from the CEB and western Tethys shelf seas. Litho- and biostratigraphy of the Bonenburg site confirm the existence of a sedimentary hiatus in the upper Triletes Beds, which are unconformably overlain by the Psilonotenton Formation. This hiatus is a feature consistent among Tr–J sections of Northwestern Europe. Our mineralogical investigation reveals that the Event Beds (Triletes Beds and Schattwald Beds) are composed of K-depleted clay minerals (e. g., kaolinite), contrasting with the unit's bracketing lithology. This clay mineral shift is indicative of a terrigenous source change and/or a transition in the climate-controlled shift in the weathering regime. These outcomes corroborate previous interpretations suggesting that this lithological unit is an expression of the environmental changes during this time interval. However, these lithological and mineralogical indices also suggest that some stratigraphic $\delta^{13}C_{TOC}$ fluctuations could have been dictated by changes in the sourced organic matter (e. g., marine versus terrestrial OC contributions). A strong correlation between the dominant OC fraction consisting of wood and $\delta^{13}C_{TOC}$ invokes consideration of a causal effect. In such a scenario, the continentally derived organic matter becomes enriched in pre-aged or fossil organic matter, recycled from intensively weathered rock and soil sections. The degraded and selectively preserved products of terrestrial plants, such as wood fragments, are known to harbor a more positive δ^{13}C signature than more easily degradable products, thereby potentially explaining the ^{13}C-enriched TOC of the Event Beds. Even though it cannot be ruled out that this shift towards more positive $\delta^{13}C_{TOC}$ in the Event Beds is a perturbation of the exogenic C reservoir, the correlation of K-depleted clay mineralogy and ^{13}C-enriched TOC warrants revisiting current notions on the stratigraphic potential of TOC-based δ^{13}C records.

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Appendix 1

Taxalist Bonenburg

Spores

Conbaculatisporites mesozoicus Klaus 1960
Deltoidospora spp. Miner 1935
Densosporites fissus (Reinhardt 1964) Schulz 1967
Limbosporites lundbladii Nilsson 1958
Lycopodiacidites rhaeticus Schulz 1967
Perinosporites thuringiacus Schulz 1962
Polycingulatisporites spp. (Simoncsics & Kedves 1961) Morbey 1975
Polypodiisporites polymicroforatus (Orlowska-Zwolinska 1966) Lund 1977
Semiretisporis spp. Reinhardt 1962
Triancoraesporites reticulatus Schulz 1962

Pollen

Cerebropollenites thiergartii Schulz 1967
Enzonalasporites vigens (Leschik 1955) Schulz 1967
Granuloperculatipollis rudis (Venkatachala & Góczán 1964) Scheuring 1978
Lunatisporites rhaeticus (Schulz 1967) Warrington 1974
Perinopollenites elatoides Couper 1958
Pinuspollenites minimus (Couper 1958) Kemp 1970
Rhaetipollis germanicus Schulz 1967
Ricciisporites tuberculatus Lundblad 1954

Dinoflagellates

Dapcodinium priscum (Evitt 1961) Below 1987
Rhaetogonyaulax rhaetica (Sarjeant 1963) Loeblich & Loeblich 1968
Suessia swabiana (Morbey 1975) Below 1987

Appendix 2

The following appendix is available under https://doi.org/10.5281/zenodo.2536746
The repository contains the R Markdown file required to reproduce the paper as well as the palynological and geochemical data sets.

Chapter 3

Macroecological patterns of the terrestrial vegetation history during the end-Triassic biotic crisis in the Central European Basin: a palynological study of the Bonenburg section (NW-Germany) and its supra-regional implications

Julia Gravendyck*, Martin Schobben, Julien B. Bachelier, Wolfram M. Kürschner.

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Chapter 4

Taxonomy and nomenclature in palaeopalynology: basic principles, current challenges and future perspectives

Julia Gravendyck*, Robert A. Fensome, Martin J. Head, Patrick S. Herendeen, Jim B. Riding, Julien B. Bachelier, Nick Turland.

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Abstract

Effective communication of taxonomic concepts is crucial to meaningful application in all biological sciences, and thus the development and following of best practices in taxonomy and the formulation of clear and practical rules of nomenclature underpin a wide range of scientific studies. The *International Code of Nomenclature for algae, fungi, and plants* (the *Code*), currently the *Shenzhen Code* of 2018, provides these rules. Although early versions of the *Code* were designed mainly with extant plants in mind, the *Code* has been increasingly used for fossil plants and, in recent decades, for organic-walled microfossils, the study of which is called palaeopalynology, or simply palynology. However, rules embodied in the *Code* do not fully reflect the needs and practices of this discipline; and taxonomic practices between fossil applications, especially in palynology, have tended to diverge from practices for extant plants. Differences in these rules and practices present specific challenges. We therefore review the *Shenzhen Code* as it applies to palynology, clarifying procedures and recommending approaches based on best practices, for example, in the designation and use of nomenclatural types. The application of nomenclatural types leads to taxonomic stability and precise communication, and lost or degraded types are therefore problematic because they remove the basis for understanding a taxon. Such problems are addressed using examples from the older European literature in which type specimens are missing or degraded. A review of the three most important conventions for presenting palynological taxonomic information, synonymies, diagnoses/descriptions and illustrations, concludes with recommendations of best practices. Palynology continues to play an important role in biostratigraphy, basin analysis, and evolutionary studies, and is contributing increasingly to our understanding of past climates and ocean systems. To contribute with full potential to such applied studies, consistent communication of taxonomic concepts, founded upon clear rules of nomenclature, is essential.

Chapter 5

Name Usage Statistics (I): Working with databases

Abstract

In taxonomy, the overview on previous works and the history of the name of a taxon and its current standing are often difficult, and picking the correct name out of a long list of synonyms can be cumbersome. However, working with databases providing data that can be used to conduct taxon user statistics, i.e. a quantitative analysis of the use of competing names, could help could help making informed decisions and revisions to support formal proposals to conserve, protect, or reject names. Currently, palynologists have two big databases, i.e. the John Williams Index of Palaeopalynology and Palynodata, but both are discontinued and compete more and more with uncurated online resources such as Google Scholar. Here, we conducted a case study for four genera with a total of 65 species, and compared the output of references for the species inventory over time by analysing more than 2000 citations and their cross-occurrences in these three databases. We found that the John Williams Index is the most accurate and extensive, but because it can only be consulted in person in London, its lack of accessibility makes Palynodata, which is available as a dataset or online, the more favourable source of information. In addition, since both databases are no longer updated, complementation, e.g. through Google Scholar, is often necessary. However, our results also showed that it does not make a big difference whether one combines the John Williams Index or Palynodata with Google Scholar for the investigated taxa since using any combinations of any two out of the three sources gives a recovery of at least 75% of all citations compared to when using all three. In conclusion, each database has its own advantages and disadvantages, and when working under time pressure, the choice of database depends on the question of the study.

“What’s in a name? That which we call a rose

By any other name would smell as sweet;”

(Juliet in Shakespeare’s Romeo and Juliet; Act II Scene II)

1. Introduction

Shakespeare’s Juliet famously suggests that a name does not reflect the essence of the object it refers to but, as Traverse (1996) pointed out, ‘a rose by any other name would be very confusing’ in nomenclature and taxonomy. Indeed, although in a scientific context the ‘name’ (or designation) is merely the label given to a concept, as the identifier of a taxon it carries subtle interpretations and assumptions about the taxon’s characteristics. Especially for genera, the choice of a particular name can imply a taxonomic opinion, and its initial or subsequent use, may influence later users. Names are often more readily accepted after impactful revisions, but for linguistic or cultural reasons, or through geological separation (long ranges), some names or concepts might be adopted by only part of the scientific community. Thereby names can experience an “evolution” of their own, independent of evidence from the natural world.

Contrary to the spirit of Shakespeare’s suggestion (by way of Juliet), the nomenclatural ideal is that a taxon has only one correct name, which would be a universal and unique identifier (Turland et al. 2018; Turland 2019). Unfortunately, taxonomic reality confronts us with both homotypic as well as heterotypic synonyms, the latter being more subjective because it depends on the author’s taxonomic opinion, and can (also) start a life of their own. In addition, any synonym might, over time, even influence the interpretation and subsequent use of competing names, even though they are, Ideally, referring to the same essence, i.e. the same taxonomically circumscribed taxon. Synonyms also tend to proliferate when taxa are poorly defined and/or prove difficult to recognise, and in any situations, just make it more difficult to determine the ‘correct’ name (Kremp & Methven 1968; Traverse 1996).

When assessing the usage, historical development and popularity of a particular taxon name, it can be helpful to study their its user statistics, i.e. when and how often the name has been chosen and how it has been used and developed over time. This process is similar to linguistic practices in studying the evolution for example of semantic change — the change of meaning, over time. In taxonomy, the frequency and the way certain names have been used over time can provide an insight into the changes in the perception and understanding of that taxon and perhaps also its subdivisions. The information gained from user statistics can be particularly relevant when revising existing taxa and/or when attempting the conservation, protection, or rejection of names (see Taxon User Statistics II). Databases that provide information on taxon citations are clearly the best sources for such user statistics.

The most extensive database in the discipline is probably the John Williams Index of Palaeopalynology (JWIP), with 23,350 pre-Quaternary paleopalynological references in 2012 (Riding et al. 2012), and subsequently about 25,550 references according to Stephen Stukins (personal communication, 20. Nov. 2020). This database consists of a non-digitised hand-written card index, stored at the Natural History Museum in London and compiled between 1968 until 31 December 2015 (Riding et al. 2012; Stephen Stukins personal communication, 20. Nov. 2020). It consists of several subindexes, of which subindex 5 gives literature references for palynomorphs sorted according to genera and species. It also provides citations and geographical, and stratigraphical information, as well as occasional remarks by the author John Williams (Riding et al. 2012). The second major database is Palynodata (PD), with 22,152 pre-Quaternary paleopalynological references compiled since 1965 initially by Gerhard O. W. Kremp, and subsequently, by a consortium of oil companies and the Geological Survey of Canada (GSC) (White et al. 2009). Unfortunately, it was only updated up to 2006 but is freely available as Geological Survey of Canada, Open File 5793 via the GSC's Geoscan website (White & Piel 2008; White et al. 2009; Riding et al. 2012). A derived searchable tool based on Palynodata is available online via www.paleobotany.ru. The third and most accessible reference resource consists of online search engines, such as Google Scholar (GS), or Web of Science. Although they are not curated like the JWIP or PD and continuously changing, they still give better access to, and a quicker search function for, publications found online.

In this study, we thus compare and evaluate the suitability, output, and respective advantages and disadvantages of all three (databases. We also investigate which one, or which combination of them, provides the best results when attempting, for example, a taxonomic revision. To do so, we provide a case study involving four genera of stratigraphic relevance to the German Triassic, and based on analysing more than 2000 citations, their cross occurrences in the three databases, and comparing the output of references for the species inventory of each genus over the past seven decades.

2. Material and methods

2.1. Taxa

For the given study, two pollen genera (*Cerebropollenites* and *Sciadopityspollenites*) and two spore genera (*Limbosporites* and *Semiretisporis*) were chosen because they contain a number of potential synonyms that are relevant to taxonomic revisions beyond a preliminary database evaluation. The genera ***Cerebropollenites*** and ***Sciadopityspollenites*** contain 15 and 28 species respectively, and ***Limbosporites*** and ***Semiretisporis*** comprise 10 and 12 species, respectively (Table 1).

Each of the three databases were searched for entries on each of the 65 species, giving a total of ca. 3000 database entries for ca. 2000 different references. References to subspecies or formae (e.g. *Sciadopityspollenites serratus* fa. *helmstedtensis*), informal descriptions (e.g. sp. A, or “barentzii”) and references not specifying the species (i.e. “sp.”) were not included. Given that the scope of this study involves a meta-analysis of database output rather than a taxonomic work, the accuracy of only about ¼ of the literature references available online through the Freie Universität Berlin Intranet or ResearchGate in spring 2020, or from the hardcopy library of the first author (Schulz inheritance; Gravendyck et al. 2020), was cross-checked. Less than 10% of these references did not contain the intended taxon name, or only gave it as a synonym, and were removed from the dataset (see details below).

Table 1: Investigated taxa in this study.

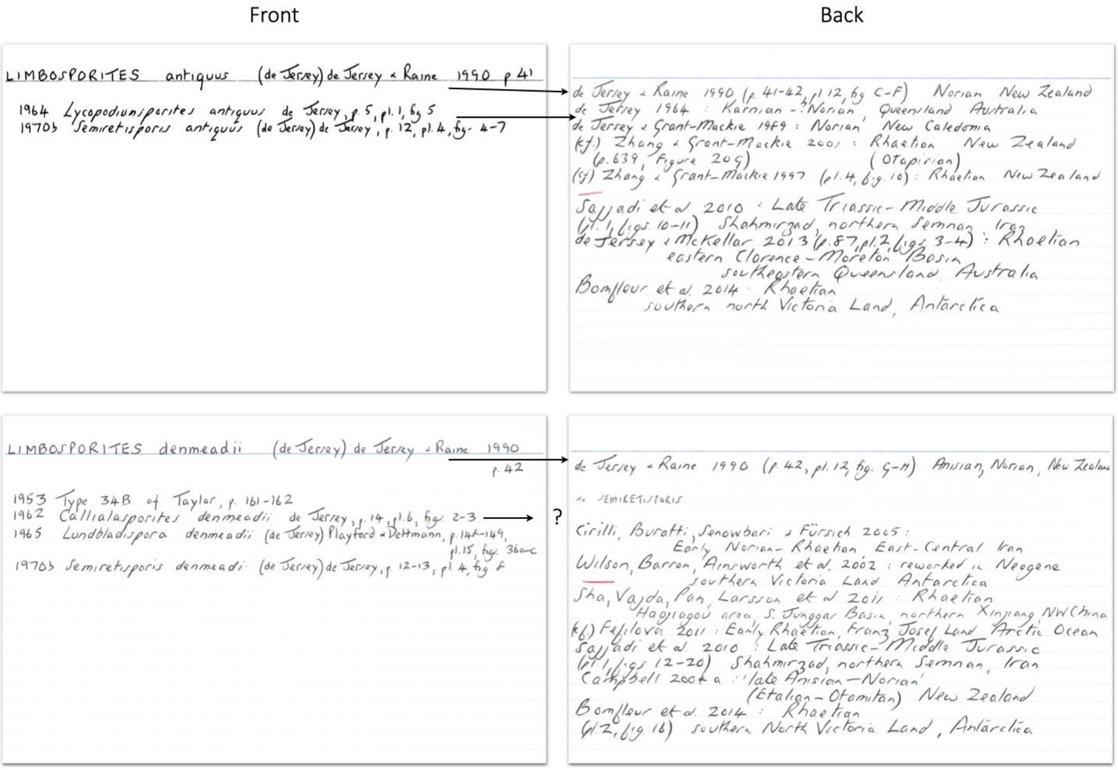
Genus	*Species*	Authority
Cerebropollenites	*carlylensis*	Pocock 1970
Cerebropollenites	*findlaterensis*	Pocock 1970
Cerebropollenites	*granulatus*	Huang 1995
Cerebropollenites	*macroverrucosus*	(Thiergart 1949) Schulz 1967
Cerebropollenites	*mesozoicus*	(Couper 1958) Nilsson 1958
Cerebropollenites	*microverrucatus*	Yu & Zhang 1982
Cerebropollenites	*minor*	Yu & Zhang 1982
Cerebropollenites	*nilssonii*	Sing & Kumar 1968
Cerebropollenites	*oriens*	Taugourdeau-Lantz 1972
Cerebropollenites	*papillosus*	Qian 1995
Cerebropollenites	*papilloporus*	Xu & Zhang 1990
Cerebropollenites	*pseudomassulae*	(Mädler 1964) Taugourdeau-Lantz 1984
Cerebropollenites	*radiostriatus*	Burden et al. 1989
Cerebropollenites	*saccificstulatus*	Ruade-Gaxiola 1967
Cerebropollenites	*thiergartii*	Schulz 1967
Sciadopytispollenites	*ambiguous*	Voloshina 1973
Sciadopytispollenites	*antiquus*	Krutzsch 1971
Sciadopytispollenites	*areolatus*	Benda et al. 1982
Sciadopytispollenites	*asper*	Benda et al. 1977

Sciadopytispollenites	*catenatus*	(Potonié 1931c) Krutzsch 1971
Sciadopytispollenites	*carlylensis*	(Pocock 1970) Fedeorova 1993
Sciadopytispollenites	*crassus*	Krutzsch 1971
Sciadopytispollenites	*eocaenicus*	Krutzsch 1971
Sciadopytispollenites	*gracilis*	Schuler 1983
Sciadopytispollenites	*krutzschii*	Takahashi & Jux 1986
Sciadopytispollenites	*largus*	Grabowska 1986
Sciadopytispollenites	*macroserratus*	(Thiergart 1949) Petrosyants in Barkhatnaya et al. 1985
Sciadopytispollenites	*macroverrucosus*	(Thiergart 1949) Iljina 1985
Sciadopytispollenites	*megaorbiculus*	Takahashi 1997
Sciadopytispollenites	*mesozoicus*	(Couper 1958) Waksmundzka 1981
Sciadopytispollenites	*miniverrucatus*	Kohlmann-Adamska in Stuchlik et al. 2002
Sciadopytispollenites	*multiverrucosus*	(Sachanova & Iljina) Iljina 1985
Sciadopytispollenites	*osmundaeformis*	Wang et al. 1981
Sciadopytispollenites	*ovalis*	Bose 1961
Sciadopytispollenites	*quintus*	Krutzsch 1971
Sciadopytispollenites	*retiformis*	Benda 1974
Sciadopytispollenites	*serratus*	(Potonié & Venitz 1934) Thiergart 1937
Sciadopytispollenites	*tuberculatus*	(Zaklinskaja 1957) Krutzsch 1971
Sciadopytispollenites	*tubulus*	Krutzsch 1971
Sciadopytispollenites	*varius*	Krutzsch 1971
Sciadopytispollenites	*verrucatus*	Dutta et al. 1970
Sciadopytispollenites	*verticilata*	Brelie 1959
Sciadopytispollenites	*verticillatiformis*	(Zauer 1960) Krutzsch 1971
Limbosporites	*antiquus*	de Jersey 1964) de Jersey & Raine 1990
Limbosporites	*balmei*	Foster 1979
Limbosporites	*crassus*	Archhangelskaya 1980
Limbosporites	*denmeadii*	(de Jersey 1962) de Jersey & Raine 1990
Limbosporites	*fovearis*	Krutzsch 1973
Limbosporites	*lundbladiae*	Nilsson 1958
	[published as *lundbladii*]	
Limbosporites	*microfoveatus*	(Zhang 1978) Bai et al. 1983
Limbosporites	*scottii*	Marcinkiewicz 1969
Limbosporites	*tubulum*	Lei 1978
Limbosporites	*vesiculosus*	Döring 1976
Semiretisporis	*achimensis*	Mädler 1964
Semiretisporis	*antiquus*	de Jersey 1964) de Jersey 1970
Semiretisporis	*denmeadii*	(de Jersey 1962) de Jersey 1970
Semiretisporis	*flaccida*	Shang-Li 1991
Semiretisporis	*gothae*	Reinhardt 1961
Semiretisporis	*hochuli*	Paterson et al. 2019
Semiretisporis	*lycopodioides*	Yu & Huang 1964 in Bai et al. 1983
Semiretisporis	*maljavkinae*	Schulz 1967
Semiretisporis	*ornatus*	Orłowska-Zwolińska 1966
Semiretisporis	*reticulatus*	Mädler 1964
Semiretisporis	*taiwanensis*	Huang 1984
Semiretisporis	*wielichoviensis*	Orłowska-Zwolińska 1966

2.2. Databases

2.2.1. John Williams Index of Palaeopalynology (JWIP)

Information from the JWIP index cards (subindex 5; see Riding et al. 2012 for details of the index organisation) were provided for the four genera as a courtesy by Niall Paterson (CASP) and Stephen Stukins (Natural History Museum London) during the Covid-19 pandemic in 2020. For each species, the JWIP includes the basionym and all other recombinations of the taxon name. Since recombinations represent citations of other names, these were not included for the current study. The references given in the JWIP include conference abstracts, theses, and industry reports. However, as grey literature these were also not included in the current study.



LIMBOSPORITES antiquus (de Jersey) de Jersey & Raine 1990 p 41

1964 Lycopodiumisporites antiquus de Jersey, p. 5, pl. 1, fig 5
1970b Semiretisporis antiquus (de Jersey) de Jersey, p. 12, pl. 4, fig. 4-7

de Jersey & Raine 1990 (p. 41-42, pl. 12, fig C-F) Norian New Zealand
de Jersey 1964 : Karnian - ?Norian, Queensland Australia
de Jersey & Grant-Mackie 1989 : Norian New Caledonia
(cf.) Zhang & Grant-Mackie 2001 : Rhaetian New Zealand
(p. 639, Figure 20g) (Otapirian)
(cf) Zhang & Grant-Mackie 1997 (pl. 4, fig. 10) : Rhaetian New Zealand
Sajjadi et al 2010 : Late Triassic - Middle Jurassic
(pl. 1, figs. 10-11) Shahmirzad, northern Semnan Iran
de Jersey & McKellar 2013 (p. 87, pl. 2, figs 3-4) : Rhaetian
eastern Clarence - Moreton Basin
southeastern Queensland Australia
Bomfleur et al. 2014 : Rhaetian
southern north Victoria Land, Antarctica

LIMBOSPORITES denmeadii (de Jersey) de Jersey & Raine 1990
p. 42

1953 Type 34B of Taylor, p. 161-162
1962 Callialasporites denmeadii de Jersey, p. 14, pl. 6, figs 2-3
1965 Lundbladispora denmeadii (de Jersey) Playford & Dettmann, p. 148-149,
pl. 15, figs 36a-c
1970b Semiretisporis denmeadii (de Jersey) de Jersey, p. 12-13, pl. 4, fig F

de Jersey & Raine 1990 (p. 42, pl. 12, fig. G-H) Anisian, Norian, New Zealand
as SEMIRETISPORIS
Cirilli, Buratti, Senowbari & Fürsich 2005 :
Early Norian - Rhaetian East-Central Iran
Wilson, Barron, Ainsworth et al. 2002 : reworked in Neogene
southern Victoria Land Antarctica
Sha, Vajda, Pan, Larsson et al 2011 : Rhaetian
Haojiagou area, S. Junggar Basin, northern Xinjiang NW China
(cf.) Fefilova 2011 : Early Rhaetian, Franz Josef Land Arctic Ocean
Sajjadi et al. 2010 : Late Triassic - Middle Jurassic
(pl. 1, figs 12-20) Shahmirzad, northern Semnan, Iran
Campbell 2004 a : 'late Anisian - Norian'
(Etalian - Otamitan) New Zealand
Bomfleur et al. 2014 : Rhaetian
(pl. 2, fig. 16) southern North Victoria Land, Antarctica

Figure. 1. Two cards from the John William subindex 5 for *Limbosporites antiquus* and *Limbosporites denmeadii*. Front sides (left) and back sides (right). Arrows indicate relationships of references between the two sides. Card images courtesy of Trustees of the Natural History Museum, London.

2.2.2. Palynodata (PD)

References from PD were retrieved from www.paleobotany.ru in spring 2020. References that included a taxon name only as a synonym, i.e. not as the name that should have been adopted according to the respective author, were not included.

2.2.3. Google Scholar (GS)

Google Scholar was preferred over other search engines such as Web of Science because it yielded output more comparable to the other two investigated databases. Using “”, each taxon was searched for hits in autumn 2020. For output connected to an available file (doc, html, or PDF), that file was cross-checked for the reference, and the record included only when the author indicated that it was the name that ought to be adopted. If the name was indicated only as a synonym, the citation was excluded.

2.3. Absolute number of references versus relative number of references

Many of the references recurred more than once in at least two or all three databases, and when we calculated the **absolute number** of references for a name, duplicates were excluded. In other words, we counted only the first occurrence of each citation towards the absolute number of citations. To calculate their percentage, i.e. the **relative number** of references of each database compared to the absolute number of references for each name, the number of citations was added for each database separately. Calculations of references per decade (from the 0-ending year to the 9-ending year; e.g. 1950–1959) were compared over 69 years.

3. Results

3.1. Accessibility and accuracy

The John Williams Index of Paleopalynology (JWIP) consists of handwritten DIN A6 paper cards. Each card has a front and a back side, with the front giving the name and basionym, and potential synonyms and sometimes other related names (Fig. 1). The back side gives a sequence of randomly ordered citations, but no further indication of which citation belongs to which name on the front side (except by using the author and the year as a cross-reference, compare arrows in Fig. 1). For citations of a particular name, one has to use common sense to figure out which citation refers to what.

It should be noted that the cards can only be consulted on site in London, UK, and that the data has to be copied by hand for subsequent transformation of data. This makes working with this information extremely time-consuming, especially if one intends to export all the information available on the cards. The random order of references, which probably partially reflects J. Williams’s personal sequence of reading the papers, and the sometimes ambiguous (albeit very neat) writing make exporting the data into a workable format such as a spreadsheet, hard work.

The citations give a lot of information (authorship, year, detailed geographic information such as country region, age information and even figure references). Except for the occasional minor error or lack of clarity, the information is very accurate. According to a randomized cross-check, most of the references that were checked were correct and reliable. Only in the entries for the genera *Semiretisporis* and *Limbosporites* did we observe some irregularities, with citations referring to other names. This is partially caused by basionyms and synonyms that are sometimes also referenced on the back side of the cards (see Fig. 1, top). This would be less problematic if this was done consistently but, unfortunately, not all synonyms mentioned on the front side are also in references on the back (see Fig. 1, bottom). Moreover, the missing title can make it hard to find a certain publication remotely, or directly using the internet. The hardcopy and full references in the library that is available on site partially compensates for that, but it is rather cumbersome compared to a simple online search. Nevertheless, although not always conclusive, especially when an author published several publications on the same material the same year, the geographical and stratigraphical information for each reference can aid an online search. Altogether, the output of the JWIP is generally very high and informative.

The Palynodata (PD) database gives a customizable sorted output, with citation of author, year and title, geographical and stratigraphical information. However, it should be noted that, at least when using the browser version, this data cannot be readily exported. In addition, compared to the JWIP, the geographic and stratigraphical information are not as refined, and usually only giving the reference for the paper at large and not specifically for the taxon in question. The biggest pitfall when studying user statistics is that this database, sometimes (though not always), also includes mention of a taxon name even if only mentioned as a synonym. In contrast, references in the JWIP generally give the name that was indicated as the name which ought to be adopted according to the respective author. Due to this difference, data from PD has to be more transformed (and double-checked) when studying user statistics. Nevertheless, the large amount of data available with a simple internet connection and that can be extracted relatively quickly is very advantageous.

Data gained from search engines like Google Scholar (GS) is highly variable, even from day to day. All the information (geography, stratigraphy) has to be extracted by the investigator and the accuracy thus depends on the standards and study question of the user. In our case, it still permitted to quickly check in which sense a name was used and whether or not it should be included in the user statistics, i.e. counting only those names that according to the (implied) taxonomic opinion of the author ought to be adopted. Due to the already digital format, data can also easily be exported and assembled in ones' own library, especially when working with citation programs.

3.2. Comparing the output

The total number of references integrated in the 3 databases represents 100% in the following comparisons (Fig. 2 and 3). The share of data recovery of that 100% per decade from 1950 till 2019 for each database shows that the JWIP gives very steady data recovery of around 50% from the 1950s–1980s and increasing thereafter (1990s–2000s), before declining to ca. 40% in the 2010s. PD has the highest values in the first half of the investigated time span (1950–1980), with a peak in the 1970s, but declines thereafter until the 2000s and has no records in 2010s (Fig. 2). GS gives the opposite trend with low (but existing) records only up to 20% until the 1990s, and values increasing steadily up to 80% until the 2010s.

Comparing the output for the entire period but split for the investigated taxa gives a more levelled impression (Fig. 3 A–C). Despite variations in between the investigated genera, the JWIP and PD have very similar overall output, with a slightly higher average (59%) (red lines in Fig. 3) of the JWIP compared to PD (54%) (Fig. 3 A–B), followed by GS with a big lag of only 30% over all decades (Fig. 3 C). However, the little output of GS before the turn of the century was compensated in the 2010s (Fig. 2).

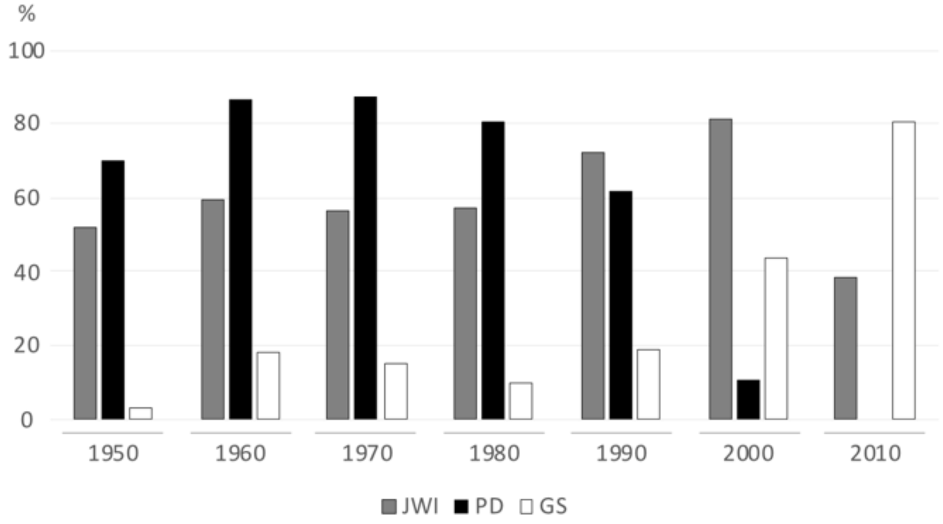


Figure. 2. Output of the compared databases as percentage of the absolute number of references per decade (from 1950–2020). JWIP = John Williams Index of Palaeopalynology; PD = Palynodata; GS = Google Scholar.

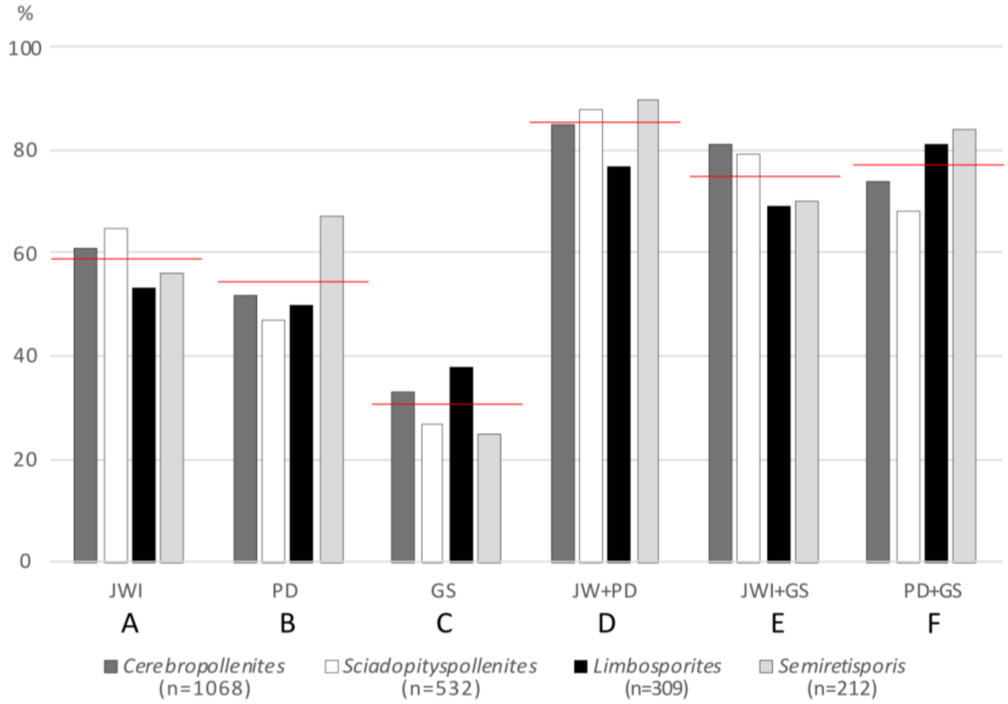


Figure. 3. Percentages of overall citations recovered from databases. JWIP = John Williams Index of Palaeopalynology; PD = Palynodata; GS = Google Scholar; n = absolute number of citations. Red Lines indicate the average percentage recovered by that database (or combination of databases).

The intergeneric changes of data output in between the JWIP and PD are driven especially by Russian and Chinese literature, which seems to be included to a lesser degree in PD. This discrepancy is not visible when comparing the JWIP with GS, which is distinguished by its rather obvious selectiveness for digital or digitised publications and creating the gap compared to the other databases.

The variation of output percentage in between genera within one and the same database is between around 12 % (JWIP and GS) and 20% (PD). The variation within one taxon between databases is between 3% and 18% more references in the JWIP compared to PD in *Limbosporites* and *Semiretisporis*, respectively (Fig. 3 A–B). Surprisingly, in *Semiretisporis*, PD has 11% more references than the JWIP. This is attributable to a lack of references for *Semiretisporis gothae*, even some very prominent ones which are given as literature references in other taxa (e.g. Mädler 1964; Schulz 1967). The fact that some of these missing references for *Semiretisporis gothae* are indicated as ‘cf.’ in the original publication can also not explain their omission in the JWIP, as such ‘cf.’ are usually also included and marked as such. The difference between the highest percentage and the lowest given by GS varies from 15% (*Limbosporites*) to 38% (*Sciadopityspollenites*). It is noteworthy that genera that include a lot of taxa described in and/or commonly used by authors who are not using English or the standard Latin alphabet, are underrepresented in PD and in our search in GS, and they are producing the biggest output difference from database to database. For example, *Sciadopityspollenites* has several taxa recombined in Russian and a 38% difference between the highest and lowest value in JWIP and GS, respectively. Similarly, *Semiretisporis* has several taxa described in Chinese or Polish and a 31% difference between the highest and lowest value in PD and GS, respectively.

3.3. Combining databases

Compared to databases standing alone, which have a relatively low output of roughly 30% (GS) to 55% (JWIP and PD) (Fig. 3 A–C), any combinations of two out of three of the databases can increase the return to 75%–85% on average at best, with the highest percentage of 85% typically achieved by combining the JWIP with the PD (Fig. 3 D–F). However, because of the lack of easy exporting functions for data in PD and especially the JWIP, this is disproportionally much more work than combining either of them with GS for an output only about 10% higher at best, since combining JWIP with GS retrieve 75% of references on average (Fig. 3 E), and 77% when combining PD with Google Scholar (Fig. 3 F).

4. Discussion

4.1. Practicality, Suitability and Output Change

In general, all databases appear based on our case study to be currently still suitable to gain information on taxon user statistics but with some limitations, depending on the study question and time available for investigation (table 2).

JWIP includes a higher number of references in total (table 2) and its slightly higher average of output than PD (Fig. 3 A) and is probably the most reliable source over the decades to get a high number of very accurate citations. Not only does it hold currently the most complete set of references, but also provides a library and, thus, a direct access to a hardcopy version of the citation. On the flipside, this index is analogous and to fully benefit of these aspects one has to travel to London working on site. This is particularly problematic in times of travel limitations, such as those imposed during the Covid-19 pandemic. Additionally, it creates a serious obstacle when operating under financial and temporal limitations, and even if the cards were available in digital form, the lack of the library is a severe loss as the cards do not provide the titles of references. These titles, however, important especially to disambiguate which publication is cited when several appeared the same year about the same material.

The analogous character of the database also poses the risk that every hardcopy library faces, the loss or misplacement of things through use. The lack of several prominent references missing in a single taxon (*Semiretisporis gothae*, see section 3.2) was especially surprising. It could be explained by either a primary bias introduced by the compiler, or secondary by the loss or misplacement of cards by the users of the index and in this given case, the number of references usually found on the card and the references missing in that taxon could explain some of the observed irregularities. Even if it is not a secondary bias introduced through loss or misplacement, one should always consider this possibility when analysing such data output since this is an inherent problem of any hardcopy collection and a growing risk when frequency of use increases. Since the cards are handwritten, exportation of the data into a workable and comparable format also needs a lot of time. For comparison, the time needed to compile the data from the JWIP was much longer than copying and pasting information from PD or GS, especially when double checking information. However, depending on the study question, the very accurate and precise data (time interval, geography, figure references) and cross-references to other synonyms, using the JWIP can still be worth it. Unfortunately, with the decreased output in the 2010s (Fig. 2) and John Williams' retirement from compiling this database after 2015, one should always consult another source for complementary recent references.

PD makes data very quickly available from two sources online through the website of the Geological survey of Canada (GSC), currently www.palynobotany.ru and https://geoscan.nrcan.gc.ca/starweb/geoscan/servlet.starweb). The Russian site is accessible through the browser, whereas PD is provided online for download by the GSC and can be run on Windows®. Since data can be sorted according to various parameters in PD, the output is quickly adjustable even if exportation of the data still has to be conducted manually when using the browser version, and takes some time. The data also appears less rigidly curated, which is probably owed to the people involved in the compilation who, although steered by a committee of experts, were not all palynologists themselves (for detail see Lentin et al. 1996). However, whether this makes a difference for the user or not depends on the study question. If one is interested in name usage, e.g. how often a name was adopted or considered to be the correct name, it makes a big difference whether the quoted references also includes names that were only cited as synonyms or not. Sometimes the references given by PD include occurrences where a name was cited to indicate or clarify synonymy, but at other times, these synonyms are not included. These inconsistencies make PD a lot less reliable and one should double-check the data according to the study questions with more scrutiny. For comparison, the JWIP only gives references for the name adopted by the author and not simply any mentioning of the name. However, if one was interested in more corpus-based work, looking for any occurrence of a name, no matter in what sense, the less differentiated output of PD might even be beneficial.

GS has proven only marginally suitable for older references compared to the two other databases. However, this might change in the future as the digitisation is further fuelled, but at the moment, a detailed taxonomical study or compilation of stratigraphic and geographic information for models (see White et al. 2009) should not be based on references from GS, as the JWIP and PD have proven themselves to provide much more abundant and precise information. One of the big pitfalls, inherent to any search engine-based output, is its high variability from IP to IP. Influenced by our browser, search history, geographical location and many other variables, the output may be very different even from one day to another and from one person to another and to some extent, the same user using different devices and/or IP addresses, and therefore biased. But the chosen example has shown that both databases, the JWIP and even more so PD, have to be complemented by another more modern source to provide younger references even at times where they were not entirely discontinued yet, but were beginning to decline (1990s and 2010s, respectively). Whether it is important to include such younger references may again depend on the study question and other constraints (see table 2). Despite its limitations, the added value of GS is undeniable for references after the turn of the century, as records strongly exceeds PD in the 2000s and the JWIP in the 2010s. It is important to note that the aim of this study was not to evaluate the overall suitability of GS as a digital source, but only to compare it with the two established databases. GS was chosen because it gave a significantly higher output than other common sources for metastudies like Web of Science, which provided an insufficient number of references to be even comparable here. To evaluate the suitability of GS today, a separate study would be needed to compile a 100% total references for the two recent decades to evaluate how many of these references are actually recovered by GS and thereby be able to better appreciate its output.

In the future, additional studies will be needed to evaluate the output and suitability of the evolving digital sources and new platforms. The new requirement to register plant names, which is not a requirement for fossil names yet but still is available, might give rise to some new databases for palynologists and paleontologists in general. It will be worth investigating how GS relates to other sources, or even how its future output compares to the one presented here.

4.2. Combining databases – which one to choose when?

In view of the discussed advantages and disadvantages, which database or combination of databases one should choose really depends on the study question, and financial and temporal limitations to conduct the study.

We found that a good workflow for taxonomic works is a preliminary consultation of PD. With www.palynobotany.ru, this database is accessible from any computer with an internet connection. The data output gives an excellent first impression of the number of citations per species or the number of species in a given genus. PD gives an elaborate and customizable output of literature references, geography, stratigraphic ranges, etc which is particularly helpful for a first overview. In many cases, the most controversial discussion of the circumscription and placement of a taxon seem to happen in the first 10–15 years after its description (compare Potonié 1956, 1958, 1960, 1966, 1970). Randomised cross-check of the given references with the closest library can give a good first impression of the standing and disputed points with the help of citations retrieved from PD. To complement the search with GS then helps to identify, whether the taxon is still in use, and the number of hits for different competing taxa can give a first insight on which is the mostly accepted name today. In many cases, this might be sufficient to clarify a taxonomic situation, especially if taxonomy is only a means to an end to answer another question which is in the focus of the study.

If irregularities are observed and/or the question is more taxonomic in its own right, e.g. a revision of a species or a genus, then the quickest way to get an overview over the number of citations over time, i.e. how commonly used and thus accepted a name is, is also to start a proper dataset from PD complemented with younger references from a search engine such as GS, to fill the gap after PD's discontinuation. According to our case study, the output might be 25% lower than it would be had the JWIP been consulted. Yet, a similar percentage would be left out if the JWIP is combined with GS. PD combined with GS is thus the most time-effective way to get a good overview. However, one should keep in mind that the references should still be checked with scrutiny as some of them might be mere synonyms.

One should also remember that the output of PD is somewhat more Western-centric. We found that publications published in other languages than English (or other Central European languages), are often not included in PD while documented in the JWIP. This might introduce an undesirable bias if taxa involved were described especially in Chinese or Russian. Whether this is the case can be fairly easily checked through PD, which is reasonably accurate in giving the first citations for most taxa. If one needs to be sure beyond 75%, or if there are indications that things might be missing, then it may be worth consulting the JWIP. However, due to its limited accessibility on site only, paired with handwritten unexportable data that has to be converted by hand into the computer, the JWIP is a bit ‘unhandy’ although the output yielded is excellent and extensive. One should note, however, that we observed for several genera that one or two species are included in the JWIP which are not in PD, and *vice versa* (compare e.g. *Limbosporites scottii, Limbosporites tubulum, Limbosporites vesiculosus*). So, if one attempted a revision of a genus, i.e. having to consider the full species inventory, a combined consultation of all available databases seems desirable. Even more so to limit the Western-centric bias. Although this is hard to avoid completely, because all databases were compiled by Western workers. Nevertheless, combination of all available databases can help be limited if consulting the JWIP which seems to contain more non-Western publications.

If one is interested in the more recent use and discussion about taxon names and associated information like stratigraphy and geographic distribution, then GS is a good source for publications after 2000. When time is limited and sources are to be consulted immediately this is a good point to start with, although further studies are needed to compare its accuracy and suitability with other search engines. In any case, it should be consulted to complement either the JWIP, PD, or both, ideally.

If one needs to get an overview and/or has a bit more time at hand for a detailed literature review, PD is again the best starting point, but should be complemented by GS for example, to fill the gap after its discontinuation after 2006. The percentage share of overall citations in our comparison was best before the 1990s for this database.

If one has easy access to the collection site in London, more time at hand, and/or if one needs a more complete reference set, especially when working on genera and/or taxa that involve a lot of Russian or Chinese literature, the JWIP is the most recommendable source of information. Its most extensive output, backed with a library directly associated, makes it a very valuable resource and workers should be encouraged to use it for detailed taxonomic work. This will not only justify its future curation to the financing authorities, but it will make very well-informed subsequent studies, honouring John William’s lifework and valuing the scientific legacy of all these visionaries, who dedicated their lifetime to compiling these databases.

4.3. Future perspectives

More than half a century ago, Robert Potoníé and his coworkers had a vision to record, sort, and continuously update palynotaxonomy, giving raise to Potonié and Kremp’s *turmae* system (Potonié & Kremp 1954), and later, to the *Synopsis der Gattungen der Sporae dispersae* (Potonié 1956, 1958, 1960, 1966, 1970), discontinued after 1970. Potonié's student Gerhard O.W. Kremp continued this legacy, financed mainly by the petroleum industry, and brought the first wave of digitisation in the 1970s to avoid a 'taxonomic chaos' (Kremp & Methven 1968; Lentin et al. 1996). Unfortunately, with funding from the industry drying up, it was again discontinued in 2006 (White et al. 2009). Similarly, John Williams compiled an extraordinary resource, but after many years of diligent and excellent work, his lifetime project is also discontinued since the 31. December 2015 (Stephen Stukins personal communication, 20. Nov. 2020). If palynology does not want to risk being discontinued itself, it needs a new wave of digitisation to preserve and update the legacy of its scientific ancestors.

Given the high quality and efforts put in both the John Williams Index of Palaeopalynology and Palynodata, it seems to be a shame to let them decay. Therefore, it might be worth discussing within the palynological community whether there are possibilities to digitise and/ or merge and/ or update these databases. We all know that our time and resources are limited, and increasingly so. However, can palynology use the current momentum towards digitisation and online resources triggered and pushed by the Corona pandemic? Like many collections, the Berlin herbarium already uses citizen-science to digitise herbarium sheets and decipher their labels for example. Can we not also use citizen-science projects to help build, digitise and/or update databases? Are there institutions who can host databases or established databases and emerging ones like the Integrative Paleobotany Portal (Pbot), that can support a concerted effort and be expanded to hold this information?

While some databases like The Lentin and Williams Index of Fossil Dinoflagellates are still striving (Fensome et al. 2019), especially terrestrial paleopalynology is hard to oversee with numerous synonyms, recombinations, and inconsistent uses. Databases provide valuable information to revise, update, and renew our taxonomy, which is at the very core of palynology, irrespective of its application. Therefore, keeping them up to date might be a necessity to keep up and stay competitive with other disciplines within and outside of palynology.

Table 2: Comparison of advantages (+) and disadvantages (–) of the compared databases

	John Williams Index of Palaeopalynology	**Palynodata**	**Google Scholar**
time interval	pre-Quaternary	pre-Quaternary	Not time specific
content	ca. 25,550 references (in 2020) (discontinued after 31st December 2015)	22,152 references (discontinued after 2006)	number of references continuously changing (continued)
compilation	compiled by the single author John Williams	compiled by a consortium of institutions and different palynologists	compiled by Google's software
accessibility	(–) accessible only on site at the Natural History Museum London	(+) easily accessible online via GSC Open File & www.paleobotany.ru	(+) easily accessible via internet (∿) variable results from IP to IP
bibliography	citation of author/s and year	citation of first author, year and title on overview page, detailed citations demands further clicks for each individual reference in browser version	variable
form	(–) handwritten, therefore (–) not readily exportable (∿) writing potentially ambiguous	digital offline on windows, online in browser, output customizable	digital but output dependent on IP, browser, search engine, keywords, … Variable not curated and potentially biased output (reference, html, file, …)
literature	(+) at the same time a repository for the cited literature (–) literature available as hardcopy only	(–) no literature available	(+) at the same time a repository for the cited literature (+/–) literature available with on click if accessible
output/ up-to-dateness	(+) good average recovery of citations over all investigated decades, BUT (–) not updated since 01/2016	(+) good recovery of especially older citations (especially until 1990s) (–) not updated since 2006	(+) increasing number of references especially from the 1990s, with upward tendency
completeness (in the given comparison)	(+) high number of references in database comparison (average 58%)	(+) high number of references in database comparison (average 55%)	(–) lowest number of references in database comparison (average 38%)
When to use (best)?/ For what best suitable?	• old-older references (before 2010) • detailed research • to avoid long literature search (of rare pieces) when on site access possible • if hard to get publications (in foreign languages and alphabets involved)	• old references (before 2000, best before 1990) • getting a quick overview (e.g. number of taxa per genus, authors of taxa., stratigraphy, geography)	• younger references (from 2000) • little time available • immediate access to literature needed • to complement either the JWIP or PD

5. Conclusion

Our study demonstrates empirically for the first time that the discontinued databases John Williams Index of Palaeopalynology and Palynodata still yield very similar output. Given the higher number of references, specialist literature, steady output throughout the decades, and higher accuracy of references, the John Williams Index of Palaeopalynology is (for the moment) the most desirable database to use if one has the time and permission to use it. Palynodata offers a quick and first overview and a still very high and fairly accurate output if time is more limited. Google Scholar cannot yet replace either of the two, but it is a useful complementary database, especially with Palynodata, because GS complements the younger references for the handy database. Such combination amounts to an output of at least 75%, irrespective which database is chosen, which might be the most cost-benefit effective combination to avoid a disproportional amount of additional time needed to consult all of them.

The presented databases all have their advantages and disadvantages, and which one or which combination of databases is the most suitable depends on the study question. All of them provide valuable information for the paleopalynologist, especially those working on nomenclature and taxonomy. After all, even if it doesn't change the essence of the objects we are working with, the names we use can make the difference between rejection and acceptance.

6. Acknowledgements

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Chapter 6

Name Usage Statistics (II): Indices to quantify name usage

Abstract

A major and recurrent issue in nomenclature and taxonomy is synonymy and the occurrence of competing names for a same taxon. Formal proposals for conservation, protection, or rejection of names are a painstaking but necessary work, which for extant plants, often requires consulting the frequency of usage of competing names in floras. In paleopalynology such information can be gathered in a cumbersome consult of the numerous publications to create a census of name usage by working, for instance, with paleopalynological databases, which provide easily accessible quantitative data on how frequently each given taxon name is used. Here, we show that such information can be employed not only for taxonomic revisions, but also to calculate three simple metrics, i.e. Citation Share (CS), Citation Rate (CR), and Establishment Index (EI), and quantify how widespread the usage of a name is on its own, or in comparison to potentially competing name(s). Using three case studies, we demonstrate how our proposed metrics, analogues to those used to evaluate academic output or diversity, for example, can easily be used to present how usage of a name of a taxon changed over the decades, especially for competing names. Independently of the study question, our proposed metrics provide a fast overview of popularity of names and abundance of the respective taxa in species inventories (CS and CR), and a concise compound metric to represent the standing of a name for competing names today (EI). Their advantage is that they encode information that would otherwise require rather lengthy enumerations and space-consuming visual representations. They are therefore an effective tool to represent data in a short and concise way to clarify disadvantageous taxonomical and nomenclatural problems, and can support informed proposals for either conservation, protection or rejection, which are typically very limited in space for the respective argument.

1. Introduction

A common endeavour in taxonomic work is to first find the 'correct' name, i.e. the name that applies to a taxon with a particular circumscription, position, and rank, according to the rules of the *International Code of Nomenclature for algae, fungi, and plants* (hereafter referred to as *Code*) (Turland et al. 2018: Art. 11). Unfortunately, this seemingly simple task is too often complicated by the occurrence of competing names, i.e. synonyms, from which one has to consider valid publication, legitimacy, priority, and several other aspects that could prevent a name from being the one that ought to be adopted (Gravendyck et al., submitted).

In paleopalynology, using databases (see Taxon Usage Statistics I) like the John Williams Index of Paleopalynology or Palynodata, can help to provide an overview about the taxa described within a genus, as well as potential synonyms, often deriving from numerous recombinations and potential confusion. Analysing usage statistics paired with a taxonomic reevaluation might even reveal that the most commonly used name might not be the correct name.

To ensure taxonomic and nomenclatural stability, the *Code* thus provides the tools to propose conservation, protection, or rejection of names (Turland 2018: Art. 14, 56 and F.2). However, in order to make such a proposal, it is important to provide a statement of the case and arguments for or against such treatment. Additionally, one should quantify how widespread the usage of the competing names is and prove that one name is threatening the other. Depending on the argument, one can then 'reject' the threatening name and thereby 'protect' the correct one, or 'conserve' that competing name which is nomenclaturally not 'correct' (McNeill et al. 2018; Turland 2019).

Quantification of the usage of a name in comparison to competing name(s), however, is often difficult to assess. For instance, sometimes new taxa are described but their names are hardly used thereafter, either because of the rarity of the taxon or because of an unfortunate series of reasons, such as a lack of efficient communication to the scientific public, e.g. through publication in a non-English language, or in a poorly accessible publication. Such names might be called "poorly established", while others are readily accepted and frequently used thereafter, and thus become "well established".

Here, we thus present three case studies on the frequency of the usage of names of taxa without and with competing synonyms to illustrate the variance of their establishment. We propose three simple metrics, the **Citation Chare (CS)** and **Citation Rate (CR)** to represent name usage for isolated names or species inventories, and the relative **Establishment Index (EI)** mainly to refer to the degree of "establishment" of a name in comparison to its competing names. We aim to demonstrate that our rather simple numerical metrics can replace lengthy decadienal representations of taxon usage which can be employed for taxonomical purposes, and provide a practical tool for nomenclature to quantify how widespread competing names are to support informed proposals for conservation, protection, or rejection.

2. Material and methods

2.1. Studied taxa

Name usage for several names of spores were compared in three case studies. The **first case study** is a species inventory of the genus *Semiretisporis*, as one might do when attempting a revision of this genus typical for the Rhaetian, and limited to the Middle/Late Triassic to Early Jurassic (Reinhardt 1961; Orłowska-Zwolińska 1966; Schulz 1967; Bai et al. 1983; Shang & Li 1991). A full species list with authorities is provided in the supplements (supplementary file 1).

Based on the overview gained from this case we chose two cases to look at in more detail, one for homotypic synonyms (case 2) and one for heterotypic synonyms (case 3).

The **second case study** is about *Callialasporites denmeadi* DE JERSEY 1962, which typically occurs in the Middle to Late Triassic (de Jersey 1962; Playford & Dettmann 1965; de Jersey 1970; de Jersey & Raine 1990a), and its subsequent recombinations as *Lundbladispora denmeadi* (DE JERSEY 1962) PLAYFORD & DETTMANN 1965, *Semiretisporis denmeadii* (DE JERSEY 1962) DE JERSEY 1970, and most recently *Limbosporites denmeadii* (DE JERSEY 1962) DE JERSEY & RAINE 1990 (de Jersey 1962; Playford & Dettmann 1965; de Jersey 1970; de Jersey & Raine 1990a).

2.2. Data acquisition

According to the principles laid out in Taxon Usage Statistics (I), citations for each taxon were retrieved from the John Williams Index of Paleopalynology (JWIP), Palynodata (PD), and Google Scholar (GS). For the second case study, due to the limited availability of the JWIP data on *Callialasporites denmeadi* DE JERSEY 1962, *Lundbladispora denmeadi* (DE JERSEY 1962) PLAYFORD & DETTMANN 1965 references from this database for these names could not be included for subsequent analysis. Data for all other studied taxa was available from PD and GS. In contrast to the previous analysis in Taxon Usage Statistics (I), citations from 2020 were also part of the analysis, to include the most recent usage of names.

2.3. Data analysis and visualisation

Quantitative data of the number of citations per decade was plotted as stacked columns (Fig. 1). However, since the focus of this study is to analyse how well a certain name is established amongst the scientific community, citations that are (co)authored by the same person who described the name for the first time (**self-citations**) are treated separately and stacked in white on the **non-author citations** (Fig. 1).

To produce numerical representation that encode information from such visual representations more concisely, we propose to calculate three metrics: (1) Citation Share, (2) Citation Rate, and (3) the compound Establishment Index. Since the author is necessarily aware of the name he created, self-citations are always deducted in these metrics.

The **Citation Share (CS)** is the percentage of the total number of non-author citations of a name divided by the total number of citations (self-citations + non-author citations = 100%). The citation share is thus independent of time and can be calculated either for a single name to quantify the numerical relation of its non-author citations in relation to self-citations (individual CS or $\mathrm{CS_I}$ in equation 1a), or for several names in relation to each other and in relation to the self-citations (group CS or $\mathrm{CS_G}$ in equation 1b).

$$\mathrm{CS_I}\ (\text{in }\%) = \frac{\textbf{non-author}\text{ citations for name in question}}{(\textbf{self-citations} + \textbf{non-author}\text{ citations for that name})} \times 100 \tag{1a}$$

and

$$\mathrm{CS_G}\ (\text{in }\%) = \frac{\textbf{non-author}\text{ citations for name in question}}{(\textbf{self-citations} + \textbf{non-author}\text{ citations for name1+name2+…})} \times 100 \tag{1b}$$

Practically, the $\mathrm{CS_I}$ for the hypothetical name *Nomen primum*, which has 10 citations from authors other than the author(s) who first published it and never cited it again, would roughly be 91%:

$$CS_I= \frac{\text{10 non-author citations}}{\text{(1 self-citation + 10 non-author citations)}} \text{ x } 100 = \frac{10}{11} \text{ x } 100 = 90.9\%$$

However, if the hypothetical name *Nomen primum* has 10 citations from authors other than the author(s) who first published it and cited it later in 2 publications, the CS would logically be lower and about 76.9%:

$$CS_I= \frac{\text{10 non-author citations}}{\text{(3 self-citations + 10 non-author citations)}} \text{ x } 100 = \frac{10}{13} \text{ x } 100 = 76.9\%$$

Now, if *Nomen primum* is rivalled by *Nomen secundum,* with also 10 non-author citations after its (later) publication, both two names would have a similar CS of roughly 45%, if none of them was cited later by their respective authorities:

$$CS_G= \frac{\text{10 non-author citations (for either name)}}{\text{(2 self-citations + 10 non-a. } \textit{N. primum} \text{ + 10 } \textit{N. secundum}\text{)}} \text{ x } 100 = \frac{10}{22} \text{ x } 100 = 45.5\%$$

However, if like in our second example, *Nomen primum* was cited later 2 times by their own authorities, it would also logically end up with a lower CS_G than its rival *Nomen secundum,* even if it is overall cited 3 times more.

$$CS_{G\ \textit{Nomen primum}}= \frac{\text{10 non-author citations (for either name)}}{\text{(3 self-cit. + 10 non-a. } \textit{N. primum} \text{ + 10 } \textit{N. secundum}\text{)}} \text{ x } 100 = \frac{10}{23} \text{ x } 100 = 43.5\%$$

$$\mathbf{CS}_{G\ \textit{Nomem secund.}} = \frac{\text{10 non-author citations (for either name)}}{\text{(1 self-cit. + 10 non-a. } \textit{N. primum} \text{ + 10 } \textit{N. secundum}\text{)}} \times 100 = \frac{10}{21} \times 100 = 47.6\%$$

Note that a name can have the maximum value close to, but never 100%, because the first publication is necessarily a self-citation by default. Thus, the higher the percentage is, the relatively more frequently an individual name is likely adopted by other authors (CS_I), or the more frequently it was chosen over competing names (CS_G), irrespectively of time.

To include a temporal element and calculate how frequently a name is used on average per year we calculate the **Citation Rate** (**CR**), dividing the total number of citations of a name (excluding self-citations) by the number of years that have passed since the name was first described. The calculation can be summarised as follows:

$$\textbf{(2)} \qquad \mathbf{CR} = \frac{\textbf{non-author}\text{ citations}}{\text{number of }\textbf{years since description}}$$

Practically, if our *Nomen primum* and *Nomen secundum* were published 10 and 5 years ago, their CR would be 1 or 2, respectively.

$$\mathrm{CR}_{\textit{Nomen primum}} = \frac{\text{10 }\textbf{non-author}\text{ citations}}{\text{10 years}} = 1$$

$$\mathrm{CR}_{\textit{Nomen secund.}} = \frac{\text{10 }\textbf{non-author}\text{ citations}}{\text{5 years}} = 2$$

The lowest possible value of the CR is zero, i.e. when the name has never occurred in non-author citations, and the higher the value, the more frequently it is used. For example, a value of 0.1 / 1 / 1.5 indicates that the name in question was used once in 10 years / once per year / thrice in two years, respectively. The CR is therefore a simple average frequency, but does not yet represent how 'established' a name is currently, i.e. how likely a name is chosen especially in comparison to other competing names.

To produce a metric that considers the proportional usage of a name in comparison to other names and relative to time, we propose to calculate an **Establishment Index (EI).** It is a compound metric that divides the Citation Share (CS) of the name in question by the number of years that have passed since its description. Theoretically the EI can be calculated for an isolated name using the CS_I , yet for isolated names this is not more informative than the Citation Share itself. For competing names, however, it integrates the relative and temporal aspects for various names, calculated as follows:

$$\text{(3)} \qquad \mathrm{EI} = \frac{\mathbf{CS_G}\text{ of name in question}}{\text{number of }\textbf{years since description}}$$

Practically, our *Nomen primum* published 10 years ago and *Nomen secundum* 5 years later, and which like in our first examples, have both the same number of self- and non-authors citations, they would thus have an EI of 4.5 and 9, respectively.

$$\mathrm{EI}_{\textit{Nomen primum}} = \frac{\mathbf{CS_G}\text{ of }\textit{Nomen primum}}{10} = \frac{45}{10} = 4.5$$

$$\mathrm{EI}_{\textit{Nomen secundum}} = \frac{\mathbf{CS_G}\text{ of }\textit{Nomen secundum}}{5} = \frac{45}{5} = 9$$

The EI of the *Nomen secundum* is logically twice as high than the EI of the *Nomen primum* because the second name has acquired the same amount of citations in only half the time, indicating not only that it is cited twice as much but also that it is the name which was favoured over the first one in recent times, and is therefore more likely to be adopted and become even more better established. If we imagine both names to be synonymous, *Nomen secundum* would pose a threat to *Nomen primum,* but lacking priority over the first name. Nomenclatural action would hypothetically be needed to ensure nomenclatural and taxonomic stability, for example the younger name could be conserved and the older name could be rejected.

The EI thus provides the metric to indicate how well a name is currently 'established' amongst the scientific community, in comparison to the other competing names. Zero values of this index indicate that the name has never been used by any members of the scientific community after its original description, or only in publications (co)authored by the author of the name itself. In contrast, the higher the value the more 'established' is the name.

3. Results

3.1. Case 1 – species inventory

Preparing a later taxonomic revision of *Semiretisporis*, we compared how often the different species names described for the genus are used in the first case study (Fig. 1). Looking at the visual representations of name usage, it is immediately apparent, that out of the 12 names the majority is hardly used at all. The seven names with very low CRs, which are below a chosen threshold of 0.1, have less than one citations in 10 years. They mostly have very low citations shares (mostly 50% or less) as well, which indicates that they were never broadly accepted (Fig. 1). Those five names that do get used more often (Fig. 1 B, C, E, H, L) are also clearly indicated by relatively higher CRs.

The most frequently used name is *Semiretisporis gothae* with almost 2 citations per year since its description 60 years ago. Additionally, it has the highest CS_I (98%), indicating that it is a very well accepted name with much fewer self-citations in relation to the non-author citations. The second most frequently used name is *Semiretisporis maljavkinae* (CR=0.49), followed by *Semiretisporis denmeadii* (CR=0.36), *Semiretisporis antiquus* (CR=0.13) and *Semiretisporis wielichoviensis* (CR=0.11). While *Semiretisporis maljavkinae* has also a high CS_I (96%), the other three names have a CS_I of less than 50% or maximum 67% (*Semiretisporis denmeadii*). A potential reason for the relatively poor acceptance by the community could suggest, that this is due to some late synonymisation with another name, leading to reduced usage of the name in later years, reducing the number of overall citations, and thus reducing the CS_I. Upon closer taxonomic inspection we realised that *Semiretisporis denmeadii* and *Semiretisporis antiquus* are indeed homotypic synonyms with earlier and later recombinations, which are looked at in case study 2 in more detail. *Semiretisporis maljavkinae* and *Semiretisporis wielichoviensis* were identified as potential heterotypic synonyms which is discussed further in case study 3.

3.2. Case 2 – homotypic synonyms

The basionym *Callialasporites denmeadi* was recombined at least three times with different genera (Fig. 2 A). The basionym was not cited again until its first recombination, and therefore its CS_G, CR, and EI are all zero (Fig. 2 A-1). Recombinations with *Lundbladispora*, *Semiretisporis*, and *Limbosporites*, depict a transitional raise and fall of the number of citations over the decades (Fig. 2 A). With each new published recombination, the former one gets cited less, giving a successional impression from one recombination to the next and all recombinations have relatively similarly low CR ranging from 0.2-0.5. However, while *Semiretisporis denmeadii* has the highest citation share of the three with a CS_G of 30%, it only has an EI value of 0.6, whereas *Limbosporites denmeadii* has EI value of 0.83 despite having CS_G of only 25%.

3.3. Case 3 – heterotypic synonyms

After the preliminary screening of the species inventory in case study 1, and the identifications of homotypic synonyms in case study 2, there were only two relatively frequently used names (CR= minimum 0.1) left: *Semiretisporis wielichoviensis* ORŁOWSKA-ZWOLIŃSKA 1966 and *Semiretisporis maljavkinae* SCHULZ 1967. To clarify how these distinguish from the other taxa and from each other, we consulted the original diagnoses and type material which suggested that they might be conspecific.

The holotype for the later name *Semiretisporis maljavkinae* was available for study (Fig. 3 B), but the holotype for *Semiretisporis wielichoviensis* was not and could not be relocated yet. If one compares the holotype and drawing from Schulz (Fig. 3 A and 3 B) with the holotype depicted in Orłowska-Zwolińska (1966, Pl. 4, Fig. 23), there is indeed no significant difference beyond some size variation. Based on the observed intraspecific variation in the Bonenburg section (Fig. 3 C and 3 D) the size appears to be variable ranging from smaller forms (Fig. 3 C) which comply in size with Orłowska-Zwolińska's holotype, to larger forms (Fig. 3 D) which comply in size with Schulz's holotype. As size is a highly variable feature in general, we consider the two holotypes to be conspecific, due to lack of other distinctive features.

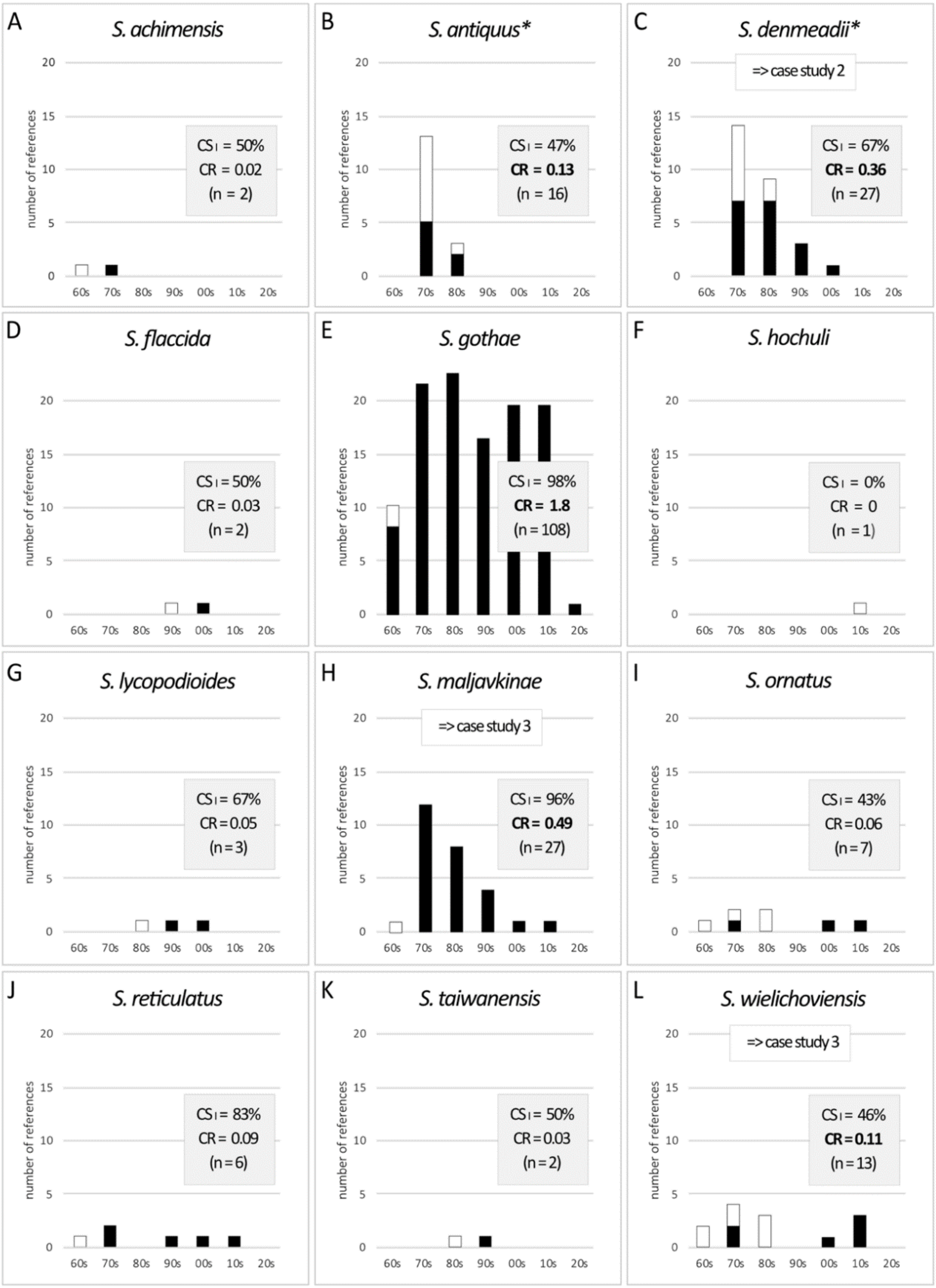


Fig. 1. Case study 1: species inventory of the genus *Semiretisporis*. Usage of the names in each case is plotted as columns per decade. Self-citations (in white) are stacked on top of citations of publications that were not (co)authored by the author of the name (grey scale-coloured columns). For each name the **Citations Share** ($\mathrm{CS_I}$ for individual names in %), **Citations Rates** (**CR**) of the overall number of self- and non-author citations (**n**) is given. Citation Rate values above a threshold of 0.1, i.e. one citation in ten years is indicated in bold. Names indicated with an asterisk (*) are homotypic synonyms, recombined with different genera.

Although described only one year apart, this makes *Semiretisporis maljavkinae* the junior heterotypic synonym of *Semiretisporis wielichoviensis* following the principle of priority. However*, Semiretisporis wielichoviensis* has a very low CS_G of 14.2% and EI of 0.27 (Fig. 1 D.1) compared to its junior synonym *Semiretisporis maljavkinae* which has a CS_G 65.85% and EI of 1.24, indicating the synonym is much better established (Fig. 1 D.2).

4. Discussion

4.1. Comparison of the metrics

4.1.1. Citation Share (CS_I and CS_G)

The CS_I (Citation Share for individual names) gives the most straight forward impression about how well a name is adopted by the scientific community. This was illustrated by many names in the species inventory (case 1) with low CS_I of 50% or less, i.e. with half or more than half of the number of citations being self-citations. One reason for such low values could be, that the name was immediately or soon afterwards recombined with another name and was thus not used much afterwards as we demonstrated for *Semiretisporis denmeadii* and which is also true for *Semiretisporis antiquus,* which was recombined with the same list of genera (Playford & Dettmann 1965; de Jersey 1970; de Jersey & Raine 1990a). Potential synonymy should therefore be considered for several of the other names with very low CS_I in case study 1, which will need additional taxonomic evaluation. The low CS_I in very recent names, e.g. *Semiretisporis hochuli* (Paterson & Mangerud 2019) on the other hand, can be explained by the limited time available for re-use of the name.

These arguments illustrate that the information encoded in the CS_I provides a good tool and starting point for subsequent taxonomic revisions. Although the same information can be provided by visual representations by different colours for self-citations and non-author citations, the numerical expression is just as effective and more precise, and save precious space and time.

The second case study of the recombinations of the basionym *Callialasporites denmeadii* showed that the Citation Share for competing names (CS_G) provides a fast overview on which name is the most commonly used name (*Semiretisporis denmeadii* with 30%), even when several names are available. It is noteworthy though that the most abundantly used names are not necessarily the currently used ones. If one looked only at the CS_G, we might get a distorted impression about current name usage. *Semiretisporis denmeadii* for example gets cited more frequently in total but was not cited in the last two decades. Instead, the recombination

Limbosporites denmeadii was adopted, but so far a lower CR (25%). The CS_G therefore gives a good first overview for competing names but cannot represent current name usage because the metric does not consider time.

4.1.2. Citation Rate (CR)

This aspect of time is then included in the CR, which gives a fast first overview on how frequently a name is used per year since its description. The first case study illustrated, how fast one can identify the most frequently used names of the species inventory. This allows fast identification of those taxa which might be most important taxa in the genus (e.g. *Semiretisporis gothae* and to some extant *Semiretisporis maljavkinae*).

Names that are used less than once in ten years (i.e. CR<0.1) are used so rarely, that it is unlikely the result of the biological scarcity of the described taxon. These are names that are assumed to be taxonomically identical to other names, which might have led to their fast synonymisation, or might be nomenclaturally problematic. They might lack valid or effective publication, which might explain the lack of acceptance amongst the scientific community as well. Names published in non-English languages (e.g. *Semiretisporis flaccida* SHANG & LI 1991) might have been less effectively communicated to the scientific public due to the language barrier and/or poorly accessible publications.

Relatively infrequent usage, i.e. less than once a year but more often than once in ten years (CR=1 to 0.1) might be explained be the relatively rarity of the respective taxon, e.g. *Semiretisporis maljavkinae*, which is much rarer, but generally co-occurs with *Semiretisporis gothae* (Schulz 1967; Morbey 1975; Gravendyck et al. 2020c). Alternatively or additionally, such relative infrequent usage might also indicate that the names was later synonymised as a homotypic synonym (case 2) or is in fact rivalled by another heterotypic synonym, which causes reduced CRs for either of the two synonyms (case 3).

These considerations demonstrate the encoded information and possible deductions that are available through the CR. Visual representation cannot illustrate such information beyond the more subjective impression of frequent, infrequent, or rare. The proposed CR permits representation of the same information in a much more concise way. On top of that, it provides a numerical value that allows easy comparison amongst taxa, for example in species inventories, and that is much more informative than just the absolute numbers of citations because of the temporal elements they include.

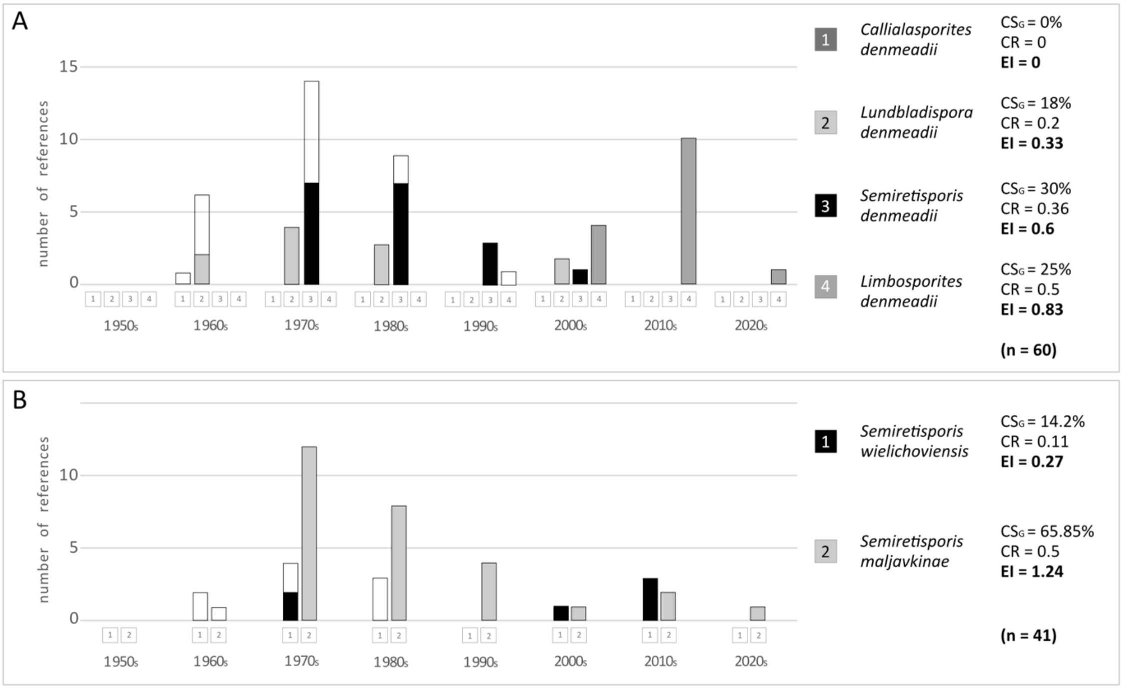


Fig. 2. Case study 2 and 3: competing names. A. homotypic synonyms. **B.** heterotypic synonyms. Usage of the names in each case is plotted as columns per decade. Self-citations (in white) are stacked on top of citations of publications that were not (co)authored by the author of the name (grey scale-coloured columns). For each name the **Citations Share** (**CS_G** in %) of the overall number of citations of all competing names (including self-citations)(**n**) is given. **Citations Rates (CR)** and **Establishment Index value (EI)** are given for each name.

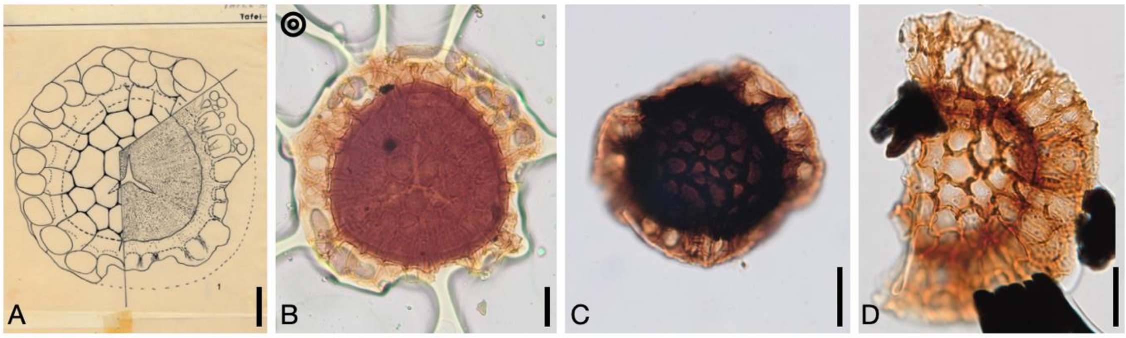


Fig. 3. *Semiretisporis maljavkinae* SCHULZ 1967. Holotype indicated with a double circle. **A.** Original ink drawing of the holotype for *Semiretisporis maljavkinae* from Schulz inheritance (Gravendyck et al. 2020a) **B.** restudied holotype for *Semiretisporis maljavkinae*. **C** and **D.** Specimens from the same taxon from the Bonenburg section (Gravendyck et al. 2020c). Holotype material from Orłowska-Zwolińska was not available for this study, but restudying the holotype from Schulz together with photographs for holotype for *Semiretisporis wielichoviensis* from Orłowska-Zwolińska (1966) and material from Bonenburg suggests that the two species are conspecific. Scale bar = 20 µm.

In screenings of species inventories like in the first case study, the CR provides and efficient tool to highlight those names that might be most relevant for taxonomic revisions, i.e. those names that have been synonymised before, or should be synonymised in the future. For competing names, however, case 2 exemplified that the name with the highest CS (*Semiretisporis denmeadii*) does not have the highest CR and vice versa. Although *Semiretisporis denmeadii* used to be the most established name in the 1970s to 1990s usage of the name decreases in the 2000s, which is likely the result of the dissemination and recombination of the species by de Jersey and Raine (1990). After a transitionary phase in the 2000s the name is not used anymore and *Limbosporites denmeadii* is used instead causing the higher CR value of the latter despite its still lower number of overall citations.

Due to the component of time in the metric, the CR represents the frequency of usage (i.e., average of non-author citations per year) and can arguably better represent the current establishment of the name than the CS_G. Yet, for the evaluation of the current establishment, the proportional aspect of names in relation to other competing names is important. Potentially conflicting results of the CS_G and CR as in case study 2, indicate that these two metrics should be combined when evaluating the actual establishment of competing names.

4.1.3. The compound Establishment Index (EI)

The EI is inspired by other compound metrics, like the Shannon-Wiener Index (Shannon 1948; Spellerberg & Fedor 2003), which combines a simple counting metric (richness, which is here similar to the CR) with a proportional metric (evenness, which is here the CS_I/CS_G,).

While the CS_I and CR are very informative for individual names (e.g. in species inventories, case 1), cases 2 and 3 demonstrated that the CS_G and CR can give conflicting impressions when comparing usage of competing names. The EI combines the advantages of both these metrics considering proportion and time, therefore indicating which is the most "established" of the competing name. It synthesises information available from visual representations and the other two metrics in one number and is therefore the most concise metric to represent more accurately the establishment of a name today.

4.2. When to use which metric

Like many other metrics to evaluate diversity, academic output, or else, it depends on the question of interest which metric, or combination of metrics, is best to look at and use. This also applies also for the metrics presented here, and especially depends on whether one is looking at isolated names (especially for taxonomic purposes) or at competing names (for taxonomic and nomenclatural purposes).

To summarise, the CS is a proportional metric independent of time. It indicates how relatively often a name was used by subsequent authors in comparison to self-citation (CS_I), or how relatively often it was chosen over other competing names by subsequent authors (CS_G). The CR represents the frequency of usage of a name (average citations pe year). The EI is a compound metric combining the temporal and proportional qualities of the CS_G and CR to express how established a name is in relation to other competing names.

If one conducts a screening of a species inventory (as in case 1) or studies a taxon that is assumed to have only **one name**, one should look at the **CS_I and CR**. The CS_I depicts how well the name was adopted by other authors. The lower the value the more self-citations the name has relatively to non-authors citations, and the less established it likely is. The CR also informs how frequently the name is actually used. Low CRs then can imply that the taxon is rare, but it might also mean that it is believed to be superfluous, i.e. that there might be another name that is used to describe this taxon. Using these metrics can thus inform taxonomic works and aid revision processes.

If one is looking at **competing names**, one could theoretically use the CS_G and CR together. To avoid conflicting or ambiguous results, and safe precious space and time, one should use the **EI**. The higher the value, the more established a name is in relation to the other names one is comparing it with. This metric is especially useful to support the evaluation of how widespread a name is and whether one name is actually threatening another, to support a proposal of (a) name/s for conservation, protection, or rejection. Especially for such proposals, which need to be detailed, but relatively short and concise (McNeill et al. 2018; Turland 2019), the EI presents and efficient tool to support and quantify the proposed argument.

4.3. Supporting a case for conservation?

Using the EI, our third case study illustrated that the younger name *Semiretisporis maljavkinae* is much more established than the name that has priority, i.e. *Semiretisporis wielichoviensis*, and which should be favoured according to the rules of the *Code* (Principle III).

Although both are non-English publications, *Semiretisporis wielichoviensis* was published in Polish and *Semiretisporis maljavkinae* in German, and the German school of palynologists was well-known, thanks to prominent figures like Potonié's and his coworkers, especially Kremp who was later very active in North-America (Piel 1994; Jansonius & McGregor 1996; Mangerud et al.

2016; Riding et al. 2016). Together with the *Synopsis der Gattungen der Sporae dispersae* (Potonié 1956, 1958, 1960, 1966, 1970), these authors brought on German palynology and publications to greater international attention, and might have fostered the increasingly dominant usage and establishment of the junior synonym *Semiretisporis maljavkinae.*

Trying to reinforce the senior synonym through a taxonomic revision might then cause more taxonomic instability than it might help. In such a case one can consider to conserve the more widely used name, i.e. *Semiretisporis maljavkinae* against *Semiretisporis wielichoviensis,* if one can demonstrate that another name is threatening the name that is ought to be adopted under the rules of the *Code* (McNeill et al. 2018; Turland 2019). With the help of the EI, we illustrated the discrepancy between the two names and quantified the necessary evidence that *Semiretisporis maljavkinae* is indeed better established and thus threatening *Semiretisporis wielichoviensis.*

A reason to support conservation of *Semiretisporis maljavkinae* could be the availability and good preservation of the holotype of *Semiretisporis maljavkinae,* while the other name would need lecto- or neotypification to ensure consistent and stable application of the name. In this context it should be considered that not even the original photograph of the holotype for *Semiretisporis wielichoviensis* can be currently reproduced, without risking copyright issues (see section 1.1). Unless one can get permission from the surviving family there is no publishable material to support a taxonomic study. Based on the given arguments one could attempt a proposal for conservation of the name *Semiretisporis maljavkinae* (which implies rejection of *Semiretisporis wielichoviensis*).

As the most concise metric of those presented, the EI provides the necessary quantitative data needed in the most space efficient way, which is important for such proposals. This compound metric thereby provides an efficient tool to aid taxonomical as well as nomenclatural works.

5. Conclusions

The present study provides three case studies that exemplify the benefits of three newly developed metrics to evaluate the quantitative usage of names over time. The CS_I and CR provide helpful tools to evaluate name usage of individual names and can thereby inform taxonomic revisions. The EI, as a compound metric consisting of the CS_G and CR, provides a powerful tool to compare name usage of competing names (homotypic and heterotypic synonyms) and can support potential proposals to conserve, protect or reject names according to Art. 14 and 56 of the *Code*. The proposed metrics summarise and synthesise information that would otherwise have to be presented in rather lengthy and space-consuming texts, and/or visual representations of name usage. We hope that the newly proposed metrics will be widely accepted to aid taxonomic, as well as nomenclatural works, to use corpus-based information available from databases in palynology and beyond.

6. Acknowledgements

We are very grateful to Stephen Stukins (Natural History Museum London) and Niall Paterson (CASP, Cambridge) for sharing photocopies of the JWI cards. JG thanks Wolfram Kürschner (University of Oslo, Norway), who organised a visit to the Geological Survey of Austria, which brought her for the first time in contact with type material and associated challenges that inspired this paper. Furthermore, we thank Maria Schauer (Freie Universität Berlin) for her diligent help with compiling part of the dataset. We sincerely thank Nicholas Turland (Botanical Garden and Botanical Museum Berlin) for his inspiring insights on taxonomy and nomenclature that informed this study and for commenting and editing on *Code* related topics of this manuscript. We thank Jim Riding (British Geological Survey), who assisted in solving copyright questions about potential reprint of Orłowska-Zwolińska's images.

Chapter 7

Revisiting the Rhaetian: review and reevaluation of types and diagnoses in view of Bonenburg's palynomorphs

Abstract

In contrast to extant botany for example, palynology is lacking comprehensive floras. Instead, the palynologist has to compile a body of literature on which he bases his subsequent classifications. Unlike aquatic palynology, the corpus of literature for terrestrial taxa is much less curated, revised and regularly updated and literature containing original diagnoses is increasingly hard to come by. This chapter provides the most comprehensive catalogue of terrestrial palynotaxonomy for the Rhaetian from the Germanic Triassic. It gathers diagnoses for some of the most important and recurrent taxa, and provides for many the first English translations. We compare the infraspecific variation observed in Bonenburg with relevant holotypes to better understand the variation included in each taxon, and make emendations, recombinations and new descriptions where necessary. Additionally, we point out the preservation of important holotype material and point out where epi-, lecto- or neotypification is needed. We also point out, that neotypification is currently problematic in palynology and paleobotany, because of a coded paradox in the *Code*. To rectify this, we also propose an emendation to the Code, to ensure future neotypification, which are needed not only in the observed holotype material, to ensure taxonomic stability and reliable application of names.

1. Introduction

Palynological studies are to a great extant based on taxonomic descriptions, therefore taxonomy is the backbone of every palynological study and its subsequent applications. Compared to the taxonomy of extant organisms, the taxonomy of fossils represents a parataxonomy that applies taxonomic principles not only to the entire unit of an organism but to parts of a plant or to parts of a live cycle of a plant (Forey et al. 2004). Each of these parts used to be referred to as a morphotaxon, each with its own name as famously exemplified by Thomas (1981 in Forey et al., 2004) for the extinct lycopod *Lepidodendron* to which at least nine different morphotaxa for different parts of the plant are associated (compare Text-Fig. 1). The spore *Lycospora* for example can be affiliated with the lycophytes through *in situ* finds in *Lepidstrobus* (Balme 1995) which illustrates how dispersed palynomorphes can be affiliated with taxa of higher rank as employed in chapter 3 for environmental reconstructions. Today the morphotaxon is replaced by the more flexible fossil-taxon concept, which can refer to a part of the plant, life-history stage or preservational state (compare chapter 6).

As opposed to the standard classification keys in extant botany, palynotaxonomical literature is a series of diagnoses usually organised in a morphology-based system of suprageneric categories (*turmae)* (Potonié 1956; Dettmann 1963). Even though artificial, i.e. not following the systematics of the assumed but often unknown mother plants, this system was first devised by Potonié and Kremp (1954), continued in Potonié (1960, 1958, 1956), further developed by (Dettmann 1963), and most recently by Burger (1994). The latest system is followed here to present the palynotaxonomy that was used for and further developed in this thesis. This *turmae*-system does not follow the *Code* and is rather intended to serve classification, and thus to function like a (classification) key (Potonié 1956).

Without an equivalent to extant classification keys or “floras”, it is challenging to gather the necessary palynotaxonomic literature to consult the original diagnoses when in doubt. Even with the support of libraries, the search is time-consuming and not always successful. While palynotaxonomy was vividly discussed, revised and continuously updated in the 1930–1980s, this evolution has slowed down in recent years for several reasons, but especially due to the reduced funding through the petroleum industry and the decreasing number of palynologists at large. Yet, the importance of taxonomy for subsequent applications remains the same.

The following chapter therefore documents the taxonomic advances that were made during this thesis and follows three main objectives. **(1)** To gather and translate (often for the first time) original diagnoses to compile a new reference work for important Rhaetian taxa. **(2)** Study and document intraspecific variation of palynomorphs in the Bonenburg section. And **(3)**, to reinvestigate relevant type material as well as the associated original material, to document the preservation of holotypes, revise several key taxa and identify potential lecto- and neotypes to ensure future taxonomic stability.

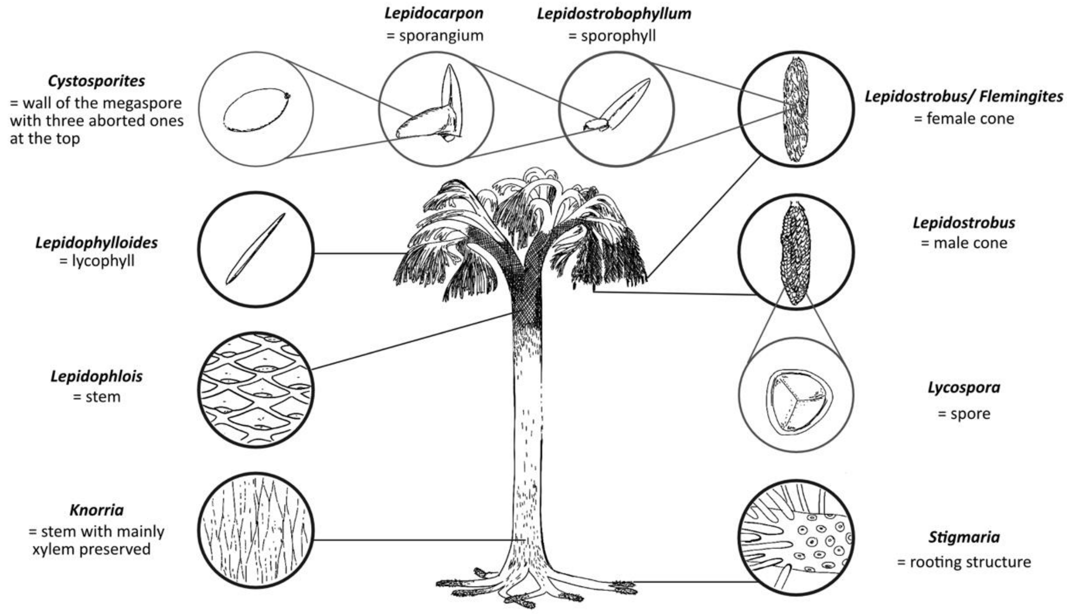


Fig. 1 Parataxonomy exemplified by *Lepidodendron*. To the mother plant of this Carboniferous lycopod at least ten different morphotaxa for the different parts of the plant or even different states of preservation of parts (e.g. *Knorria* and *Lepidophlois*) of the plant can be associated. Redrawn and altered after Thomas 1981 in Forey et al., 2004)

2. Materials and methods

2.1. Materials

Aside the new material from Bonenburg and reference material from Kuhjoch (Austria, Bonis et al., 2009), St. Audrey's Bay (UK; Bonis et al., 2010; Bonis and Kürschner, 2012) and Rødby (Denmark; Lund (1977), most part of it stored at GEUS in Denmark), we searched for original and type material from some of the most important palynotaxonomic works covering the TJ–transition: Couper (1958), Klaus (1960), Mädler (1964b), Nilsson (1958), Orlowska-Zwolinska (1966), Reinhardt (1961, 1964), Schulz (1962, 1967), and Thiergart (1949). Unfortunately, many collections are very hard to find nowadays and due to death, reorganiisation of institutions, or relocation of collections from one place or institution to another, many types remained untraceable or were not available for study. The following descriptions (in chronological order of publication) document the current whereabouts of the studied holotype material and their provenance. Detailed lists of type material, number of slides available, and their respective preservation are given in Appendix III.

Luckily, more than half of the desired material could be restudied and used for comparison with the Bonenburg material. In the following table, the respective storage locations are referred to using the standardized abbreviations of the Index Herbariorum (http://sweetgum.nybg.org/science/ih/) when possible; otherwise the intra-institutional abbreviations are used (see Table 1).

Table 1: Overview of consulted collections referred to in this thesis. Collections that are listed in the standard international (paleo)botanical collection database (Index Herbariorum) are in the following referred to with their standardized abbreviation. Collections that are not registered are referred to by their intra-institutional abbreviation.

Abbreviation	Institution	intra-institutional abbreviation	City	Country	Authors for type material
BHUPM	Natural History Museum	MfN	Berlin	Germany	Thiergart
/	Bundesanstalt für Geowissenschaften und Rohstoffe	**LBEG/BGR-H**	Hannover	Germany	Mädler,
/	Bundesanstalt für Geowissenschaften und Rohstoffe – Dienstbereich Berlin Spandau	**BGR-S**	Berlin-Spandau	Germany	Schulz
/	Geological Survey NRW	**GD NRW**	Krefeld	Germany	R. Potonié
/	Geological Survey of Austria	**GBA**	Vienna	Austria	Klaus
CGE	Sedgwick Museum of Earth Sciences – University of Cambridge	UCM	Cambridge	UK	Couper

2.1.1. Thiergart collection (1938, 1949)

According to Thiergart (1949), his **collection** (Text-Figs. 2.1 and 2.2) was supposed to be stored at the paleobotanical collection (of the author) in Berlin. However, after his death, the curator of the paleobotanical collection of the **BHUPM** at the time, Frau Dr. Barbara Mohr, had transferred all type material together with most of the the slide collection to the microscope slide collection of the BHUPM, where they are currently stored at the external storage in the Reuchlinstraße. Only one box was still stored in the herbarium of the BHUPM in the Invalidenstraße. However, in a first attempt to trace the Thiergart material, the staff of the BHUPM denied the presence of any material of this author in their collection. After inquiring with other Germany collections (BGR, BGR-S, GD NRW), there was growing evidence for its presence in the BHUPM collection. After personal communication with the former curator, she confirmed that she had picked up the Thiergart material personally and that it should be stored in the external storage of the Reuchlinstraße despite lack of information in the database.

The first author spent two days in the collection going through all slide boxes, i.e., opening every single one and looking for slides from the localities that Thiergart had worked on. Eventually the collection was found, camouflaged by contradictory labelling on the back of the boxes. On top of that Thiergart had used a particular labelling system with coloured dots for different regions (e.g. Berlin, Germany, Mediterranean). Red dots were used for German material and led to a confusion with “type material”, which is traditionally marked with a red dot, and resulted in an inconsistent separation of one part of Thiergart’s material, which was stored in the herbarium instead of the external storage together with the rest. In the end, the type material for two of Thiergart’s publications could be discovered (Thiergart 1938, 1949). Ironically, the older of the two collections (1938) is in excellent condition and is presumably prepared with Canada balsam. This part of the collection is mainly from the Cenozoic however, and therefore of limited value (but see chapter 8) in regard to the here studied Rhaetian interval. In contrast, the latter publication (1949) covers (amongst other intervals) the TJ–transitions and provides for several taxa their very first documentation. Unfortunately, these slides are poorly labelled and due to their preparation with glycerin jelly, most of the slides are in a poor to very poor condition and of limited use. In the course of this thesis, the Thiergart collection was curated for the BHUPM, and holotypes were marked and given inventory numbers. The material was borrowed and studied in Berlin in 2019–2020.

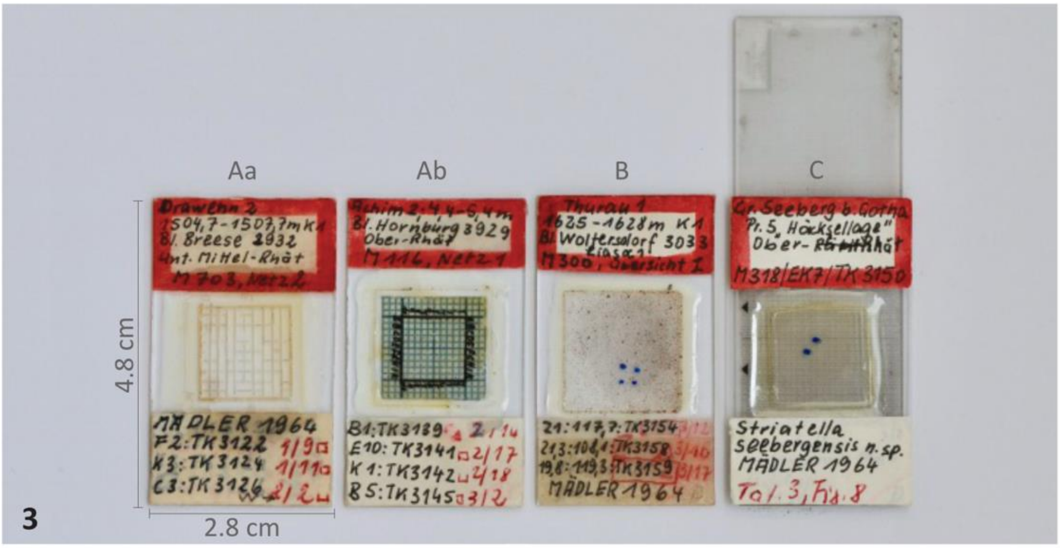
Fig. 2 Overview of slides and slide preparations. 1. Thiergart (1949) collection; glycerine jelly mount, without cover slip seal. Red dots and blue points to indicate location of the type were added in the course of this study. **2.Thiergart (1939) collection**; presumably Canada Balsam (contradictory to indication in the original publication). **3. Mädler (1964b) collection**; glycerine jelly with perfectly preserved cover slip seal; different kind of mounts: Aa. Net type 1; Ab. Net type 2; B. strew mount. C. single grain preparation. Slides significantly smaller than standard slide size. **4. Klaus (1960) collection** with double cover slip mounts held in pouches, or remounts on standard microscope slides. **5. Schulz (1962, 1967) collection**; glycerine jelly mount with Canada balsam as cover slip seal.


Hannover-sche Gegend
Pollenites macro-verrucosus
Deyow 1
253-55 m
a
Pollenites reclusus
Behring Berlin Alsenstr.
393-94 m

1


110 a
Marga
Canada Balsam
112 a
Marga
117 a
serratus (2x)
Canada-Bals.

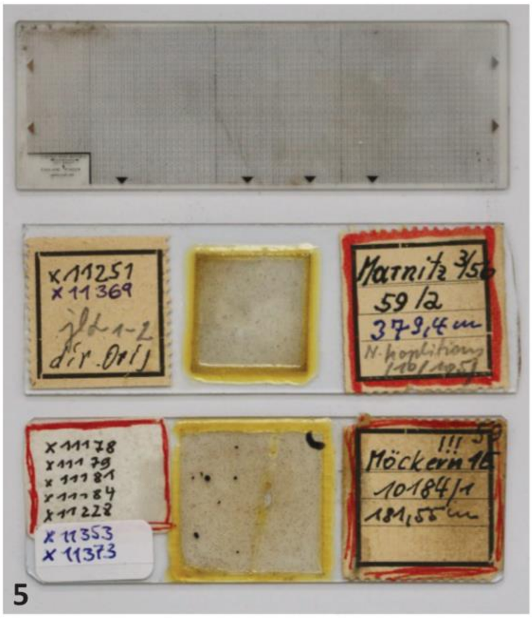
2


Aa
Ab
B
C
4.8 cm
2.8 cm
MÄDLER 1964
Striatella seebergensis n. sp.
MÄDLER 1964
Taf. 3, Fig. 8

3


Circulina meyeriana
KL. 1960
Taf. 36, Fig. 58
Nr. 383
TRIAS
Rhät
Hallein-D.
Rosstr. Bdm.
S. 165
AT 28
Zebrasporites kahleri
KL. 1960
Taf. 30
Nr. 360
TRIAS
Karn
Bleiberg
2. Schieferh.
KL. 1960.
Duplicisporites granulatus
LESCHIK 1955
Kl. 1960. Taf. 35
Fig. 53 Nr.
TRIAS
Karn
Hallein (Salzb.)
Halobiensch.
1960
AT 31

4


x 11251
x 11369
Marnitz 3/56
59/2
Möckern 1E
10184/1
181,55 m

5

2.1.2. Couper collection (1953)

The **Couper collection** (Text-Fig. 3) for the publication Couper (1958) is well curated and accessible through the Sedgewick Museum for Earth Sciences in Cambridge. Since the original publication, the material is stored at the same institution and was at the time of request already included in the collections' database. The material was borrowed and studied in 2020.

Fig. 3 Overview of loan from the Couper collection from Sedgewick Museum in Cambridge (UK). 17 slides that are associated with Couper (1958) were borrowed. All slides are strew mounts. Each specimen has its own inventory number, i.e. one slide can have several inventory numbers (marked on blue labels).

2.1.3. Klaus collection (1960)

The **Klaus collection** (Text-Figs. 2.4 and 2.3) is stored at the Geologische Bundesanstalt **(GB)** in Vienna and was consulted in summer 2017. Overall, the type material for Klaus (1960), which should consist of 56 slides is in fairly good condition. Nevertheless, some types and holotypes [*Saturnisporites* (≡ *Aratrisporites) fischeri; Patinasporites iustus, Elipsovelatisporites plicatus*] are missing, could not be relocated and are supposedly lost through a remounting process (*Praecirculina maljavkina)*, broken (e.g., *Anapiculatisporites telephorus*), or difficult to study and could not be photographically documented (e.g., holotype for *Paraconcavisporites lunzensis*). A full list of all consulted specimens and their respective preservation states can be found in Appendix III.

Compared to other collections studied for this thesis, Klaus used a unique mounting method that he did not describe in his 1960 publication. He used thick paper or lino, trimmed to the standard shape and size of a microscope slide. In the middle where one would normally put the cover slip, the paper/lino is punched out in the shape of a circle. A hard plastic foil is treated in the same way and mounted on top of the paper/lino creating a pouch. The palynomorphs are mounted as single grain preparations between two cover slips. These are then inserted in the pouch in between the paper/lino and plastic (Text-Fig. 4 and 5 C, D). This mounting method allows the photographic documentation from both sides of the palynomorph. On the flipside, it is a rather fragile mount, and the cover slip is easily moved (Text-Fig. 5 C) or damaged up to the point of breaking (Text-Fig. 5 D). As a result, several slides seemed to have been remounted later as standard preparations with a cover slip mounted on a microscopic glass slide (Text-Fig. 5 A and B). The overall preservation is relatively good. Although the available camera equipment slightly hindered photographic documentation (compare Text-Fig. 5. E, F) and had to be strongly processed to make the palynomorphs visible. The majority of slides still available and comparably well preserved (in contrast to the Schulz material for example). In some slides the glycerine jelly is intact in the crucial places, but in the majority of slides it is degraded unfavourably (compare Text-Fig. 5 E, F). The material was studied in Vienna at the GB in 2017.

Fig. 4 Overview of the Klaus collection at the Geological Survey of Austria (Vienna). 58 slides that are associated with Klaus (1960) could be recovered. Most of the slides (41) were inventoried at the time (2017) and found in the collection database (47). All slides are single pollen grain mounts and slide has one inventory number.

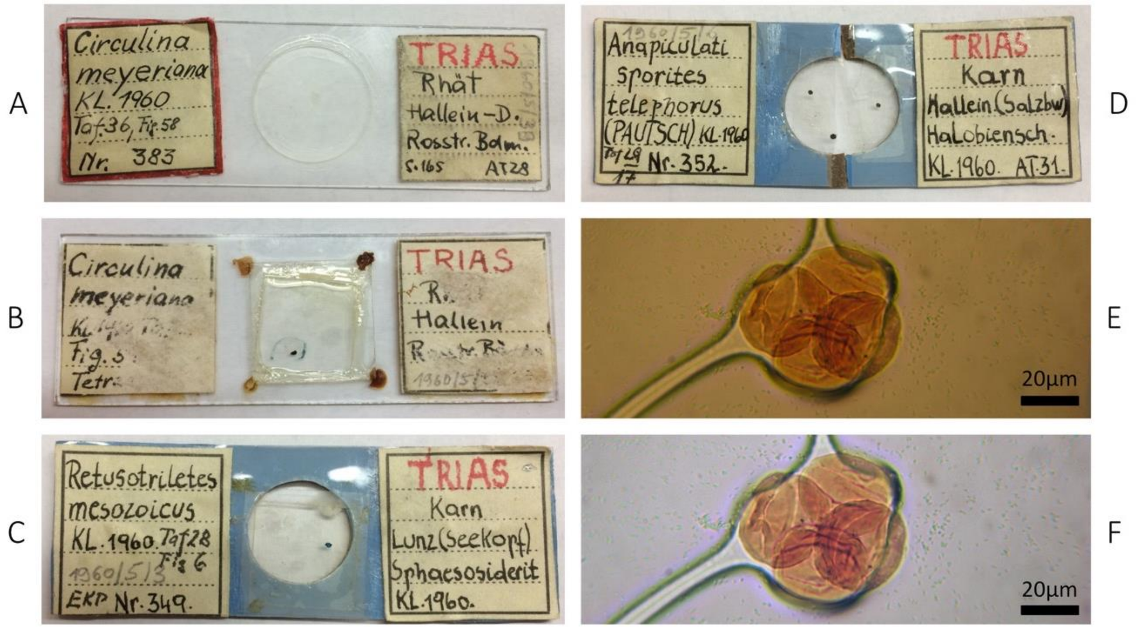


Fig. 5 Overview of slide preparations and preservation from the Klaus collection. A. Standard glass mount which was probably mounted later to repair a broken slide. **B.** The original cover slip seems to have been remounted under another cover slip, the labels of these type of mounts appear more damaged, probably as the result of the remounting. **C.** Supposedly the original mounting method used by Klaus. The majority of the slides are mounted with this technique of a double cover slip being held by a pouch made of lino in the standard microscope shape and size. This mount is rather fragile and some of the slides have broken (**D**) or were remounted like in A and B. Due to the available equipment at the GB, the palynomorphs could be only documented with a digital camera mounted on the microscope. The lighting was not optimal (**E**) and photographic documentation depicted in this thesis was achieved through photo-manipulation to gain a better white balance. **E+F**. *Classopollis meyeriana* tetrad before (**E**) and after (**F**) manipulation. The glycerine jelly has dried out, like in most slides and is representing the standard preservation state of many palynomorphs of the collection, although several palynomorphs are still enclosed by an intact glycerine jelly mount. For a complete list see Appendix III.

2.1.4. Mädler collection (1964b)

The **Mädler collection** (Text-Fig.2.3) is housed in the holotype collection of the BGR in Hannover **(BGR-H)** as stated in Mädler (1964b) and referenced with the type-catalogue numbers (TK.-Nr.) 3114-315. and was borrowed for the purpose of this study. The slides are not normal microscope slides but slides of 4.8 x 2.8 cm in size. In general, the material is in excellent condition, mounted in glycerin jelly with the framing seal still intact, in contrast to other slides of the author authors studied herein. Some specimens are in a mixed-mounts (Text-Fig. 2.3. B), others are mounted as single grains (Text-Fig. 2.3. C), or in a net (Text-Fig. 2.3. Aa/b). For future reference without Mädler’s microscope coordinates available, England Finder coordinates are given for studied specimen in mixed mounts and single grain mounts. The Mädler slide was put on the England

Finder slide as shown in (Text-Fig. 2.3. C). The material was borrowed and studied in Berlin in 2018-2020.

2.1.5. Schulz collection (1962, 1967)

The **Schulz collection** (Text-Fig. 2.5) was uncovered by accident. Originally looking for the holotype of *Cerebropollenites thiergartii*, the first author contacted the BGR in Spandau. Schulz (1967) had written that the collection would be stored at the Zentrales Geologisches Institut (ZGI). Schulz was working for this institution until shortly after the fall of the Berlin Wall (Gravendyck et al. 2020a). His entire office was cleared a couple of weeks before the inquiry, leaving the BGR with a vast collection of paperwork, literature, slides and a few residues. For the purpose of this thesis, the collection was sorted, and type slides identified for further study. The hereby further curated collection of material from Schulz (Schulz & Krutzsch 1961; Schulz 1962, 1967) is stored at the BGR in Spandau **(BGR-S)** together with collections of Ibrahim, Döring, Bruckmann and Krutzsch. The holotypes are stored in the type collection, and the inventory number is given for each of those studied. Additional slides were made from residues and mounted in Entellan® to facilitate fluorescence microscopy, and are also stored at the BGR-S.

2.2. Methods

2.2.1. Microscopy

Qualitative Palynology, i.e. taxonomic work, was conducted at an Olympus CX31 mounted with an Olympus SC50 camera. Most specimens were studied with an x100 oil immersion objective. Some taxa were additionally studied with a Zeiss Axio Imager 2 fitted with an ApoTome.2 and Zeiss AxioCam camera. The ApoTome facilitates images similar to an impression obtained by an SEM, but without the need of additional preparation, and in an easier way than with a confocal microscope. However, the resolution is not as good as with either of these more sophisticated microscope techniques.

Transference from one microscope to another was facilitated by an England Finder (EF). For the Olympus microscope the EF can be used normally. Most of the investigated holotype material dates back to before EF references were standard practice; only the variable microscope coordinates are available. In the process of restudying holotype material, we provide EF coordinates, where not available so far.

Specimens from type or original material that were studied are indicated with (!) after their respective reference. Where suitable, a description of the condition of the studies specimens is given under “**Preservation of the Type”**.

2.2.2. Terminology

In general terminology for descriptions and revisions follows that of Punt et al. (2007). Basic and recurrent terminology is explained in the following visuals (Text-Figs. 6–9).

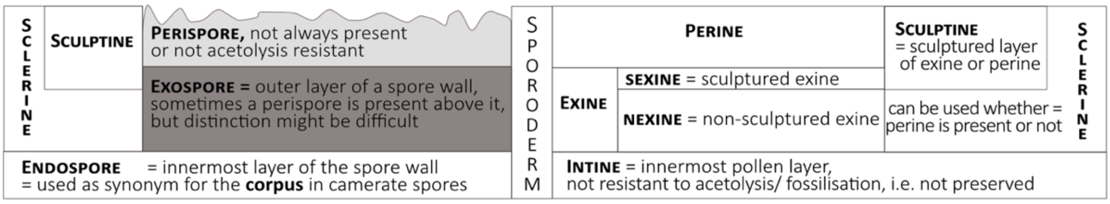


Fig. 6 Sporoderm stratification. Left: spores, Right: pollen. Altered after Erdtman (1952) and Punt et al. (2007).

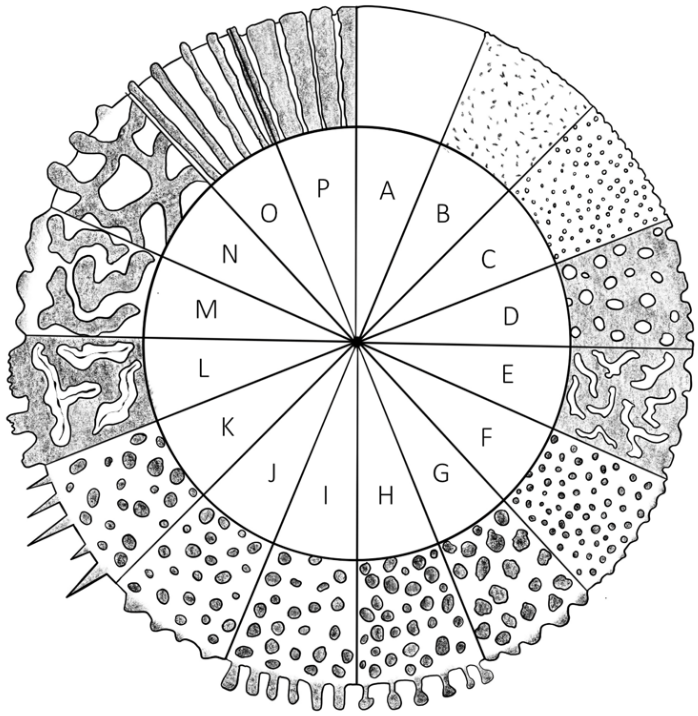


Fig. 7 Schematic diagram of exine surface structures: A–unsculptured, B–P with various sculpturing modes with each sector showing a in profile (optical section, as at equator) around the outer periphery and bird-view elsewhere. A–laevigate, B–scabrate, C–punctate, D–foveolate (with foveolae), E–vermiculate, F–granulate (with grana, i.e. less than 1 μm), G–verrucate (with verrucae, i.e. bigger than 1μm), H–pilate (with pila consisting of a columella and a caput), I–baculate (with bacula), J–conate (with coni), K–spinose (with spinae), L–cristate (with cristae), M–rugulate (with rugulae, i.e. elements longer than 1 μm), N–reticulate (with muri; note that muri also occur in striate patterns), O–cicatricose, P–canaliculate/fossulate (with fossulae). Altered after Playford and Dettmann (1996)

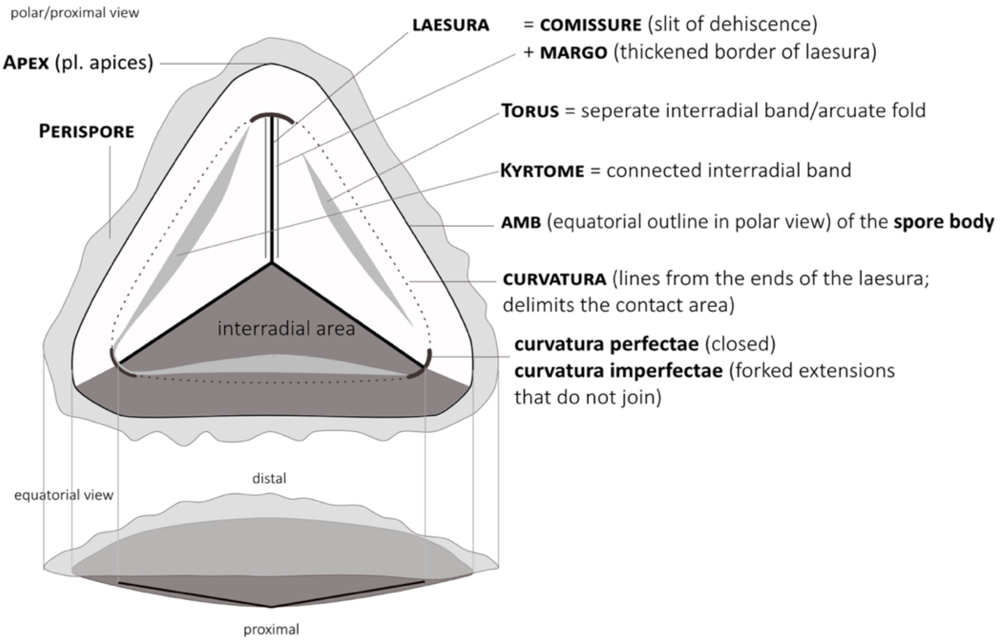


Fig. 8 Overview of spore terminology used in the following. Terminology according to Punt et al. (2007); not exhaustive.

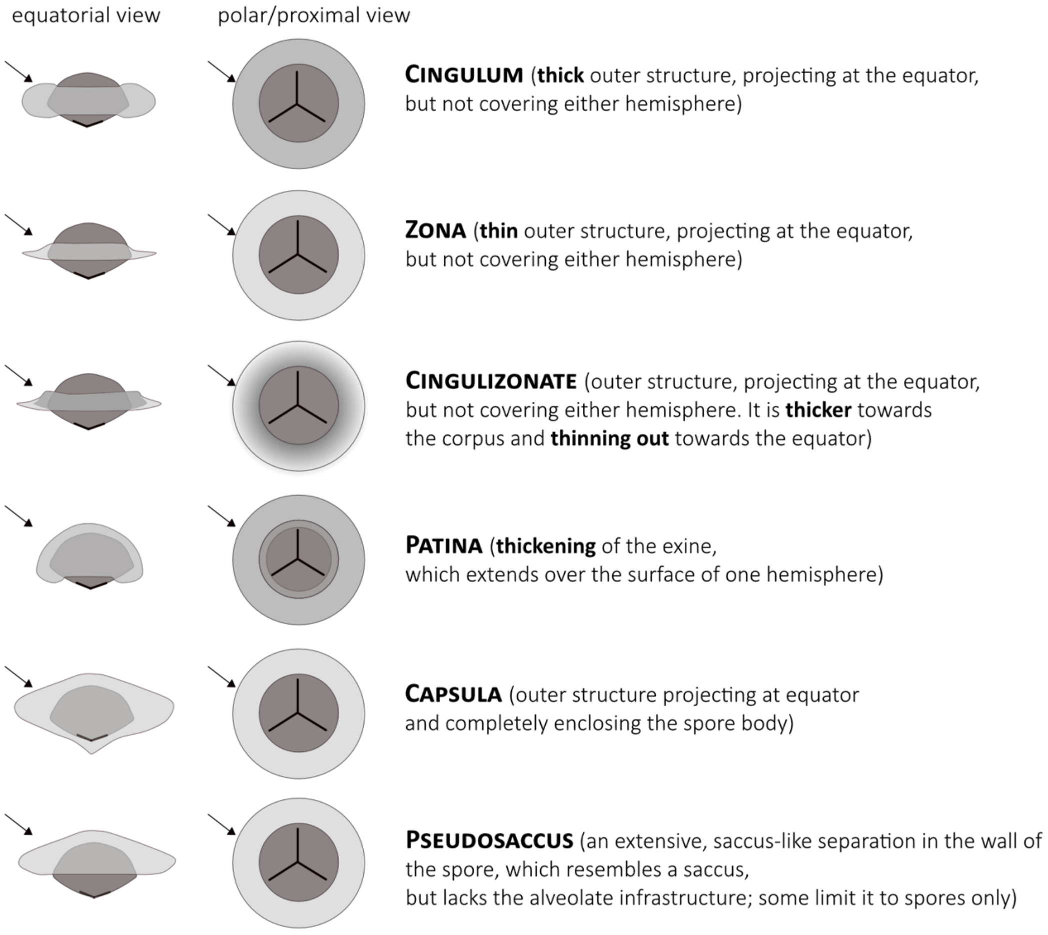


Fig. 9 Overview of different forms of “flanges” (= equatorial extensions). Terminology according to Punt et al. (2007) and Traverse (2007). Diagrams altered after Punt et al. (2007).

3. Systematic Palynotaxonomy – refiguring the Rhaetian

Here a selection of significant original diagnoses or descriptions (where available) is presented. These are referred to as "**diagnosis"** irrespective of whether they are in fact a diagnosis or a description. Firstly, because several are a hybrid of both and secondly to distinguish it better from the "**descriptions**" of our specimens from Bonenburg. For the many diagnoses we provide the first English translations. Note that English translations exist for generic diagnoses/descriptions from the Jansonius and Hills Card Index (Jansonius & Hills 1976) (available online with all supplements published after 1976 https://cdm22007.contentdm.oclc.org/digital/collection/p22007coll22), but not for species diagnoses/descriptions. Several of the translations by Jansonius and Hills are generally broad and often include interpretations rather than neutral translations that retain the ambiguities of the original texts. With the new translations, the following catalogue presents one of the most comprehensible catalogues of descriptions for the Germanic Triassic and is complemented by reinvestigation of type material of key taxa. The Bonenburg material is compared with this material and where possible, specimens from Kuhjoch (GSSP section for the base of the Jurassic) complement the discussion. Although this is an extensive catalogue it is not a complete list of the taxa identified in Bonenburg and a more comprehensive list with full author citations can be found in the supplementary Table 1 for chapter 3.

Type material that was investigated for this study is indicated with a "(!)". Synonymy lists are strictly restricted to homotypic synonyms (indicated with an "≡") and heterotypic synonyms (indicated with an "=“). Listings of other records or misapplications and indicated separately. Specimens found in Bonenburg are described under "**Description"** to provide additional information on observations and morphological variation. Comments and taxonomic/nomenclatural discussions can be found under "**Remarks**".

Anteturma **SPORITES** H. POTONIÉ 1893

Turma **MONOLETES** IBRAHIM 1933

Suprasubturma **ACAVATOMONOLETES** DETTMANN 1963

Subturma **AZONOMONOLETES** LUBER 1935

Infraturma ***Apiculatimonoletes*** BURGER 1994

Polypodiisporites POTONIE 1931 ex POTONIE 1956

Type: *Polypodiisporites favus* POTONIÉ 1931, Braunkohle 16: 556, Fig. 3

Preservation of the Type: presumably lost. Since the original publication lacks clear indication of the original material from which the type was described there is little chance for original material, so neotypification is needed.

Diagnosis: Genotypus 57 µm, monolete bohnenförmige Mikrosporen. Exine mit flachen ± polygonalen Platten oder flachen Verrucae so dicht bedeckt, daß zwischen ihnen nur ein ± schmalrinniges negatives Reticulum verbleibt. Die Platten können ganz flach oder ± leicht gewölbt sein, extrema lineamenta der Sporen dementsprechend ± leicht gewellt (Potonié, 1956, p. 78).

Engl. Translation: Type specimen 57 µm, monolete bean-shaped microspores. Exine with flat ± polygonal plates or flat verrucae so densely covered, that between them only a ± narrow negative reticulum remains. The plates can flat or ± slightly dome-shaped, the resulting outline is slightly undulated.

Remarks: For discussion and distinction see (Jansonius and Hills, 1976; card 2102)

Polypodiisporites polymicroforatus (ORLOWSKA-ZWOLINSKA 1966) LUND 1977

Pl. 1, Figs. 1–23

Holotype/Basionym: *Foveosporites polymicroforatus* ORLOWSKA-ZWOLINSKA 1966, Geological Quarterly 52: 1011, Pl. 3, Figs. 19–21

Preservation of the Type: doubtful; inquiries for material were so far unsuccessful.

Synonymy:
≡ 1966 *Foveosporites polymicroforatus* ORLOWSKA-ZWOLINSKA 1966, p. 1011, Pl. 3, Fig. 19–21
= 1967 *Convolutispora microrugulata* SCHULZ 1967, p. 570. Pl. 6, Fig. 7–9 (!)
= 1967 *Convolutispora microfoveolata* SCHULZ 1967, p. 571. Pl. 6, Fig. 10, 11

Engl. Translation of the Diagnosis: Size 36–47 μm. Spore with circular outline. Trilete mark delicate, often badly visible. Exine very thick (up to 3–5 μm thick), strongly carved with deep, small and very numerous pits both on the proximal and distal side. Ornamental elements have a round or elongated shape, sometimes they merge together. The outline of the spore is, due to the coarse and heavily carved exine, appears serrated (after Orłowska-Zwolińska, 1966, p. 1011).

Description: The morphological as well as preservational variation is particularly noteworthy in this taxon (see Pl. 1, Figs. 1–23). The verrucate ornamentation is fairly uniform, but size and also exine thickness appears to be variable. Orłowska-Zwolińska (1966) as well as well as Schulz (1967) indicate a size the range between 36–47 μm and 35–48 μm, respectively. Many of the species from Bonenburg, but also from Kuhjoch from the same time-interval are between 25–50 μm, and mostly in the lower half of that size range. Particularly apparent is the variation in colour, not only from sample to sample but also within one sample (compare Pl. 1 Figs. 2–5 for Bonenburg and Figs. 12–13 for Kuhjoch and see the overview in Text-Figs. 10 and 11).

Remarks: *Polypodiisporites polymicroforatus* is a stratigraphically very important species. An acme in the Middle and Upper Rhaetian had already been noted by Lund (1977) and more recently a *Polypodiisporites polymicroforatus* abundance interval has been employed to correlate the Central European sections spanning the TJ–transition (Lindström et al. 2017b).

Lund (1977) has synonymised *Convolutispora microrugulata* SCHULZ 1967 and *Convolutispora microfoveolata* SCHULZ 1967 denoting them junior synonyms of his newly combined *Polypodiisporites polymicroforatus*. However, he did not consult the type-material, in contrast to some of his other recombinations. After our consultation of the type material of Schulz (1967) we could not with certainty relocate the holotype for *Convolutispora microrugulata* (Pl. 1, Fig. 22) and not relocate the holotype for *Convolutispora microfoveolata.* Given the variety of spores observed in these slides and seen the inconceivable differences in the original photomicrographs, the two forms are considered conspecific and on top of that conspecific with the holotype for *Polypodiisporites polymicroforatus.* The latter has priority and is therefore applied here. Schulz' recombination with *Convolutispora* is also not followed here.

Schulz' decision might have been influenced by the problematic character of the laesurae. In the discussed forms we have a dominant long laesurae, with a much shorter perpendicular slit (Pl. 1, Figs. 18, 23) this is often not clearly perceivable however (Pl. 1, Figs. 14, 15, 20). Sometimes the perpendicular slit is hardly visible, wherefore the spore appears monolete, but depending on the position and prismatic effects it can appear more trilete (Pl. 1, Fig. 11), which has probably influenced Schulz to recombine It with *Convolutispora* HOFFMEISTER, STAPLIN & MALLOW 1955, which is a trilete genus, rather than the monolete genus *Polypodiisporites* POTONIÉ 1931 ex POTONIÉ 1956. *Polypodiisporites* is used here, since it is not uncommon in several species to find the perpendicular slit, and the typical opening pattern (Pl. 1, Figs. 16, 17) justifies Lund's recombination.

Botanical affinity: Uncertain. Bonis (2010) assigned them to the Filicales.

Suprasubturma PERINOMONOLETES DETTMANN 1963

Subturma AZONOPEROMONOLETES BURGER 1994

Infraturma ***Apiculati*** BURGER 1994

Aratrisporites LESCHIK 1955 emend. PLAYFORD & DETTMANN 1965

Type: *Aratrisporites parvispinosus* LESCHIK 1955, Schweizerische Paläontologische Abhandlungen 72: 38, Pl. 5, Fig. 4; B53/1a

Synonymy: = 1960 *Saturnisporites* KLAUS, p. 142, Pl. 32, Fig. 32, 33

Diagnosis: Mikro- oder Isosporen, deren Zone mit Stacheln bis zu einer Höhe von 3 μm besetzt ist. (Das Innere der Stacheln ist undurchsichtig und fest, das der Dornen zum Teil hell und hohl)(Leschik, 1955, p. 38).

Engl. Translation: Micro- or isospores whose zone is occupied by spinae up to a height of 3 μm. (The inside of the spinae is opaque and firm, that of the spines partly light in colour and hollow.)

Emended Diagnosis*:* Meiospores monolete, bilateral. Spore wall (sclerine) two-layered, cavate; consisting of an outer structured layer (sculptine) loosely enveloping, but proximally attached to, a homogeneous inner layer. Sculptine surface finely patterned (the pattern being formed by an arrangement of structural elements) and with sculptural elevations including grana, coni, spinulae, spinae, and saetae. Laesura enclosed within elevated lips which are proximal extensions of sculptine (Playford and Dettmann, 1965, p. 151).

Remarks: Thiergart (1949) already depicted specimens that comply with the circumscription of *Aratrisporites*, but did not describe a new genus, but only the new species "*Pollenites Saturni n. sp*" as a "flat ball, enclosed by a thin ring. No germination opening." (own translation). This description rather seems to serve a genus circumscription than to distinguish an individual species of what was then described by Leschik (1955) as *Aratrisporites*. Unfortunately, the type material has to be accounted for as lost, making a reevaluation or better distinction of the species impossible. The rather poor pictures can also not disambiguate the situation. Later authors are therefore advised to refrain from using this poorly circumscribed species.

Although the majority of authors (eg. Klaus, 1960; Leschik, 1955; Schulz, 1967) consider *Aratrisporites* to be a zonate spore, Potonié (1958), maybe inspired by Thiergart's assignation to *Pollenites*, speculated weather it could be the saccus of a monosaccate pollen. Subsequently, Bharadwaj and Singh (1964) restudied and emended the genus accordingly, also interpreting it as a pollen grain. Playford and Dettmann (1965) revised this again, reinterpreting the palynomorph as a cavate, i.e. not zonate, spore. Cavate is a synonym for "camerate" in spore terminology, which means that there is a cavity in between the endospore or spore corpus and the outer wall which is separated from the corpus (Punt et al. 2007). This interpretation is followed here. Also in agreement with Playford and Dettmann (1965), a separation of *Saturnisporites* Klaus 1960, based on the elevated laesurae tips appears superfluous. This is further supported when comparing the type/holotype material for the two genera.

Following Palynodata available from Palynodata there are 65 species formally described and this abundant number of species, with often minute to hardly comprehensible differences, makes an overview confusing. Based on in situ finds and comparison with extant *Isoetes* spores, it seems very likely that these type of spores were produced by Isoetales (Taylor et al., 2009 and citations therin; Schulz, 1967). Given the long existence of this plant group, form variations in the spores might reflect speciation in the mother plants over time, which makes it interesting to record such variations, which could also serve as stratigraphic markers. Yet, when authors describe similar species from different time intervals, this suggests the assumption that they were only differentiated, because they originate from different time intervals. Especially in the Upper Rhaetian and Lower Jurassic reworking might explain the occurrence of certain taxa (compare Gravendyck et al., 2020b). To be able to identify reworking however, it is important to clearly identify existing or non-existing differences of species described from different time to better estimate their temporal distribution. As a first, but not yet complete, attempt to revise the genus *Aratrisporites* and to provide a better overview of the described species, the literature and type material of Thiergart, Leschik, Klaus, Schulz and Reinhard was critically assessed in the following (compare Table 2).

Botanical affinity: *In situ* finds were reported in *Cyclostrobus* and *Lycostrobus* by Helby and Martin (1965), and in *Annalepis zeilleri* by Grauvogel-Stamm and Duringer (1983), which is now known as *Lepacyclotes* (Kustatscher et al. 2015); see also Taylor et al. (2009).

Fig. 10 Spore colour alteration throughout the detailed sampling I. D–1 to D–5 from the black Contorta Beds, D–10 from the grey layer in between the Contorta and the Triletes Beds. In several samples specimen of varying colour/preservation occur.

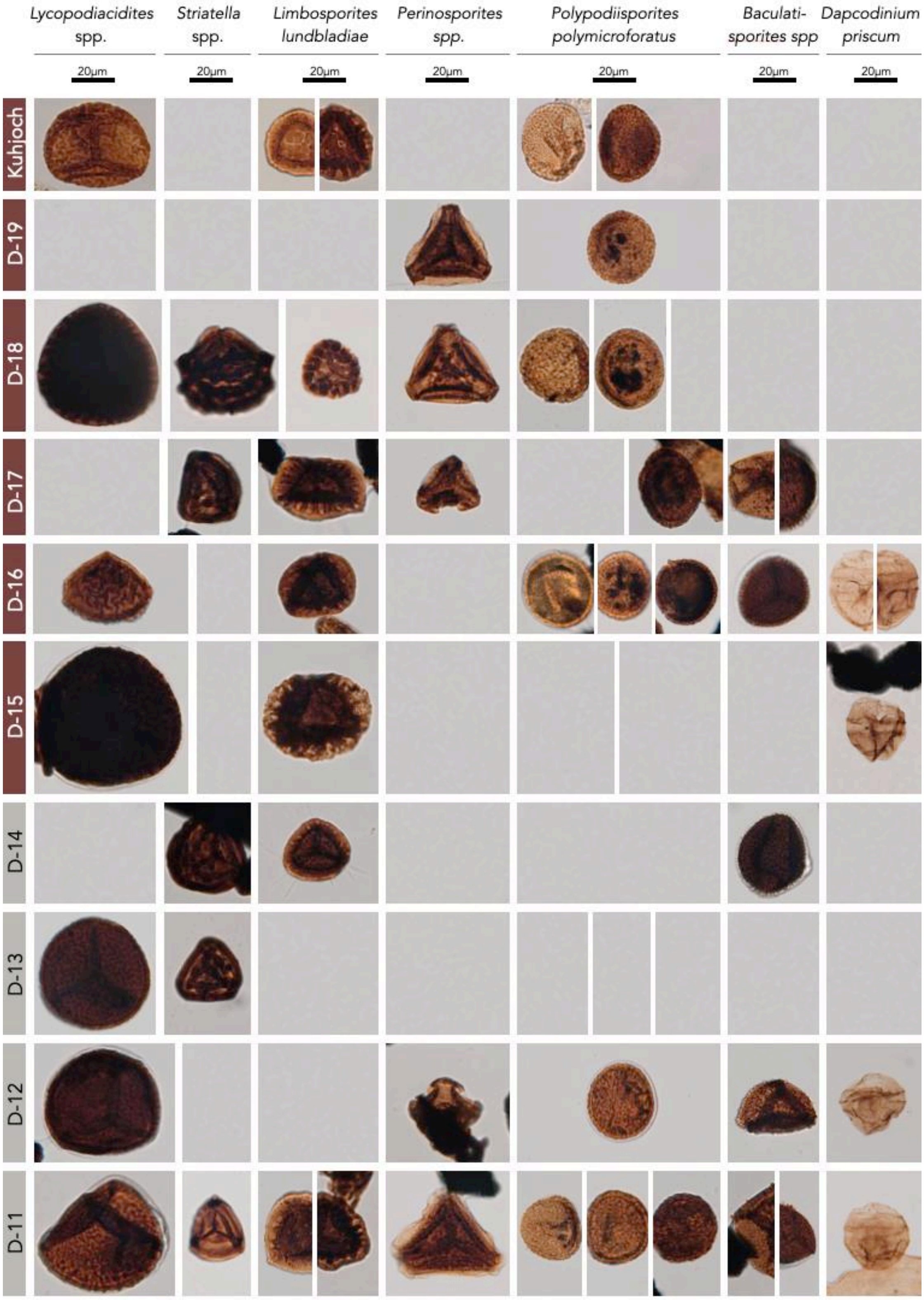


Fig. 11 Spore colour alteration throughout the detailed sampling II. D–11 to D–14 from the grey layer in between the Contorta and the Triletes Beds. D–15 to D–19 from the reddish Triletes Beds. One sample from Kuhjoch from the Schattwald Beds in comparison. In several samples specimen of varying colour/preservation occur.

Table 2: Overview of *Aratrisporites* species described by Thiergart, Leschik, Klaus, Schulz and Reinhard. Characteristics are assembled from original descriptions and restudying the type material. Similar species are grouped together.

species name	Author	Width of equatorial sculptine projection (relative to corpus)	ornamentation	Length (longest side)	Length spinae
centratus	Leschik 1955	1/5–1/6	Finely granulate, with smooth sculptine	69 μm	/
fimbriatus	Klaus 1960	1/3	granulate with rel. long spinae (2/3 of the length of “zona”)	33–44 μm	“rel. long”
palettae	Klaus 1960	1/7–1/9	Infrapunctate – infragranulate with scattered hairs (sometimes thickened at the end)	70–100 μm	“more or less long”
fischeri	Klaus 1960	1/2	Infrapunctate – infragranulate, + few hairs	80–100 μm	2–3μm
granulatus	Klaus 1960	1/6–1/8–(1/10)	Finely granulate (to regulate)	40–55 μm	/
minimus	Schulz 1967	1/10	Infragranulate – finely punctate	30–38 μm	/
parvispinosus	Leschik 1955	1/5–1/6 (Holotype)	Finely granulate with spinae	62.5 μm	
paraspinosus	Klaus 1960	1/3–1/5 (Holotype)	Finely granulate with spinae that are thickened at the base	50–65 μm	
saturni	Thiergart 1949	1/5	?	40 μm	?
scabratus	Klaus 1960	1/6	Punctate-granulate	50–70 μm	/
coryliseminis	Klaus 1960	1/5–1/6	Granulate (to rugulate)	42–65 μm	/
crassitectatus	Reinhard 1964	1/6–1/8	punctate	40–50 μm	/

Aratrisporites centratus LESCHIK 1955

Holotype: *Aratrisporites centratus* LESCHIK 1955, Schweizerische Paläontologische Abhandlungen 72: 38, Pl. 5, Fig. 1, B56/1a

Diagnosis: Zentralteil: Kontur oval. Exospor mit Körnelungsskulptur. Glatte, stark lichtbrechende Membran mit einer Dicke von ca. 0,5 μm. Peripherer Teil; Der Hautrand ist perforiert (Leschik, 1955, p. 38).

Engl. Translation: Central part: outline oval. Exospore with granulate sculpture. Smooth, strong refractive membrane of 0.5 μm thickness. Peripheral part; the edge of the membrane is perforated.

Remarks: According to Palynodata, there are only 11 citations of this name, the last in 1998. At this point it remains questionable, whether the specimen is actually only a badly preserved *Aratrisporites parvispinosus*. The original photographs of Leschik makes such a distinction doubtful, especially when comparing the photographs of the two holotypes (Pl. 5 Figs 1 and 2 in Leschik, 1955). A final decision cannot currently not be made given the lack of type material for comparison.

Aratrisporites fimbriatus (KLAUS 1960) MORBEY 1975

Pl. 2, Fig. 14

Holotype/Basionym: *Saturnisporites fimbriatus* KLAUS 1960, Geologisches Jahrbuch A, Sonderband 5: 142, Pl. 32, Figs. 32–33, Bleiberg 198 (! Here refigured in Pl. 2, Fig. 14)

Preservation of the Holotype: well preserved, glycerin-jelly intact.

Synonymy:

≡ 1960 *Saturnisporites fimbriatus* KLAUS 1960, p. 142, Pl. 32, Fig. 32, 33, EK Nr. 364, GB (!)
= 1960 *Saturnisporites palettae* KLAUS 1960, p. 144, Pl. 32, Figs. 32, 36, EK Nr. 366, GB (!)
= 1965 *Aratrisporites palettae* (KLAUS 1960) PLAYFORD & DETTMANN 1965, p. 152
= 1966 *Saturnisporites spinosus* ORLOWSKA-ZWOLINSKA 1966, p. 1014, Pl. 9 Fig. 45
= 1967 *Aratrisporites palettae* (KLAUS 1960) SCHULZ 1967, p. 591, Pl. 16, Figs. 5,6

Diagnosis: Monolete Sporen mit Zona und Zentralkörper. Beide oval. Die Breite der Zone entspricht etwa $^{1}/_{3}$ der Breite des Zentralkörpers, gemessen an der schmalen Stelle des Ovaloides. Die monolete Marke besteht aus einem deutlichen ± dicken, sanft geschlängelten Wulst, welcher in Längsrichtung das gesamte Korn bis zum äußeren Zonenrand durchzieht und von einer meist kenntlichen Dehiszenznaht geteilt wird. Zentralkörper und Exine sind fein punktiert und besitzen verhältnismäßig lange, nicht sehr dicht aufgesetzte Haare. Am Äquatorrand stehen, gemessen auf einem $^{1}/_{4}$ 15–20 Haare, deren Länge etwa $^{2}/_{3}$ der Zonenbreite entspricht. Zentralkörper tiefdunkelbraun, Zona gelb (Klaus, 1960, p. 142).

Engl. Translation: Monolete spores with a zona and central body. Both oval. The width of the zona corresponds to side of the ovaloid. The monolete mark consists of a clear ± thick, gently meandering thickening, which transverses the whole grain longitudinally until reaching the outer edge of the zone. It is often parted by an often-visible dehiscence. Central body and exine finely punctate and with relatively long, not very densely distributed hairs. Measured on a $^{1}/_{4}$ of the outline of the equator of the spore there are 15–20 hairs. Their length corresponds to approximately $^{2}/_{3}$ of the width of the zona. Central body intensely dark brown, zona yellow.

Emended Diagnosis: Miospores monolete, bilateral, camerate. Amb and intexine ellipsoidal. Exoexine punctate or scabrate, attached proximally to a thin, laevigate or scabrate intexine. Exoexinal width between equator and margin of intexine ca. $^{1}/_{3}$–$^{1}/_{9}$ width of intexine. Distal surface and equator ornamented with spinae or saetae up to 7 μm in height. Sutura sinuous with labra 1–3 μm in width, extends to margin of intexine or to equator, where curvaturae imperfectae may develop (Morbey, 1975, p. 23).

Description: Our specimen (Pl. 2 Fig. 5) is 63 μm long and 47 μm wide and thus ovaloid in shape. The corpus width is ca. 43 μm. The colour is very dark brown and given the somewhat less distinct sculptine, which is only visible through its slightly lighter colour. It reaches only ca. 5 μm beyond the spore corpus wide and thus ca. $^{1}/_{9}$ of the corpus diameter and within Klaus' given size range of *Aratrisporites palettae*. The monolete mark is slightly meandering. The spinae are scattered and about 26 of them are visible. They are ca. 5 μm long, wider at the base and thinning to the tip. Compared to the holotypes of *Saturnisporites fimbriatus* as well *as Saturnisporites palettae*, our specimen has fewer spinae, but overall, size, shape, sculptine-corpus ratio and ornamental elements is very similar to the holotype of *Saturnisporites palettae* and complying with the circumscription of *Aratrisporites fimbriatus*, even though fewer spinae are present.

Remarks: The ornamentation of *Aratrisporites fimbriatus* is very similar to that of *Aratrisporites palettae* leading Morbey (1975) to synonymise the two. He argues, that the specimen depicted by Schulz (1967) on Pl. 16 Fig. 5 and 6 represents an intermediate form of the two species with the same ornamentation but with an intermediate width of the equatorial sculptine projection (i.e. the distance between equator and margin of the intexine). This, he argues, renders a species distinction obsolete and emended the circumscription accordingly, also incorporating new phrasing following the genus revision of Playford and Dettmann (1965). Both specimens are documented for the Carnian by Klaus (1960) and Schulz reports *Aratrisporites palettae* from the middle Rhaetian, which is the same occurrence as in Bonenburg. Even if the two were not synonymised, their stratigraphic value is very limited as they seem to occur together. Finally, the size seems to be the only differentiating characteristic. Given the high intraspecific variability of this characteristic in many taxa, Morbey's argument to synonymise the two species is followed after comparing the two holotypes and regarding them as variants of the same species with strong variation in size and width of the sculptine projection in relation to the corpus width.

Aratrisporites fischeri (KLAUS 1960) PLAYFORD & DETTMANN 1965

Pl. 2, Fig. 6

Holotype/Basionym: *Saturnisporites fischeri* KLAUS 1960, Geologisches Jahrbuch A, Sonderband 5: 144, Pl. 32, Fig. 35, Hallein-Dürnberg AT 31

Preservation of the Holotype: is missing and has to be accounted for as lost. Lecto- or neotypicfication necessary.

Diagnosis: Große, ± ovale, monolete Mikrosporen mit relativ kleinem Zentralkörper und breiter Zona. Ihre Breite misst etwa den $^1/_2$ Durchmesser des Zentralkörpers an der schmalen Seite. Die monolete Marke besteht im Bereich des Zentralkörpers aus einem wulstigen, etwas geschlängelten Strang, welcher verflachend in die Zone übergreift, um dort in Form von mehreren, unregelmäßigen kleinen Fältchen in diese zu verlaufen. Die Exine ist fein infrapunktiert bis infragranuliert, sowohl am Zentralkörper wie auch auf der Zone; außerdem mit Haaren vereinzelt besetzt. Diese sind etwa 2–3 μm lang und 1/2–1 μm breit (Klaus, 1960, p. 144).

Engl. Translation: Big, ± oval, monolete microspores with relatively small central body and wide zona. Their width measures about the $^1/_2$ diameter of the central body on the narrow side. The monolete mark consists (in the area of the central body) of a thickened, slightly vermiculate string, which flattens when merging with the zona to dissolve there in the form of several irregular small wrinkles. The exine is finely infrapunctate to infragranulate, both on the central body as well as on the zona; with scattered hairs. These are about 2–3 μm long and 0.5–1 μm wide.

Remarks: Unfortunately, the holotype could not be studied and has to be accounted for as lost, which makes a comparison at this point more difficult. Standing out from the circumscription and the original photographs is the very large equatorial sculptine projection, which is half as wide as the corpus itself. Specimens with a similar sculptine-corpus ratio were not found in Bonenburg for comparison and evaluation of variation and potential overlap with other species, but should be part of future studies of Carnian material and potential lectotypification to substitute for the missing holotype.

Aratrisporites granulatus (KLAUS 1960) PLAYFORD & DETTMANN 1965

Pl. 2, Fig. 13

Holotype/Basionym: *Saturnisporites granulatus* KLAUS 1960, Geologisches Jahrbuch A, Sonderband 5: 143, Pl. 32, Fig. 34, Eisenkappel 167 (! here refigured in Pl. 2, Fig. 13)

Preservation of the Holotype: well preserved, glycerin-jelly intact.

Diagnosis: Monolete Mikrosporen von rundlich-ovalem Umriß, dunklem Zentralkörper und schmaler Zona. (Etwa $^{1}/_{6}$–$^{1}/_{8}$ des Zentralkörperdurchmessers an der schmalen Stelle.) Die Dehiszenzmarke besteht aus einem deutlichen dicken, oft in der Mitte gewundenen Wulst, welcher sich gegen den Rand des Zentralkörpers gewöhnlich verliert und ohne Kontur allmählich in die Zona übergeht. Dort wird die Zone meist etwas breiter, sodaß der Umriß mehr spindelförmig wirkt. Die Exine ist fein granuliert und zeigt bei bestimmter optischer Einstellung ein enges, negatives Reticulum imperfectum (Klaus, 1960, p. 143).

Engl. Translation: Monolete microspores of rounded-oval outline, dark central body and narrow zona. (About $^{1}/_{6}$–$^{1}/_{8}$ of the central body's diameter measured at the narrow side.) The laesurae consists of a clear thick, often with a meandering thickening in the middle, which becomes less pronounced towards the edge of the central body and gradually merges into the zona without contour. There, the zona is usually somewhat wider, so that the outline appears more spindle-shaped. The exine is finely granulated and shows, in a particular optical setting, a narrow negative reticulum imperfectum.

Remarks: Like in *Aratrisporites coryliseminis* Klaus describes a negative reticulum. When restudying the specimen this observation cannot be confirmed. A certain focal plane might give this impression only when the grana optically "melt into each other" when the image is not sharp. Here the ornamentation is thus considered to be granulate only. In comparison to other species this specimen stands in between *Aratrisporites scabratus* (and synonymised species) and *A. minimus*. Since biology is usually a continuum rather than seperate boxes, a distinction of the said species appears difficult and might only represent transitional (maturation) stages. Different preservation stages can further complicate this. Playford and Dettmann (1965) for example argued, that *Aratrisporites granulatus* would be distinguished from *Aratrisporites coryliseminis* by having thicker lips, a thinner sculptine and a broader elliptical amb. The appearance of the holotype of *Aratrisporites coryliseminis* appears indeed more hyaline but compared to the rather dark *Aratrisporites granulatus* this might be simply a matter of preservation. Similarly, the thickness of the lips and roundness of the outline is a combination of folding and infraspecific variation that is highly variable and thus not a very reliable characteristic for species distinction.

For the time being this species is kept sperate, but future studies should further investigate, how this circumscription relates to other described species and their respective temporal and geographical distribution.

Aratrisporites minimus SCHULZ 1967

Pl. 2, Figs. 16–17

Holotype: *Aratrisporites minimus* SCHULZ 1967, Paläobotanische Abhandlungen Abteilung B 2: 592, Pl. 16, Fig. 7–9, Wellmitz 1

Preservation of the Holotype: The holotype could not be relocated yet, but the slide is available although in poor condition with the glycerine gelatine desiccated. Holotype potentially lost.

Diagnosis: Größe 30-38 μm (Holotypus 30 μm). Ä-Kontur in Pollage oval, Zentralkörper dunkler als die ihn umgebende häutige Pseudozona oder das Pseudoperispor. Breite des Pseudoperispors am Äquator 2-5 μm. Exine des Zentralkörpers und des Pseudoperispors infragranulat bis fein punctat. Monolete Dehiszenzmarke deutlich, meist leicht gewellt, als schmaler, durch eine Sutur getrennter Exinenwulst ausgebildet, der auf dem Pseudoperispor ausläuft oder bis zum Umriß des Pseudoperispors oder der Pseudozona reicht. Sporen in Äquatorialansicht kahnförmig (Schulz, 1967, p. 592).

Engl. Translation: Size 30–38 μm (holotype 30 μm). Equatorial outline in polar view oval, central body darker than the surrounding membranous pseudozona or the pseudoperispore. Width of the pseudoperispore at the equator 2–5 μm. Exine of the central body and the pseudoperispore infragranulat to fine punctate. Monolete dehiscence mark distinct, usually slightly wavy. It is formed by a narrow exinal ridge which is separated by a suture, which ends on the pseudoperispore or extends to the outline of the pseudoperispore or the pseudozona. Spores in equatorial view boat-shaped.

Description: Our specimen (Pl. 2. Fig. 17) is very small, with 29 μm length and 23 μm width even smaller than the size range given by Schulz. The (pseudo-)zona is ca. 3 μm wide. The corpus is, contrary to the original diagnosis lighter in colour that the (pseudo-)zona. The monolete mark is slightly undulating, the commissure is not visible. The ornamentation is not very distinct, probably finely punctate to infrapunctate. Despite these differences, the ornamentation and overall size complies with the diagnosis and allows tentative assignation of the given species.

Remarks: Schulz writes that the new species is mainly distinguished by its smaller size. It is doubtful, whether size alone might be criterion enough to erect a new species. On the other hand, such a narrow sculptine projection only occurs in few other species (e.g. *Aratrisporites palettae*), which are then distinguished by different ornamentation, which is not present in the species in question. A similarly narrow, yet still broader sculptine projection occurs in *Aratrisporites granulatus.* A different stage of development might explain the smaller size of *Aratrisporites minimus* and weaker development of ornamental traits and narrow sculptine projection. Yet, in a system that describes morphospecies, the latter argument is not enough to dismiss Schulz' species, as long as there are other distinctive characteristics, such as the different ornamentation. For future studies in *Aratrisporites* it might be interesting to explore, whether the small size of this spore, and other taxa like *Pinuspollenties minimus*, typically occurring right after the mass extinction could be connected to what is described as the "Lilliput effect" (e.g. Harries and Knorr, 2009) in animals.

Aratrisporites scabratus KLAUS 1960

Pl. 2, Figs. 8, 10

Holotype: *Aratrisporites scabratus* KLAUS 1960, Geologisches Jahrbuch A, Sonderband 5: 147, Pl. 5, Fig. 37, 38, Einzelkornpräparat Nr. 368, GB (!)

Preservation of the Holotype: Due to the preservation of the slide and the particular mounting technique of Klaus and air bubbles, it was technically not possible to photographically document the specimen. The preservation of the spore itself is only ok.

Synonymy:	= 1960	*Aratrisporites coryliseminis* KLAUS 1960, p. 147, Pl. 33, Fig. 39, 40, EK Nr. 369, GB (! here refigured in Pl. 2, Fig. 11)
	= 1964	*Aratrisporites crassitectatus* REINHARD 1964, p. 54, Pl. 1, Fig. 4, (! here refigured in Pl. 2, Fig. 12)

Diagnosis: Monolete Mikrospuren mit häutiger heller Zona und etwas dunklerem Zentralkörper. Die an den Enden der monoleten Marke einwärts aufgebogene Zone mißt in ihrer Breite etwa $^1/_6$ des Durchmessers des Zentralkörpers an der schmalen Seite. Die Sutur kann im Zentralteil gelegentlich klaffen. Sekundärfalten können Zentralkörper und Zona durchlaufen. Artcharakteristisch ist u. a. die Exinenornamentation. Diese ist in der Zona fein punktiert bis granuliert. Das Muster ist hauptsächlich eine Struktur, kommt aber an die Außenfläche als schwach angedeutete Skulptur durch. Verstreut stehen manchmal ein paar große Grana. Größe: Längendurchmesser etwa 50–70 μm (Klaus, 1960, p. 147).

Engl. Translation: Monolete microspores with a membranous, bright zona and a slightly darker central body. The monolete mark is bent inwardly at the ends of the zone and measures in width about $^1/_6$ of the diameter of the central body on the narrow side. The suture may occasionally gape in the central part. Secondary folds can pass through the central body and zona. Characteristic is amongst other things the exine ornamentation. On the zona, the ornamentation is finely punctate to granulate. The pattern is mainly ornamental structures, but protrudes at the outer surface as a dimly indicated sculpture. There are sometimes a few large grana scattered around. Size: Length about 50–70 μm.

Description: Our specimens are slightly folded (Pl. 2, Fig. 9–10), with the monolete mark bent inwards on one side (Pl. 2, Fig. 9), just as described by Klaus. They measure ca. 50 and 68 μm in length and 42 and 51 μm in width. In the first specimen (Pl. 2, Fig. 9) the corpus measures 34x 25 μm and the sculptine is 10 μm wide on one side of the corpus, and ca. 5 μm on the other. It is thus bigger in relation to the corpus compared to Klaus's diagnosis, but the darker corpus and lighter coloured sculptine, the typical finely granulate ornamentation and typical secondary folds allow assignation to this species. The second specimen (Pl. 2 Fig. 10) is bigger but has the same proportions as Klaus' holotype.

Remarks: Klaus mainly distinguishes *Aratrisporites scabratus* KLAUS 1960 (Pl. 2, Fig. 8) and *Aratrisporites coryliseminis* KLAUS 1960 (Pl. 2, Fig. 11) with the latter being granulate to rugulate rather that punctate-granulate (compare Table 2). This distinction is only a small one and when restudying *Aratrisporites coryliseminis* we could not see rugulate structures that would justify a distinction. Furthermore, an alleged distinction in the width of the equatorial sculptine projection (which Klaus interprets as a zona) is mentioned in the text but cannot be seen when comparing the two holotypes. Naturally, the width is dependent on the place where it is measured, but even when taking an average of multiple places, no such distinction appears justifiable. Both *Aratrisporites scabratus* and *Aratrisporites coryliseminis* are described on the same page in the same publication, however *Aratrisporites scabratus* which is therefore considered to have priority over the latter.

The holotype for *Aratrisporites crassitectatus* REINHARD 1964 (Pl. 2, Fig. 12) is still available for study (personal communication with the University of Freiberg, 2020). Unfortunately, the material is not permitted to leave the premises of the collection and could not be studied on site due to the Covid-19 pandemic. Based on the original photomicrograph we do not consider the depicted specimen to taxonomically differ from *Aratrisporites scabratus.* Final evaluation pends investigation of the holotype, but for the time being the species are tentatively synonymised here.

Aratrisporites parvispinosus (LESCHIK 1955) emend. PLAYFORD 1965

Pl. 2 Fig. 1

Holotype: *Aratrisporites parvispinosus* LESCHIK 1955, Schweizerische Paläontologische Abhandlungen 72: 38, Pl. 5, Fig. 4, B 53/1a

Synonymy: = 1960 *Aratrisporites paraspinosus* KLAUS 1960, p. 148, Pl. 33, Fig. 43,44 (! here refigured in Pl. 2, Fig. 2)

Diagnosis: Zentralteil: Kontur oval bis kreisförmig. Exospor feine Körnerskulptur, unter 1 μm dick, Strangbildung schwach ausgeprägt. Peripherer Teil: Skulptur der Membran feinkörnig, unter 1 μm dick. Auf dieser stehen lose verteilt zarte spitze Dornen bis zu einer Hohe von 2,5 μm. Zone ungleichmässig breit (Leschik, 1955, p. 38).

Engl. Translation: Central part: Outline oval to circular. Exospore sculpture finely granulate, less than 1 μm thick, thickening of the laesurae slightly pronounced. Peripheral part: Sculpture of the membrane finely granulate, less than 1 μm thick. On this are loosely distributed delicate and pointed thorns with a height of up 2.5 μm. Zona unevenly wide.

Emended Description: Microspores monolete, bilateral; plano-convex to biconvex with strongly arched distal surface. Amb elliptical to subcircular. Laesura straight or curved, indistinct to perceptible, extending beyond inner body, often to equator; accompanied by faint to conspicuous, elevated lips (1.5–3 μm high) formed by extensions of proximal sculptine. Spore wall (sclerine) two-layered, cavate: sculptine (outer layer) proximally attached to, but otherwise loosely enveloping, the clearly-defined inner layer. Sculptine about 1 μm thick (hence often folded), structured, having finely patterned surface bearing sparsely distributed, conspicuous, simple, delicate spinae that usually taper rapidly from broad, subcircular bases. Dimensions of spinae: length and basal diameter about 1–4 μm; spacing about 2–20 μm. Delicate tips of spinae often severed leaving resistant spine bases. Spinose sculpture reduced or absent proximally, clearly evident at equator. Inner layer homogeneous, seemingly smooth, approximately 0.5 μm thick (Playford, 1965, p. 194).

Remarks: Unfortunately, consulting the holotype for *Aratrisporites parvispinosus* LESCHIK 1955 was not possible, as Leschik's material could not be located for this study. For the time being the holotype has to be considered as lost. Nevertheless, the remaining photograph can give some information, although the designation of a new type would be desirable. After consulting and comparing Klaus' type material and comparing it with photographs of the holotype of *Aratrisporites parvispinosus*, we consider *Aratrisporites paraspinosus* KLAUS 1960 to be a junior synonym. Although Leschik has not included a more elaborate description like Klaus has, the picture of his holotype depicts the same size relationships between zona and corpus and the same type of ornamentation (also compare Table 2). The latter is in both types finely granulate and although Klaus considers it to be distinctive for *Aratrisporites paraspinosus* to possess spinae that are thicker at the base and rounded at the tip, the same characteristics can be seen from the photograph of *Aratrisporites parvispinosus* (Pl. 2. Figs. 1–2).

Turma TRILETES (Reinsch 1881) emend. Dettmann 1963

Suprasubturma ACAVATITRILETES Dettmann 1963

Subturma AZONATI Burger 1994

Infraturma ***Laevigati*** (Bennie & Kidston 1886) emend. R. Potonié 1956

Calamaspora Schopf, Wilson & Bentall 1944

Calamaspora tener (Leschik 1955) emend. Mädler 1964

Pl. 3 Figs. 3–4

Holotype/Basionym: *Laevigatisporites tenuis* Leschik 1955, Schweizerische Paläontologische Abhandlungen 72: 12, Pl. 1, Fig. 20; B 51/1c

Synonymy: = 1955 *Punctatasporites flavus* Leschik, p. 31, Pl. 4, Fig. 2
= 1958 *Calamaspora mesozoica* Couper, p. 132, Pl. 15, Fig. 3,4

Diagnosis: Äquatorkontur kreisformig. Exospor glatt und hyalin. Die Membran ist sehr dünn, unter 0.7 μm. Dadurch erscheint die Spore sehr hell. Auf die geringe Dicke des Exospors ist die verhältnismassig starke Faltenbildung zurückzuführen. Die flächigen breiten Falten überwiegen die schmalen und wulstigen. Infolge der Faltenbildung ist die kleine Y-Marke nicht immer zu sehen. Sie liegt hier in der Nähe der Umrisslinie. Länge der Strahlen 7 μm. Größe: 41.5 μm (Leschik, 1955, p. 12).

Engl. Translation: Equatorial outline round. Exospore smooth and hyaline. Membrane is very thin, less than 0.7 μm. Because of that the spore appears very bright. The very thin exospore explains the proneness to folding. There are more broad flat folds compared to the padded ones. Because of the numerous foldings, the trilete mark is often not visible. The trilete mark in this case lies close to the equatorial outline. Length of the laesurae 7 μm. Size: 41.5 μm.

Emended Description: Sporen mit dünner, glatter Exine, von kreisrunder oder annähernd kreisrunder Gestalt, die meist sekundär verfaltet überliefert sind. Y-Strahlen etwa dem halben Radius der Spore entsprechend, eher etwas kürzer. Felder zwischen den Y-Strahlen selten etwas dunkler als die übrige Exine. Größe 30–45 µm (Mädler, 1964a, p. 92).

Engl. Translation of Emended Description: Spores with thin, smooth exine with round or almost round equatorial outline and most of the time preserved with secondary folds. Laesurae about the length of half the spore radius, tendentially a bit shorter. Area between the laesurae rarely a bit darker than the exine. Size: 30–40 µm.

Description: The specimens are typically very hyaline, and when the trilete mark is not clearly visible (Pl. 3, Fig. 3) it can be difficult to distinguish this taxon from aquatic elements without using fluorescence. In the Triletes Beds, specimens are often preserved visible darker as in the depicted specimen (Pl. 3, Fig.4). Some specimens show darkening around the trilete mark as reported in the emended diagnosis of Mädler (compare Pl. 3 Fig. 4).

Botanical affinity: Spores of this kind were documented *in situ* in Upper Triassic/Jurassic *Equisetites* sp. and *Equisetites arenaceus* (Couper 1958; Kelber & Van Konijnenburg-van Cittert 1998).

Remarks: Comparison with the specimen of *Calamaspora nathorstii* Klaus 1960 (Pl. 3, Figs. 1–2) depicted no difference to *Calamaspora tener*. Klaus used the name applied to *in situ* spores rather than the name for dispersed ones. The latter is applied here to be more precise. Other synonymisation is followed as laid by Mädler (1964a); see further discussion in there.

Punctactisporites (IBRAHIM 1933) POTONIÉ & KREMP 1954

Holotype: *Punctatisporites punctatus* IBRAHIM 1933, Dissertationsdruckerei Konrad Triltsch, p. 21, Pl. 2, Fig. 18

Synonymy: = 1958 *Todisporites* COUPER, p. 134, Pl. 16, Fig. 6

Diagnosis: Sporen mit Y-Marke, bei denen die Oberfläche des Exospors fein sandig erscheint (Ibrahim, 1933, p. 21).

Engl. Translation: Spores with Y-mark whose surface of the exospore appears finely sandy.

Emended Diagnosis: Trilete Iso- oder Mikrosporen, Äquatorkontur kreisförmig oder doch stark angenähert kreisförmig mit nur sehr schwacher Erinnerung an die Dreiecksform, Umrißlinie glatt. Exine also skulpturlos. Struktur nicht erkennbar oder durch Punktierung bis Infrareticulierung oder Infragranulierung gekennzeichnet (die nicht mit einer sich durch rauhe Umrißlinie bemerkbar machenden Granulierung verwechselt werden darf), vielleicht auch nur lokal, zum

Beispiel längs der Y-Strahlen sichtbar punctat. Strahlen der Y-Marke meist länger als $^1/_2$ Radius des Äquatorschnittes; dadurch und durch mangelnde Kontaktareen von *Calamospora* unterscheidbar (Potonié & Kremp 1954).

Engl. Translation of Emended Description: Trilete iso- or microspores, amb circular or subcircular with only very weak reminiscence of a triangular shape, outline smooth. Exine laevigate. Structure not recognizable or punctate, infrapunctate to infragranulate (which should not be confused with grana which would be perceivable as an uneven outline), perhaps only locally, for example, along the Y-rays visible. Rays of the trilete mark usually longer than $^1/_2$ radius of the equatorial plane; thereby and through the lack of contact area distinguishable from *Calamospora*. (altered after Jansonius and Hills, 1976; card 2286)

Botanical affinity: Ferns. Found *in situ* in Marattiales in *Danaeopsis* (Middle–Upper Triassic in Australia, South America and Europe; Kustatscher et al., 2012b), Osmundaceae (various *Todites* species) and Gleicheniaceae (*Wingatea plumosa* (DAUGHERTY) LITWIN 1985 (Triassic))(Balme 1995).

Remarks: Lund (1977) already points out that the holotypes for *Punctatisporites* and *Todisporites* COUPER 1958 depict the same characteristics, but explains that the former is usually used for Paleozoic specimens while the latter is more commonly used for Mesozoic specimens. Lund (1977) for example follows the proposal by Kedves and Simoncsics (1964) to treat them as synonymous and use *Punctatisporites*, i.e. the name with priority, irrespective of temporal occurrence, because the later name was nomenclaturally superfluous at the time of its description. This opinion is concurred here. It is important to keep this synonymy in mind when comparing data in between different Mesozoic sections (e.g. like in chapter 3), as authors tend to use either or of these two names. For further discussion see Jansonius and Hills (1976; card 2286), who discuss emendations which are not adopted here.

cf. *Punctactisporites* sp.

Pl. 3, Fig. 5

Description: Our specimen is tentatively assigned to this taxon. The trilete mark is a bit short compared to the type of the genus. Although it also shows similarities with *Stereisporites*, the amb is more rounded and therefore more similar to *Punctatisporites*. The specimen does not show curvaturae perfectae although it is folded a bit at the end of two of the three laesurae and is therefore not assignable to *Retusotriletes*. It complies best with the emended description by Potonié and Kremp (1954).

Retusotriletes NAUMOVA 1953

Retusotriletes mesozoicus KLAUS 1960

Pl. 3 Fig. 6–10

Holotype: *Retusotriletes mesozoicus* KLAUS 1960, Geologisches Jahrbuch A, Sonderband 5: 28, Pl. 28, Fig. 6, GB (! here refigured in Pl. 3, Fig. 7)

Preservation of the Holotype: The slide itself is in mediocre condition with a desiccated mounting medium, which allows a less clear view on the specimen. The main characteristics, i.e. the curvaturae, is partially still visible (Pl. 3, Fig. 7), but due to the changed light refraction not as clearly as in the original photograph (Pl. 3, Fig. 6). Therefore, an epitype would be useful to disambiguate this for the future. We propose the specimen shown in Pl. 3, Fig. 9 to serve as such in later effective publication of this manuscript.

Diagnosis: Trilete Mikrosporen mit ± kreisrundem Äquatorumriß und deutlichen, großen Kontaktareen. Die ± schwachen Wülste der Y-Marke verbinden sich zu Curvaturae perfectae und lassen zum Äquatorumriß nur einen verhältnismäßig schmalen Raum frei. Die nicht dicke Exine (um 1 μm) ist schwach gefleckt (bis scabrat) jedenfalls nicht vollkommen einförmig glatt (Klaus, 1960, p. 28).

Engl. Translation: Trilete microspores with ± circular amb and distinct, large contact areas. The weak laesurae of the Y-mark connect to curvatura perfectae and leave only a relatively narrow space between the curvatura and the equatorial outline. The not thick exine (around 1 μm) is weakly spotted (to scabrate), at least not completely uniformly laevigate.

Botanical affinity: Clubmosses. Asides the affinity with Rhyniophyta, Balme (1995) describes the spores of Zosterophyllales generally as retusoid, and for seven of the circa eleven genera (*Discalis*, *Nothia*, *Rebuchia*, *Sawdonia*, *Oricilla*, *Serrulacaulis*, *Zosterophyllum*) from the Devonian around the world are reported to show spores *in situ* that comply with the circumscription of *Retusotriletes* (Balme 1995).

Description: Our best-preserved specimen (Pl.3, Fig. 9) is subcircular and measures ca. 33 μm in diameter. The exine is ca. 0.9 μm thin and mostly smooth only scabrate in a few places in the contact areas. The most distinctive characteristic, the curvaturae perfecta is very well visible, especially at the lower two apices. The trilete mark itself is visible only as a hairline. Altogether, the specimen complies very well with the original diagnosis.

Infraturma ***Apiculati*** (BENNIE & KIDSTON 1886) emend. POTONIÉ 1956

e.1. Elements small (up to 1.5 μm) BURGER 1994

Baculatisporites THOMSON & PFLUG 1953

Type: *Sporites primarius* WOLFF 1934, Arbeiten aus dem Institut für Paläobotanik und Petrographie der Brennsteine 5: 66, Pl. 2, Fig. 51

Diagnosis: Skulptur aus locker angeordneten Stäbchen, die im Grundriß nicht verlängert sind (Thomson and Pflug, 1953, p. 56).

Engl. Translation: Sculpture consists of loosely arranged rods that are not elongate when seen in horizontal section.

Botanical affinity: This type of spores are found *in situ* in *Todites hartzii* and *Osmundopsis plectophora*, both of which belong to the Osmundaceae (Pedersen and Lund, 1980; van Konijnenburg-van Cittert, 2000).

Remarks: Krutzsch (1967) studied a variety of extant Osmundaceous species and subsequently emended the genus to include all forms, granulate, baculate and verrucate alike, that occur in the extant affinity (see more elaborate summary in Jansonius and Hills (1976); card 219). Given the multiple occurrence of very similar spore types in ferns (Balme 1995), this appears as a potentially problematic simplification which is not followed here for the sake of keeping different forms of ornamentation taxonomically separate. This primary separation still permits secondary lumping of the botanical affinities depending on the respective study question (e.g. SEG analysis Abbink et al., 2004a, 2004b).

Baculatisporites comaumensis (COOKSON 1953) POTONIÉ 1956

Pl. 1, Figs. 24–33

Holotype/Basionym: *Trilites comaumensis* COOKSON 1953, Australian Journal of Botany 1: 470, Pl. 2, Fig. 27, 28

Diagnosis: Spores more or less spherical, 29–59 μm in diameter, trilete, the tetrad scar extending to the periphery. Wall thin, rather closely ornamented with blunt rod-like processes, about 1.2 μm long (Cookson, 1953, p. 470).

Description: Our specimens comply very well with the original description in size, ornamentation and length of the laesurae. In comparison to the holotype however, the laesurae are accompanied by a thickening. The colour is variable and increasingly dark with the progressing transition from the Contorta Beds to the Triletes Beds (Pl. 1, Fig. 24–33), but within the Triletes Beds within sample variation as well (e.g. Text-Figs. 10 and 11). We also observed a potentially aberrant specimen in the detailed sampling just prior to the base of the Triletes Beds (Pl. 1, Fig. 33). Although it cannot be entirely excluded to be an effect of folding, it appears, that the trilete mark is double forked, i.e. like two Y-marks grown together.

Trachysporites NILSSON 1958

Type: *Trachysporites fuscus* NILSSON 1958, Publications from the Institutes of Mineralogy, Paleontology and Quaternary Geology, University of Lund 53: 38, Pl. 2, Fig.1, Präp.-Nr. 91 (Höör)

Diagnosis: Azonate, trilete Miosporen mit uregelmäßiger Skulptur und wechselnder, dreieckiger oder annähernd kreisrunder Form. Skulptur nicht regelmäßig granulat, verrucat, oder reticulat, sondern meist von verschiedenen Elementen an einem und demselben Individuum bestehend: Granula, Verrucae, Baculae, Clavae, kurze und breite Dornen und Leisten usw. (Nilsson, 1958, p. 38).

Engl. Translation: Azonate, trilete miospores with irregular sculpture and alternating, triangular or subcircular shape. Sculpture not regularly granulate, verrucate, or reticulate, but usually composed of different elements on one and the same individual: granules, verrucae, baculae, clavae, short and broad spines and ridges, etc.

Botanical affinity: Ferns. Presumably based on morphology after Bonis (2010).

Remarks: For distinction of similar genera like *Conbaculatisporites*, read the discussion there.

Trachysporites asper NILSSON 1958

Pl. 1, Figs. 37, 38

Holotype: *Trachysporites asper* NILSSON 1958, Publications from the Institutes of Mineralogy, Paleontology and Quaternary Geology, University of Lund 53: 39, Pl. 2, Fig.3, Präp.-Nr. 91 (Höör)

Diagnosis: Grösse 38–41 µm. Dreieckige Spore mit meist schwach konvexen Seiten und abgerundeten Spitzen. Y-Strahlen fast bis zum Äquator reichend; Lippen nicht verdickt. Exine dünn (etwa $^3/_4$ µm), schwach gefärbt, mit sehr feinen Granula und kurzen Dornen dicht besetzt (Nilsson, 1958, p. 39).

Engl. Translation: Size 38–41 µm. Triangular spore with mostly slightly convex sides and rounded apices. Y-rays almost reach the equator; margo not thickened. Exine thin (about $^3/_4$ µm), slightly coloured, densely covered with very fine granules and short spinae.

Description: Our specimen (Pl. 1, Fig. 36) is triangular with slightly concave sides and rounded apices and measures ca. 36 μm, i.e. slightly smaller than noted in the original diagnosis. Two of the laesurae almost reach the equator, one of them seems to reach it, but might be an artefact of the positioning of the spore. The ornamentation is dominated by fine granules. Spines are absent, only a few bigger baculae can be seen, the exine is rather thick, ca. 1.5 μm which could make this specimen also comply with *Trachysporites fuscus*, the smaller size and the very fine ornamentation however suggests assignation to *Trachysporites asper* due to lack of other discriminating characteristics.

Remarks: Although Nilsson (1958) has described a very diverse ornamentation of granules and spinae, neither the majority of our specimen, nor his own representations of them show this.

Trachysporites cf. *asper* NILSSON 1958

Pl. 1, Fig. 37

Description: The depicted specimen is almost perfectly triangular with only one of the sides slightly concave. It is ca. 46 μm in diameter and thereby a bit bigger that the size range given in the original description. The trilete mark is very straight and almost reaches the equator. The ornamental elements are small grana and bigger baculae. The granules are ca. 1 μm high and densely distributed. The exine is ca. 1 μm thick.

Trachysporites sp. A NILSSON 1958

Pl. 1, Fig. 38

Description: The depicted specimen is almost perfectly triangular with slightly more convex sides than in the other observed specimens. It is ca. 45 μm in diameter. The trilete mark is very straight and almost reaches the equator, but in comparison to the other species it possesses tori in the interradial area. The ornamental elements are small grana and very densely arranged. The exine is ca. 1 μm thick.

Remarks: Nilsson (1958) already depicted a specimen just like this with the same tori.

e.3. Elements medium to large, height at least 2x width BURGER 1994

Conbaculatisporites KLAUS 1960

Type: *Conbaculatisporites mesozoicus* KLAUS 1960, Geologisches Jahrbuch A, Sonderband 5: 125–126, Pl. 29, Fig. 15, single grain sample Nr. 355, GB (! here refigured in Pl. 1, Fig. 35).

Diagnosis: Trilete Mikrosporen von ± dreieckigem Äquator umriß. Die Dreieckseiten können gerade, konkav oder schwach konvex gebogen sein. Ist letzteres der Fall, dann muß immer noch die Dreieckform deutlich bleiben. Y-Strahlen etwa $^{2}/_{3}$ des Sporenradius, zuweilen auch etwas länger, aber nie ganz bis zum Äquator reichend; meist ziemlich gerade, zart, jedenfalls ohne nennenswerte Aufwulstungen. Die Exinen-Skulptur ist distal und proximal bis zum Apex in ähnlicher Weise ausgebildet. Sie besteht aus Baculae in ähnlicher Dichte und Größe wie bei *Baculatisporites* THOMS. & PFLUG, welche einer dünnen bis mäßig dicken Exine ± senkrecht aufsitzen. Vielfach ist die Anordnung der Baculae an den stark abgerundeten Dreickspitzen dichter; auch sind sie dort etwas länger und auffälliger ausgebildet. Die Dicke und Länge der Baculae ist innerhalb der Gattung Variationen unterworfen. Sekundärfaltungen selten. Größenvariation: Etwa 33–50 μm (Klaus, 1960, pp. 125–126).

Engl. Translation: Trilete microspores of ± triangular equator outline. The sides of the triangle can be straight, concave or slightly convex. If the latter is the case, then the triangle shape still has to remain clear. Y-rays about $^{2}/_{3}$ of the spore radius, sometimes a little longer, but never quite reaching the equator; usually quite straight, delicate, at least without significant thickenings. The exine sculpture is formed distally and proximally to the apex in a similar manner. It consists of baculae in similar density and size as in *Baculatisporites* THOMSon & PFLUG, which are ± perpendicular to a thin to moderately thick exine. In many cases, the arrangement of baculae on the strongly rounded apices is denser; They are also a little longer and more conspicuous. The thickness and length of the baculae is subject to variations within the genus. Secondary folds rare. Size variation: About 33–50 μm.

Botanical affinity: Ferns – Osmundales? The strong similarity with *Baculatisporites* sp. suggests a similar affinity as some authors have assumed (Bonis 2010). Even though Pederson and Lund (1980) report an *in situ* find of spores that comply with the circumscription of *Conbaculatisporites mesozoicus* in *Clathopteris mesicoides* this is based on Harris (1931) publication with illustrations of rather poor quality which might obscure such a small distinction. In view of intraspecific variety within a single sporangium in extant plants, the first suggestion is followed here.

Remarks: *Trachysporites* and *Conbaculatisporites* are very similar but are distinguished by the fact that *Trachysporites* possesses multiple different types of ornamental elements together, while *Conbaculatisporites*, although the same in shape, possesses only baculae.

Conbaculatisporites mesozoicus KLAUS 1960

Pl. 1, Figs. 34–35

Holotype: *Conbaculatisporites mesozoicus* KLAUS 1960, Geologisches Jahrbuch A, Sonderband 5: 125–126, Pl. 29, Fig. 15, single grain sample Nr. 355, GB (! here refigured in Pl. 1, Fig. 35).

Preservation of the Holotype: The holotype was still embedded by the mounting medium at the time of study in 2018, but the glycerin jelly had already strongly desiccated (Pl.1, Fig. 35). Due to the limited quality of the available photographic equipment, the ornamentation could not be documented as nicely as in the original photograph, yet the baculae are still clearly visible.

Diagnosis: Trilete Mikrosporen von annähernd dreieckigem Äquatorumriß mit manchmal konkav, bis leicht konvexen Seiten. Stark abgerundete Dreieckspitzen. Exine ziemlich dünn und durchsichtig. Y-Strahlen zart, etwa $^2/_3$ des Radius lang. Der Exine sitzen ziemlich dünne, am Ende abgerundete Baculae auf. Sie sind etwa doppelt so lang wie dick. An der Basis gelegentlich geringfügig erweitert. Gegen die Mitte der Dreieckseiten im Äquatorumriß ersichtlich, sind sie kürzer und auch nicht so dicht wie an den abgerundeten Ecken der Dreiecksform. Die Anordnung ist so, daß zwischen zwei Baculae eher noch ein weiteres Stäbchen Platz hätte. In der Fläche erscheinen sie nicht ausgesprochen regelmäßig angeordnet. Größe: 39–48 μm (Klaus, 1960, pp. 125–126).

Engl. Translation: Trilete microspores of approximately triangular equatorial outline with sometimes concave to slightly convex sides. Strongly rounded apices. Exine pretty thin and transparent. Y-rays delicate, about $^2/_3$ of the radius long. Exine with quite thin baculae, which are rounded at the end. They are about twice as long as thick. Occasionally slightly wider at the base. Towards the center of the triangle, which is visible at the equatorial outline, they are shorter and less dense than at the rounded corners of the triangular shape. They are arranged in a way, that between two baculae, another one would have place. In overall view they do not appear very regularly arranged. Size: 39–48 μm.

Porcellispora SCHEURING 1970 emend. MORBEY 1975

Type: *Conbaculatisporites longdonensis* CLARKE 1965, Palaeontology 8: 299, Pl. 36, Fig. 1

Synonymy: = 1973 *Naiaditaspora* ORBELL, p. 10, Pl. 5, Figs. 1–3

Diagnosis: Grosse, in Polansicht annähernd runde Mikrosporen mit kräftig ausgebildeten Int- und Ectexinen. Die Meridiankontur ist stark abgeflacht. Die Distalseite weist einen lockeren, nicht sehr regelmässigen Besatz an unterschiedlich grossen Echini, Coni und Baculae auf. Die Proximalseite ist mit bedeutend kleineren und feiner ausgebildeten stachel-, haar- und baculaförmigen Skulpturelementen verziert, die ebenfalls locker und unregelmässig verteilt sind, deren Dichte und Grösse gegen den Proximalpol zu aber abnimmt. Die Y-Marke ist (ausser im aufgeplatzten Zustand) nie scharf und deutlich ausgebildet sichtbar. Sie wird oft nur durch ein variabel geformtes, oft gefeldert erscheinendes helles Feld in Polnähe angedeutet, von dem zuweilen unregelmässig verlaufende Exineneinrisse in Richtung der Y-Strahlen ausgehen. Dieses Feld geht auf eine proximale Exinenverdünnung zurück (Scheuring, 1970, p. 103).

Engl. Translation: Large microspores with subcircular amb and strongly developed intexine and ectexine. Strongly flattened in lateral view. The distal face covered more or less densely with echini, coni and baculae that are rather irregularly distributed and variable in size. Proximal face ornamented with significantly smaller and finer spiny, rod-, or hair-shaped elements that also are distributed In a loose and irregular fashion, and that become smaller and sparser towards the proximal pole. The Y-mark is never sharp and distinctly developed (except when burst open and gaping). It is often only indicated by a brighter region in the polar area which is variable in shape and often apparently subdivided into fields, occasionally with irregular cracks in the exine running in the direction of the trilete rays. This region is caused by thinning of the proximal exine. (altered after Jansonius and Hills (1976), card 2119)

Emended Diagnosis: Miospores proximally hilate, occasionally trilete or with a polar exinal tear irregular in shape. In structure, generally zonate or cinguli-zonate. Amb triangular to circular. Exine two-layered. Equatorially, int- and exoexine of variable thickness between specimens. Distal surface ornamented with a variety of processes, mainly spinae, coni, bacula, and verrucae. Individual specimens dominated by one process type or characterised by a combination of process types. Proximal surface similarly ornamented, ornamentation comparatively reduced. Equatorial ornamentation similar to distal in development, often fused in part, seldom totally (Morbey, 1975, p. 23).

Botanical affinity: Liverworts – Marchantiophyta (Balme 1995).

Remarks: It is worth noting the synonymy with *Naiaditaspora*, which is a much-used name in British sections, but describing the same genus. Only two other species are formally described: *Porcellispora magna* SMTO-SZENTAI 1996 in Hungary and *Porcellispora bella* MIAO et al. 1984. in China. Given the rather broad range of ornamentation covered by *Porcellispora* as such and *Porcellispora longdonensis* in particular, might have caused the relatively small number of species described.

Porcellispora longdonensis (CLARKE 1965) SCHEURING 1970 emend. MORBEY 1975

Chapter 3, Fig. 7.37

Holotype/Basionym: *Conbaculatisporites longdonensis* CLARKE 1965, Palaeontology 8: 299, Pl. 36, Fig. 1

Synonymy: = 1967 *Baculatisporites kajperianus* ORLOWSKA-ZWOLINSKA, p. 48, Pl. 1
= 1973 *Naiaditaspora harrisii* ORBELL, p. 10, Pl. 5, Figs. 1–3.

Diagnosis: not available

Emended Diagnosis: Miospores proximaly hilate, occasionally trilete. Irregular exinal tears common where hilum or trilete mark indistinguishable. In structure, generally zonate or cinguli-zonate. Amb convexly triangular to circular. Proximal profile flat to convex, distal profile convex. Exine two-layered. Intexine laevigate or punctate, thin or equatorially thickened. Exoexine extended into a well-developed or rudimentary zona, upto [sic] ca. 13 μm in width. Modification of the zona is dependent upon the development of the equatorial ornamentation. Distal surface ornamented with randomly spaced spinae, coni, bacula, tubercula, grana, and occasional gemmae. Processes unequal in size, sparse or dense in distribution, upto [sic] ca. 12 μm. in height and ca. 5 μm in diameter. Individual specimens dominated by one process type or a combination of types. Proximal surface ornamented with random, often densely distributed, spinae, coni, bacula, and grana, upto [sic] ca. 3 μm in height and ca. 2 μm in diameter, reduced in size and density at the proximal pole. Suturae, where evident, simple, gaping (Morbey, 1975, p. 23).

Description: Our specimen's amb is convexly triangular and ca. 97.5 μm big and therefore in the middle of the size ranges given by Morbey (1975)(68–111 μm), but bigger than the range 60–85 μm given by Scheuring (1970). A zona is clearly visible through its hyaline appearance and ca. 7–10 μm wide. A trilete mark is not visible. The distal side depicts mostly baculae and some spinae of up to 6 μm length. The sculptural elements are rather evenly spaced with 1–6 μm in between them.

Infraturma ***Murornati*** POTONIE & KREMP 1954

e.1. *Reticulati* BURGER 1994

Tigrisporites KLAUS 1960

Type: *Tigrisporites halleinis* KLAUS 1960, Geologisches Jahrbuch A, Sonderband 5: 140, Pl. 31, Fig. 28, 30 (!, here refigured in Pl. 4, Fig. 23)

Synonymy: = 1972 *Tappanispora* SRIVASTAVA, p. 859, Pl. 1, Fig. 1, 2

Diagnosis: Trilete Mikrosporen mit ± dreieckigem Äquatorumriß. Die Ecken sind flach abgerundet. Y-Strahlen dünn, ohne begleitende Wülste bis zum Äquatorumriß gerade, zuweilen besonders in Apex nähe etwas geschlängelt. Keine durch Falten oder auf andere Art gekennzeichneten Grenzen von Kontaktarealen. Proximal ist die Exine – glatt oder wenig und nur fein verziert. Distal hingegen, etwa im Äquator beginnend verlaufen ziemlich kurze, gewundene kräftige Rugae, welche sich vorwiegend in radialer Richtung anordnen und den Umriß gekerbt gewellt erscheinen lassen. Etwa auf halbem Radius münden diese Wülste in den nicht rugulaten, sondern entweder glatten, granulierten, punktierten oder anders verzierten, dunklen zentralen Fleck der Distalseite Dieser und die Radialrugae kennzeichnen neben anderen Merkmalen die Gattung. Größe:Etwa 40–68 μ (Klaus, 1960, p. 140).

Engl. Translation: Trilete microspores with an ± triangular equatorial outline. Apices are flatly rounded. Y-rays thin, without accompanying thickenings, extending to equator, straight but sometimes sinuous towards the apices. Contact areas not indicated by folds or other characteristics delaminating the borders of the contact areas. Proximal exine smooth or minutely sculptured. Distally however, beginning at the equator, with rather short, strongly sinuous rugae, mostly in radial direction, causing a serrate or corrugated outline**.** Approximately in the middle of the radius, the rugae run into not rugulate but smooth, granulate or punctate or other such sculptural elements, forming a darker spot in the middle of the distal face. This dark spot and the radially arrange rugae are characterizing the genus amongst other things. Size: ca. 40–68 μm.

Emended Diagnosis: Trilete miospores. Outline subtriangular to subcircular in polar view. Distal surface ornamented with rugulae; distal pole consisting of an area of exinal thickening without rugulate ornamentation. Proximal surface smooth to weakly rugulate to distinctly rugulate. Trilete rays extending to the equator (van Erve, 1977, p. 56).

Botanical affinity: Clubmosses? Tentative affinity based on Bonis (2010) and Schulz (1967)

Remarks: Note that this translation differs significantly from the translation given by Jansonius and Hills (1976, card 3417), which is rather a free summary and interpretation of the characteristics than a translation. Based on comparison of the two diagnoses of *Tigrisporites* and *Tappanispora* SRIVASTAVA 1972, there is no notable difference that would justify the latter name, which is thus considered a junior synonym as it was superfluous at the time of its description.

Tigrisporites halleinis KLAUS 1960

Pl. 4, Fig. 23, 24

Type: *Tigrisporites halleinis* KLAUS 1960, Geologisches Jahrbuch A, Sonderband 5: 140, Pl. 31, Fig. 28, 30 (!, here refigured in Pl.3, Fig. 29)

Synonymy: = 1967 *Tigrisporites microrugulatus* SCHULZ, p. 571, Pl. 7, Figs. 1–3

Diagnosis: Trilete Mikrosporen von ± dreieckigem Umriß mit stark abgerundeten bis abgeflachten Dreieckspitzen. Y-Strahlen auf der sonst glatten Distalseite sind gerade, nur in Apexnähe leicht geschlängelt, dünn, reichen bis zum Umriß. Auf der Distalseite finden sich zwei Exinenornamentationen, welche sich etwa auf 1/2 Radius begegnen. Nach außen zu etwa 1.5 μ breite, in sich gebogene, im allgemeinen radial gestellte Runzeln von maximal etwa 10 μ Länge, welche bis zum Äquator heraufreichen und diesen gewellt und gekerbt erscheinen lassen. Nach innen gegen den Zentralteil verlieren sich die Rugae, werden hingegen von einem ± runden, durch verstreute Runzeln abgegrenzten, infragranulaten dunkleren Exinenfleck abgelöst. Sein Radius entspricht ungefähr $^1/_3$ bis $^1/_2$, der Länge eines Y-Strahles (Klaus, 1960, p. 140).

Engl. Translation: Trilete microspores of + triangular outline with strongly rounded to flattened apices. Y-rays on the otherwise smooth distal side are straight, only slightly sinuate near the apex, thin, reaching to the outline. On the distal side there are two types of exine ornamentation, which meet circa in the middle of the radius. Outwardly about 1.5 μm wide, in themselves curved, generally radially arranged wrinkles with a maximum length of about 10 μm, which reach up to the equator and make it appear wavy and sinuate. Inwardly, towards the central the rugae are partly dissolved, and are replaced by a distinct, infragranulate, darker exine spot. Its radius is roughly $^1/_3$ bis $^1/_2$ of the length of a laesura.

Remarks: Schulz (1967) described the new *Tigrisporites microrugulatus*. Although we could not yet relocate the holotype, the form photograph he depicts is indistinguishable from our specimen (Pl. 4, Fig. 24). We also compared our specimen with the holotype for *Tigrisporites halleinis* (Pl. 4, Fig. 23) and could not find a notable difference, except for variety and size and preservation. The less radially arranged rugulate, that Schulz mentions, is an almost imperceivable difference and interpreted to be part of the infraspecific variation. Due to the lack significant differences, we see not need for species differentiation and therefore synonymise the two species here.

Triancoraesporites SCHULZ 1962

Type: *Triancoraesporites reticulatus* SCHULZ 1962, Geologie 11: 311, Pl. 2, Fig. 12–13, Möckern 1E – 10184/1, R46.3, BGR-S: X11184 (!, here refigured in Pl.).

Diagnosis: Trilete Mikrosporen mit meist deutlicher Y-Marke, r= $^1/_2 - ^2/_2$. Wand zweischichtig, Ä-Kontur hat die Form eines dreifachen T-Ankers mit starken seitlichen Einbuchtungen. Oberfläche verschieden, glatt oder mit Skulptur versehen (Schulz, 1962, p. 311).

Engl. Translation: Trilete microspore with a trilete mark visible in most of the cases, r= $^1/_2 - ^2/_2$. Wall two-layered, equatorial outline has the shape of a trimeric T-anchor with strong lateral invaginations. Ornamentation variable, smoot or sculptured.

Botanical affinity: Clubmosses–Lycopodiales according to Schulz (1967) and Bonis (2010).

Remarks: Schulz (1967) highlights the differences between the genus *Waltzispora* Staplin 1960 whose outline is reminiscent but different from the current spores who on top of that vary in their ornamentation. He therefore erects the new genus *Triancoraesporites*. It is a small genus with only three formally described species: *Triancoraesporites ancorae*, *Triancoraesporites communis* and *Triancoraesporites reticulatus*. Given that *Triancoraesporites communis* was already synonymised by the author himself (compare Schulz 1967) only the two presented below are still valid. Both seem limited to the TJ–transition, wherefore the genus has great stratigraphic value. One known occurrence outside this time-range, i.e. the Turonian (Medus et al. 1980) has to be dismissed, as the publication depicts a spore with an outline that does not possess the typical trimeric T-anchor shape, but a triangular spore-body with round perispore, probably assignable to *Zebrasporites*.

Triancoraesporites ancorae (REINHARDT 1961) SCHULZ 1962

Pl. 3, Fig. 21–25

Holotype/Basionym: *Waltzispora ancorae* REINHARDT 1961, Geologie und Mineralogie 3: 705, Pl. I, Fig. 14

Synonymy: = 1962 *Triancoraesporites communis* SCHULZ, p. 311, Pl. 2, Fig. 14–15

Diagnosis: Äquatorumriss dreieckig-konkav, dreieckspitzen stark abgestumpft, schwach T-förmig. Sporenwand glatt, ca. 1 µm stark, zweischichtig. Schwache Verdickungen an den sechs Ecken der T-förmigen Dreiecksspitzen. Y-Marke deutlich (Reinhardt, 1961, p. 705).

Engl. Translation: Equatorial outline triangular-concave, apexes strongly rounded, weakly T-shaped. Spore wall smooth, ca. 1 μm thick, two-layered. Weak thickening at the six corners of the T-shaped apices. Trilete mark clearly visible.

Description: Our specimens (Pl. 3, Figs. 21–25) are between 30–40 μm in diameter. The invaginations of the outline in between the apices are between 3–6 μm deep but vary in the degree to which they are pronounced anchor-shape (compare Pl. 3, Figs. 21 and 25). The spore wall is two-layered and about 1 μm thick, but slightly thinner at the tip of the apices and thickening towards the six corners of the T-shaped apices. The laesurae are ca. $^{2}/_{3}$ of the length of the spore radius. The area around the laesurae is darker in colour.

Remarks: Size variation, depth of invagination and colour around the laesura might be connected to maturation, with smaller specimen with less deep invaginations and darker colouring, whilst bigger specimen depict deeper invaginations are more uniform colour. In fact the entire species might be a premature stage leading up to *Cornutisporites seebergensis*. Since they are still two ends of morphological variation they are treated separately, however. Interestingly, some species show the beginning formation of a perispore similar to *Zebrasporites* (Pl. 3, Fig. 26), or beginning reticulation (Pl. 3, Figs. 26 and 27) similar to *Triancoraesporites reticulatus*. It is unclear whether this could be an effect of hybridiisation, causing chimeric spore forms or whether this is an aberration caused by environmentally induced mutagenesis for example. The occurrence of this forms can only be reported from the transitionary interval between Contorta and Triletes Beds

Triancoraesporites reticulatus SCHULZ 1962 ***emend***.

Pl. 3, Fig. 28–38

Holotype: *Triancoraesporites reticulatus* SCHULZ 1962, Geologie 11: 311, Pl. II, Fig. 12–13, Möckern 1E – 10184/1, R46.3, BGR-S: X11184 (!, here refigured in Pl. 3, Fig. 29).

Preservation of the Holotype: The preservation is rather poor, the cover slip was cracked through the middle and the glycerin jelly is completely dried out, but remains as “grainy” little lumps throughout the slide obstructing the view aside the different light refraction. The main characteristics, i.e. the outline, with the typical shape of a trimerous anchor and rounded apices, the trilete mark and reticulate distal side, are still discernable.

Diagnosis: Größe 33–41 μm (Holotypus 35 μm) Ä-Kontur des Sporenkörpers triangulär mit schwach gerundeten Ecksektoren, aber trotzdem flach zugespitzten Ecken und starken seitlichen Einbuchtungen. Die Form hat die Gestalt eines dreifachen T-Ankers. Distal ist die Oberfläche der Sporen uregelmäßig reticulat, der Äquatorrand dadurch leicht gewellt. Y-Marke meist bis zum

Äquatorrand reichend, nahe dem Äquator undeutliche Aufspaltung der einzelnen Strahlen (Schulz, 1962, p. 311).

Engl. Translation: Size 33–41 μm (holotype 35 μm). Equatorial outline of the body of the spore triangular with weakly rounded apex-areas, but still flat and pointed apices and invaginations of the outline. The specimen has the shape of a trimerous anchor. On the distal side, the surface of the spores is irregularly reticulate, the equatorial outline through this slightly undulated. The trilete mark, most of the time, reaches the equator, and splits there indistinctly into sperate rays.

Description: The best-preserved specimen (Pl. 3, Fig. 35) measures ca. 33 μm in diameter and fits the original description very well. Only the point where the laesurae meets the apex does not seem to split "indistinctly" as Schulz puts it, but rather merge with a thickened "cap" at the apex.

Remarks: After restudying the holotype of Schulz, the "thickened cap" is visible on the proximal side, and although varying in thickness from apex to apex (an in between specimens), sometimes to the extent of being inconspicuous, which has probably caused Schulz to describe it as a "indistinct" split. Comparing with other specimens from Bonenburg, this seems to be a characteristic feature of this species. We propose the following emended description incorporate our observations infraspecific variations together with insights from restudying the holotype.

Description/Diagnosis *emend.*: Size 33–41 μm (holotype 35 μm). The spore has the shape of a trimerous anchor. The invaginations at the sides in between the apices, make the apex-areas stand out, giving them the appearance of an anchor. These invaginations are less pronounced than in *Cornutisporites* SCHULZ 1962. Apices weakly rounded. On the distal side irregularly reticulate, which makes the equatorial outline appear slightly undulated. The trilete mark reaches almost to the equator and merges into a "thickened cap", i.e. a thickening which is thickest at the tip of the apex and becomes thinner towards the corners of the apex area, where the invaginations begin. The laesurae merge with this thickening shortly before, to almost at the equator and thus forms a feature comparable to a curvatura imperfecta, even though not always well developed at all apices. Laesurae not accompanied by a darkening like in *Triancoraesporites anchorae*.

e.2. *Rugulati* BURGER 1994

Lycopodiacidites (COUPER 1953) emend. POTONIÉ 1956

Type: *Lycopodiacidites bullerensis* COUPER 1953, New Zealand Geological Survey Paleontological Bulletin 22: 26, Pl.28, Fig. 9.

Synonymy: ≡ 1963 *Lycopodiacdisporites* DANZÉ-CORSIN & LAVEINE, p. 77
= 1983 *Labrorugospora* ZHANG, p. 35

Diagnosis: Free, anispopolar, trilete, laesura long, reaching to sculptured distal surface. Spores triangular to sub-circular in polar view, tetrahedral to sub-tetrahedral in lateral view. Proximal face smooth or with greatly reduced sculpture, distal face always clearly and heavily sculptured, sculpture varied (Couper, 1953, p. 26).

Emended Diagnosis: Größe des Genotypus nicht angegeben, sonst 37–43 μm, trilete Miosporen, Äquator und Meridian ± kreisförmig, Exine abgesehen von den Kontaktareen rugulat. Es sei von Rugae gesprochen, weil die einzelnen Zierelemente nicht regelmäßig wall- oder mauerförmig sind, sondern mehr gestreckten und geschlängelten Verrucae gleichen, die nicht immer gleiche Höhe und gleichbleibende Breite haben. Die ± langgestreckten bis geschlängelten Verrucae verlaufen unregelmäßig und zeigen z. T. conus- bis baculumförmige Fortsätze (Potonié, 1956, p. 39).

Engl. Translation: Size of the type not specified, otherwise 37–43 μm, trilete miospores, equator and meridian ± circular, exine apart from the contact area rugulate. The ornamental elements should be called rugae, because they are not regularly wall-shaped, but resembling more some stretched and meandering verrucae, which do not always have the same height nor a constant width. The elongated to meandered verrucae run irregularly and show conus- to baculum-shaped processes.

Botanical affinity: Clubmosses–Lycopodiales. Most authors (Abbink 1998; Bonis 2010; Kustatscher et al. 2010, 2012a) follow the assignation to the Lycopodiales suggested by Filatoff (1975), while others follow Balme's assignation to ferns (Balme 1995; Mander et al. 2010; Paterson et al. 2016). *In situ* finds are still lacking and morphological comparison does not render either possibility more or less likely. Due to only minor occurrences, we did not put too much emphasis on this decision and followed the majority for the sake of comparison, until further evidence is given.

Remarks: Zhang (1983) described the new genus *Labrorugospora*, with *Lycopodiacidites kuepperi* Klaus 1960 as the type for the genus, and distinguished it based on the shorter trilete rays and the thin and broad margo (Jansonius and Hills, 1976; card 4458). After studying the said holotype and comparing it with other *Lycopodiacidites* specimen (see below) this designation is considered superfluous, as these characteristics are visible and variable in all of the species in *Lycopodiacidites*.

Klaus (1960) points out that the distinguishing characteristic to *Camarozonosporites* is the uniform exine thickness at the equator in *Lycopodiacidites,* while it is thinner at the apices in *Camarozonosporites*, which is otherwise very similar, although generally smaller.

Lycopodiacidites rhaeticus SCHULZ 1967 ***emend***.

Pl. 4, Fig. 18, 19, 21, 22

Holotype*:* *Lycopodiacidites rhaeticus* SCHULZ 1967, Paläontologische Abhandlungen Abteilung B 2: 574, Pl. 8, Figs. 1,2, Möckern 1E, X 11304 BGR-S (!, here refigured in Pl. 4, Fig. 18)

Preservation of the Holotype: The holotype is in perfect condition.

Diagnosis: Größe 55–64 μm (Holotypus 64 μm). Ä-Kontur dreieckig-konvex. Exine durchschnittlich 1,5 μm dick, distal mit maximal bis 15 μm langen, unregelmäßig gewundenen, relativ schmalen Rugae verziert, die konzentrisch, weniger radial angeordnet sind. Skulptur auf kleinem dunklen Zentralfleck des distalen Polfeldes fehlend, Exine lediglich fein granulat bis fast glatt. Exine der Proximalseite mit vorwiegend radial angeordneten, fein rugulaten Elementen verziert. Y-Marke deutlich, Länge der Strahlen r: $^{3}/_{5}$–$^{4}/_{5}$, werden fast ausnahmslos von 3–4 μm breiten, kräftigen Tori begleitet. Umrißlinie unregelmaßig wellenförmig (Schulz, 1967, p. 574).

Engl. Translation: Size 55 – 64 μm (holotype 64 μm). Amb triangular-convex. Exine on average 1.5 μm thick, distally ornamented with a maximum of 15 μm long, irregularly wound, relatively narrow rugae which are arranged concentric rather than radially. Sculpture missing on a small dark central spot of the distal pole field, Exine only finely granular to almost smooth. Exine of the proximal side ornamented with predominantly radially arranged, finely rugulate elements. Y-mark distinct, length of the rays r: $^{3}/_{5}$-$^{4}/_{5}$, which are almost always accompanied by 3–4 μm thick tori. Outline irregularly wavy.

Description: Our specimens (Pl. 4, Figs. 21–22) measures about 53 and 62 μm and are seen from the distal side with the proximal one shining through. The amb is triangular-convex almost sub-circular. The exine appears smooth and is ca. 1.5–3 μm thick in the interradial sides and is only minutely thinner at the apices. Some specimens are very dark (Pl. 4, Fig. 21), but highly intense light, or increased contrast shows, that the distal rugae are up to 2 μm thick and are hamulate forming a pattern of an open reticulum. The laesurae almost reach the equator with a length of ca. $^{4}/_{5}$ of the spore radius and are accompanied by a 2 μm thick margo. The very dark specimes typically occur in the Triletes Beds (text Figs. 10 and 11)

Remarks: *Lycopodiacidites rhaeticus* sometimes occurs in tetrads. Schulz uses the term "Tori", which can cause some confusion due to the inconsistent use of the term. Punt et al. (2007) define torus as an arcuate invagination or protuberance of the exine more or less paralleling the laesura of a spore in the interradial area. They also clarify though, that the term is connected to kyrtome, which some people prefer to use for connected tori. It is crucial to differentiate, that both terms are used for thickenings in the interradial area outside of the laesurae. After studying the holotype, we can confirm, that the thickening that Schulz refers to is directly associated with the laesurae and should thus be called a margo. We propose the following emendation to translate and update the terminology and include more of the observed intraspecific variation observed in Schulz' original material.

Description *emend*. Size 50–65 μm (holotype 64 μm). Amb triangular-convex. Exine on average 1.5–3 μm thick, distally ornamented with a maximum of 15 μm long, hamulate, relatively narrow rugae. Exine of the proximal face more finely rugulate and predominantly radially arranged. Y-mark distinct, length of the laesurae variable, $^{3}/_{5}$ of the spore radius to almost reaching the equator. Laesurae bordered by a 2–4 μm thick margo, that is not always equally distinctly visible. Due to the ornamentation the outline appears irregularly wavy/undulate

Lycopodiacidites rugulatus (COUPER 1958) SCHULZ 1967 ***emend*.**

Pl. 4, Fig. 12, 13, 15–17

Holotype/Basionym: *Perotrilites rugulatus* COUPER 1958, Palaeontographica Abteilung B 103: 147, Pl. 25, Fig.7, 8.

Preservation of the Holotype: The original slide is available, but the holotype could not be relocated yet.

Synonymy: = 1960 *Lycopodiacidites kuepperi* KLAUS, p. 135, Pl. 31, Fig. 27 (!, here refigured in Pl. 4, Fig. 12)

Diagnosis: Trilete, laesurae reaching almost to equator, commissures flanked by a weakly developed margo; equatorial contour rounded-triangular to almost circular; proximal and distal surfaces sculptured with low, occasionally anastomosing, rugulae 2 to 3 μm wide, forming a distinct rugulate to rugulo-reticulate sculpture pattern; exine consists of two distinct layers, an outer, thin layer (considered here as a perine) carrying the rugulate sculpture, and an inner, unsculptured layer, about 2.5 to 3 μm thick (Couper, 1958, p. 147).

Description: Our specimen (Pl. 4, Fig. 13) measures 52 μm in diameter and is seen from the distal side with the proximal one shining through. The amb is triangular-convex almost sub-circular. The exine appears smooth and is at the thickest part 8 μm thick but less than 1 μm at the apices, i.e. at the ends of the laesurae. The rugae on the distal side are very thick, almost 4 μm, but also form an open reticulum as in *L. rhaeticus*. The commissure is opened in our specimen and the margo is about 3.2 μm thick.

Remarks: After restudying the holotype of *Lycopodiacidites kuepperi* KLAUS 1960 we consider it conspecific with *Lycopodiacidites rugulatus.* Klaus gave no distinguishing characteristics from the older name, and since we could not see any, we consider them to be synonymous. Schulz (1967) recombined the species with *Lycopodiacidites* based on the absence of a perispore. Indeed, looking at the original photographs, there is no indication for a perispore. Possibly the relatively large rugulate and the thick exine have caused Couper's interpretation as a perispore. Pending reevaluation of the holotype we propose the following emendation. It should be noted that, depending on the position (it is sometimes difficult to distinguish between *Lycopodiacidites and Camarozonosporites* (Pl. 4, Fig. 11, 14). Although the latter is supposed to be smaller and distinguished by heterogeneous exine thickness, there appear to be some intermediate forms (Pl. 4, Fig. 14) that make classification difficult.

Description/Diagnosis *emend.*: Rounded-triangular to subrounded trilete spores. Laesurae variable in length, up to almost reaching the equator. Laesurae with a weakly to distinctly developed margo. Hamulate ornamentation with thicker muri than in *Lycopodiacidites rhaeticus*. Ornamentation finer and predominantly radially arranged on the proximal face (muri up to 1μm thick). Muri on distal face 2–4 μm thick.

Subturma **AURICULATI** SCHOPF 1938 emend. POTONIÉ & KLAUS 1954

Infraturma ***Laevigati*** BURGER 1994

Cosmosporites NILSSON 1958

Type: *Cosmosporites elegans* NILSSON 1958, Publications from the Institutes of Mineralogy, Paleontology and Quaternary Geology, University of Lund 53: 37, Pl. 1, Fig. 18, Präp. Nr. 5, KT 26,7/108,8

Diagnosis: Endexine in den Dreieckspitzen verdickt und stark eingebuchtet. Y-Strahlen etwa 1/2 Radius. Umrisslinie eben (Nilsson, 1958, p. 37).

Engl. Translation*:* Endexine thickened and indented at the apices. Laesurae ca. ½ of the radius. Outline smooth/even.

Cosmosporites elegans NILSSON 1958

Chapter 3, Fig. 7.14

Holotype: *Cosmosporites elegans* NILSSON 1958, Publications from the Institutes of Mineralogy, Paleontology and Quaternary Geology, University of Lund 53: 37–38, Pl. 1, Fig. 18, Präp. Nr. 5, KT 26,7/108,8

Diagnosis: Größe 24 μm. Dreieckseiten schwach konkav, Dreieckspitzen stumpf abgerundet. Y-Strahlen eng, wohl kaum mehr als ½ Radius; Lippen nicht verdickt. Exine sehr dick (bis 2,5 μm), zweigeteilt; Ektexine etwas dicker (etwa 1,5 μm) als Endexine (bis etwa 1 μm). Endexine am dicksten in den mittleren Partien der Dreieckseiten und in den Dreieckspitzen; Endexine an letzterer Stelle stark eingebuchtet. Innere Struktur verschwommen, schwach sichtbar. Umrisslinie eben (Nilsson, 1958, pp. 37–38).

Engl. Translation: Size 24μm. Sides of the triangle weakly concave, apices bluntly rounded. Laesurae narrow, hardly more than ½ radius; tori not thickened. Exine very thick (up to 2.5 μm), two-layered; ectexine slightly thicker (ca. 1.5 μm) than the endexine (ca. 1 μm). Endexine thickest in the middle part of the sides of the triangle and at the apices; endexine at the latter strongly indented. Inner structure blurred, weakly visible. Outline smooth/even.

Description: Our specimen is ca. 30 μm in diameter and therefore slightly bigger than the holotype. Moreover, the laesurae reach the equator and are therefore double the length compared with the holotype. A very distinct characteristic in our specimen is the forking extensions of the laesurae where they meet the apex, i.e. depicting curvaturae imperfectae. The exine is thinner (ca. 1.25 μm) and thus only half as thick as in the holotype. Despite these differences, the overall smooth habitus with typical indentions at the apices identifies our specimen as *Cosmosporites elegans*. Described differences in sizes might well be a result of different developmental stage or maturity.

Remarks: The genus is still monotypic. It should not be confused with *Cosmosporites* RICHARDSON 1960, which was a homonym at the time of description and was therefore later renamed (Jansonius and Hills, 1976; card 619). Our description of the specimen is very similar to that of (Achilles 1981) who gives similar sizes (27–33 μm) and exine thickness (ca. 1 μm). The laesurae of the depicted specimen in Achilles also reach the equator.

Subturma TRICRASSATI BURGER 1994

Infraturma ***Laevigati*** BURGER 1994

Camarozonosporites (PANT 1954) ex POTONIE 1956

Type: *Rotaspora cretaceus* WEYLAND & KRIEGER 1953, Palaeontographica Abteilung B 95: 12, Pl. 3, Fig. 27

Synonymy: ≡ 1963 *Camarozonisporites* DANZE-CORSIN & LAVEINE, p. 84

Diagnosis: Genotypus ca. 25 μm (nach Photo), trilet, Äquator fast kreisförmig mit schmalem Cingulum, das sich in den Bereichen der den Äquator ± erreichenden Y-Strahlen stark verschmälert. Beim Genotypus scheinen Kyrtome angedeutet zu sein, Exine glatt, Äquator des Cingulums unbedeutend gewellt (flexuos) (Potonié, 1956, p. 65).

Engl. Translation: Type approx. 25 μm (according to photo), trilet, equator almost circular with narrow cingulum, which narrows strongly in the areas of the Y-rays, which reach the equator. In the type, kyrtomes appear to be visible, exine smooth, equator of the cingulum insignificantly wavy (flexuos).

Botanical affinity: Clubmosses? Tentatively assigned based on Schulz (1967), who argues with the similarity to extant species. Not found *in situ* yet.

Remarks: *Uvaesporites* can be differentiated by the different kind of ornamentation (see Pl. 4, Fig. 10).

Camarozonosporites laevigatus SCHULZ 1967

Pl. 4, Fig. 7–9

Holotype: *Camarozonosporites laevigatus* SCHULZ 1967, Paläontologische Abhandlungen Abteilung B 2: 572, Pl. 7, Fig. 7–9, Möckern 1E, 10184/3, X 11300 BGR-S (1)

Preservation of the Holotype: Although the slides holding the holotype is available it could not be relocated.

Diagnosis: Größe 33–35 μm. Ä-Kontur dreieckig konvex. In Verlängerung der Y-Strahlen ist die Exine meist kuppelartig nach außen gewellt, Exine ca. 1 μm dick. Von den Ecken aus verbreitert sich der "Exinenwulst" und misst in Seitenmitte 3–4 μm. Proximal ist die Exine glatt, distal glatt bis infrapunctat. Strahlen der Y-Marke deutlich, fast gerade, r=$^3/_4$. Strahlen werden beiderseits von etwa 2 μm breiten, wulstartigen Verdickungen der Exine begleitet (Schulz, 1967, p. 572).

Engl. Translation: Size 33–35 μm. Amb triangular convex. In extension of the Y-rays, the exine is usually dome-like curled outwards [?], Exine about 1 μm thick. From the apices the exinal thickening widens and measures 3–4 μm in the middle of interradial side of the spore. Proximal, the exine is smooth, distally smooth to infrapunctate. Y-mark rays clearly visible, almost straight, r=$^{3}/_{4}$. Rays are accompanied on both sides by a ca. 2 μm wide, thickening of the exine.

Description: Our specimens are 26/33/35 μm in diameter, i.e. with a larger size range than in the original diagnosis. The exinal thickening is less than 1 μm at the apices of the slightly convex triangular spores. In the interradial sides of the spores the exine can be up to 3 μm. The exine is very smooth (Pl. 4, Figs. 7, 8) or slightly ornamented (Pl. 4, Fig. 9) which is also visible in the photograph of the holotype. The laesurae vary in length and can reach almost to the equator. They are accompanied by a very weak margo which is thinner at the ends of the laesurae and thicker at their sides.

Remarks: While both *Camarozonosporites rudis* and *Camarozonosporites laevigatus* occur already from the Norian onwards, *Camarozonosporites laevigatus* is a typical Rhaetian from, occurring temporarily more abundantly in the Latest Triassic and is thus used in some zonation schemes (e.g. Fisher and Dunay, 1981; Suneby and Hills, 1988).

Camarozonosporites rudis (LESCHIK 1955) KLAUS 1960

Pl. 4, Figs. 1–6

Holotype/Basionym: *Verrucosisporites rudis* LESCHIK 1955, Schweizerische Paläontologische Abhandlungen 72: 15, Pl. 1, Fig. 15

Synonymy: = 1967 *Camarozonosporites golzowensis* SCHULZ, p. 573, Pl. 7, Fig. 10, 11, Golzow 3 (!, refigured here in Pl. 4, Fig. 5)

Diagnosis: Äquatorkontur fast kreisförmig. Exospor deutlich zweischichtig. Die Ektexine ist sehr dünn; darunter liegt die fast 4 μm dicke Endexine. Auch hier liegen die Skulptur- und Strukturelemente in der Endexine. In der proximalen Lage zeigen die plattgedrückten bandartigen Wülste eine gewisse Ordnung. Ca. 3,5 μm von der äußersten Äquatorkontur entfernt scharen sich die verbreiterten Wülste im Zentralteil der Spore. Unterbrochen werden sie nur von den Wülsten der Y-Marke. Mit der Endexine werden sie durch dünnere Stränge verbunden. Länge der Strahlen der Y-Marke 16 μm; sie reichen bis zum Rand (Leschik, 1955, p. 15).

Engl. Translation: Equatorial outline almost circular. Exospore clearly two-layered. The ektexine is very thin; underneath is the almost 4 μm thick endexine. Again, the sculptural and structural elements are in the endexine. In the proximal position, the flattened band-like thickenings show some order. Approximately 3.5 μm from the outermost equatorial contour, the thickened ridges gather in the central part of the spore. They are only interrupted by the laesurae of the Y-mark.

They are connected with the endexine by thinner thickenings. Length of the laesurae of the Y mark 16 μm; they reach to the equator.

Emended Diagnosis: Kleinere trilete Mikrosporen mit wenig verzierter bis glatter Proximalseite (Fig. 14) und durch dicke Rugae kräftig vielfach verfalteter Distalseite von ± abgerundet dreieckigem Umriß (Fig. 12). Die Exine ist zwischen den abgerundeten Dreieckspitzen dicker als an diesen, wodurch sich im optischen Schnitt in Äquatorhöhe das Bild einer an den Dreieckseiten verschmälerten Äquatordifferenzierung ergibt. Die Rugae reichen bis etwa zum Äquator herauf oder enden knapp davor distalwärts, wodurch der Umriß leicht gewellt erscheinen kann. Die Y-Strahlen besitzen kräftige Wulstränder, welche bis ganz oder annähernd zum Äquator reichen. Die Rugae der Distalseite sind dick, gelegentlich kennzeichnend hakenförmig gebogen und ineinander übergehend. Sie schließen zwischen sich ein schmales, absolut imperfectes negatives Reticulum ein. Kennzeichnend für die Art ist neben den erwähnten Merkmalen die geringe Zahl dicker Rugae und die wulstartigen dicken Ränder der Y-Marke. Im Meridianschnitt werden etwa 5–8 Wülste getroffen. Größe: 34–(38)–42 (Klaus, 1960, p. 136).

Engl. Translation: Rather small trilete microspores with little ornamented to smooth proximal side (Fig. 14) which depicts multiple folds by thick rugae on distal side, which has a rounded triangular outline (Fig. 12). The exine is thicker between the rounded apices than at these, resulting in narrowed exine at the apices, when seen in an optical cut in the equatorial region. The rugae reach up to the equator or end just before it, making the outline slightly wavy. The Y-rays are accompanied by thickening, which extend to, or almost to the equator. The rugae on the distal side are thick, occasionally characteristically curved in a hook shape and merging into one another. They enclose between them a narrow, absolutely imperfect negative reticulum. Characteristic of the species is, in addition to the features mentioned, the small number of thick rugae and the thickenings along the Y-mark. In a meridian section about 5–8 rugae are cut. Size: 34–(38)–42.

Description: The majority of studied specimens is between 25–35 μm (Pl. 4, Fig. 1–6). The thinning of the exine at the apices is clearly visible and allows assignation to this taxon. SEM study of a spore gives an clear impression of the imperfect reticulum.

Remarks: It is unclear how this species is to be distinguished from *Lycopodiacidites rugulatus*. The characteristic ornamentation, size, shape and even the thinned exine at the apices are found in intermediate forms (Pl. 4, Fig. 14). We restudied the holotype for *Camarozonosporites golzowensis* Schulz 1967 (Pl. 4, Fig. 5) and we could not find any notable difference, wherefore the two names are synonymised here.

Infraturma ***Murornati*** Burger 1994

Zebrasporites Klaus 1960 emend. Schulz 1967

Type: *Zebrasporites kahleri* Klaus 1960, Geologisches Jahrbuch A, Sonderband 5: 137, Pl. 30, Fig. 18, 19, 20, GB (!, here refigured in Pl. 5, Fig. 5).

Preservation of the Type: The glycerin jelly has desiccated, but the specimen is still in position and unbroken, displaying the described characteristics.

Synonymy: = 1962 *Thuringiasporites* Schulz, p. 309, Pl.1, Figs. 3–6

Diagnosis: Trilete Mikrosporen mit der Dreiecksform mit konvexen Seiten genähertem Äquatorumriß. Ecken des Dreieckes abgeflacht bis gerundet. Von Ecke zu Ecke ziehen sich meist konkave, zuweilen auch gerade oder schwach konvexe, meist scharf gerandete und aufgewulstete Konturen der Kontaktarea, welche in sich geschlossen die Enden der Y-Strahlen umgreifen (Taf. 30, Figs. 19, 20). Diese reichen bis ganz oder nahe an den Arealrand und sind meistens besonders in Apexnähe von Wülsten begleitet. Die Proximalseite ist glatt bis fein verziert (Taf. 30, Fig. 20). Die Distalseite hingegen trägt markante Wülste. (Taf. 30, Figs. 18, 19.) (Radiale Distalrugae.) Es ist kennzeichnend, daß diese jeweils in Richtung senkrecht auf die Dreieckseiten verlaufen und bis an den oft zarten Sporenrand reichen. Am Zentralteil der Distalhemisphäre treffen sich diese leicht geschlungenen Wülste und schließen sich gelegentlich zu wenigen, unregelmäßigen, häufig offenen Netzmaschen. Die Anzahl, Dicke und sonstige Beschaffenheit der jeweils auf eine Dreieckseite senkrecht stehenden Wülste wechselt je nach Art. Die Wülste können auch noch den Äquatorumriß zu leichten Undationen verformen. Größe: Etwa 28–75 µm (Klaus, 1960, p. 137).

Engl. Translation: Trilete microspores with triangular shape and convex sides.[1] Apices of the triangle flattened to rounded. From apex to apex there are mostly concave, sometimes also straight or slightly convex, mostly sharp–margined thickenings of the contact area, which encompass the in themselves closed ends of the laesurae. These [the laesurae] reach entirely or close to the end of the contact area and are most of the times, especially in the region of the apex, accompanied by thickenings. The proximal side is smooth to finely ornamented (Pl. 30, Fig. 20). The distal side on the other hand depicts distinct thickenings (Pl. 30 Figs. 18, 19). (Radiale distal rugulae)[2]. It is characteristic, that they [the thickenings] run perpendicular to the apices and

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[1] Ambiguous German sentence. Here the interpreted disambiguation is given. If literally translated the sentence reads: "Trilete microspores with triangular shape and convex sides approximated equatorial outline."

[2] Klaus' "rugae" are here translated with rugulae, as the term "rugae" following current terminology *sensu* Punt et al. (2007) today is used as a synonym for colpus, while the term "rugulate" describes a pattern of ornamentation of elements more than 1 µm long.

reach as far as the delicate edge of the spore. At the central part of the of the distal hemisphere these undulating thickenings meet and sometimes connect to few, irregular often open mesh/network. The number, thickness and other characteristics of the thickenings on the distal side changes according to the species. The thickenings can cause slight undulation at the equatorial outline. Size: ca. 28–75 µm.

Emended Diagnosis: Trilete Mikrosporen, Umriss dreieckig konvex, Exine an den Dreieckseiten zonaartig verbreitert oder aufgewulstet, Dehiszenzmarke nicht bis zum Äquator reichend. Ektexine glatt oder mit wulstförmigen, radial angeordneten Verdickungen.

Engl. Translation of emended Diagnosis*:* Trilete microspores, equatorial outline a convex triangle, exine at the sides of the triangle broadened or bloated in a zona-like fashion, laesurae do not reach the equator. Ectexine smooth or with muri-like, radially oriented thickenings.

Botanical affinity: Ferns – Filicales? Tentatively assigned based on Bonis (2010) and Schulz (1967).

Remarks: It should also be noted, that the original description of the distal ornamentation as "rugae" is problematic. Following current terminology *sensu* Punt et al. (2007) rugae are is used as a synonym for colpus. Today it would be thus more correct to translate "rugae" with rugulae. According to Punt et al. (2007) "rugulate" describe a type of ornamentation consisting of elongated sexine elements more than 1 µm long, arranged in an irregular pattern that is intermediate between striate and reticulate. In fact, the above-described pattern is regular and more like striae, i.e. parallel elements, on the edges of the distal hemisphere with muri sometimes forming a reticulate-like ornamentation in the center of the distal hemisphere. The English translation thus now contains "rugulate" as the closest term capturing Klaus' ambiguous expression, but the more adequate term from a taxonomical perspective is "muri", which is now adopted in the translation of Schulz' emendation.

There are seven described species of *Zebrasporites* (*Z. kahleri* KLAUS 1960 (!) – type of the genus; *Z. corneolus* KLAUS 1960 (!), *Z. fimbriatus* KLAUS 1960 (!), *Z. interscriptus* (THIERGART 1949) KLAUS 1960 (!; lost); *Z. laevigatus* SCHULZ 1962 (!), *Z. sinelineatus* BÓNA 1966, *Z. rectus* ZHANG 1984. Klaus, due to the limited occurrence of this genus, with its main occurrence from the Carnian to the Rhaetian, already points out the significance of this genus for Triassic stratigraphy (1960). A good understanding of the distinctive features is therefore desirable. While *Zebrapsorites kahleri*, *Zebrapsorites corneolus* and *Zebrapsorites fimbriatus* are typical for the Carnian, *Zebrapsorites interscriptus, Zebrapsorites laevigatus*, *Zebrapsorites sinelineatus* and *Zebrapsorites rectus* are described from the Rhaetian of Hungary and China respectively. While *Zebrapsorites interscriptus, Zebrapsorites laevigatus* are used regularly among different authors and geographical regions, *Zebrapsorites sinelineatus* and *Zebrapsorites rectus* are used primarily by their authors without subsequent documentation by other authors.

It is noteworthy, that one of the described and much used name *Zebrapsorites laevigatus* does not meet the above-described criterion of the radiale distal rugulae as the name "laevigatus" already suggests. In his distinction to other species, Klaus uses the radially oriented distal rugulae as the most distinctive feature of this genus (1960), consequently the original phrasing of the genus diagnosis could not include *Zebrapsorites laevigatus*. Schulz (1967) rectified this in the emended diagnosis to include such forms.

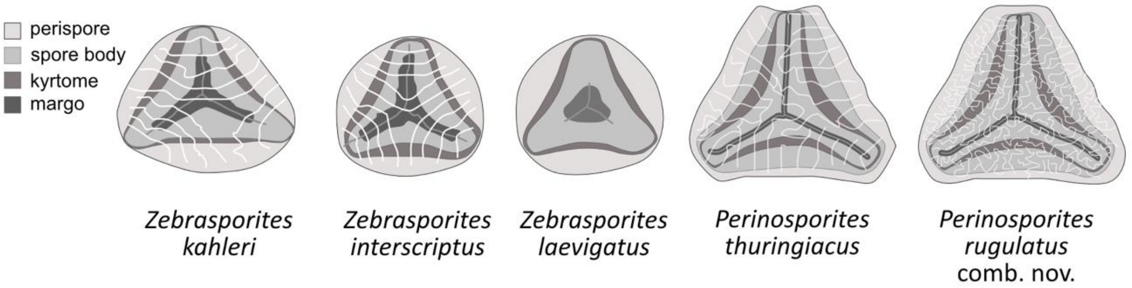


Fig. 12 Comparison of *Zebrasporites* and *Perinosporites*. Morphological characters are grey scale coded according to the legend.

Zebrasporites interscriptus (THIERGART 1949) KLAUS 1960 ***emend***.

Holotype/Basionym: *Sporites interscriptus* THIERGART 1949, Palaeontographica Abteilung B 89: 13, Pl. 2, Fig. 9, sample Helmstedt (!, refigured here, Pl. 6, Fig. 1)

Preservation of the Holotype: Two specimens potentially representing the holotype were found. Based on the surrounding material one can be identified as the holotype. Because it is partially covered by organic material and since it is not embedded any more it is uninformative and is here considered destroyed. Lectotypification is excluded because no original material is available anymore. Neotypification is however excluded because under the current phrasing of the code, the illustrations, also considered original material still exist. They are however not eligible for typification. See detailed discussion below (section 1.4.3)

Synonymy:
≡ 1962 *Thuringiasporites interscriptus* ssp. *interscriptus* SCHULZ, p. 309, Pl.1, Fig. 3
= 1962 *Thuringiasporites interscriptus* ssp. *rugulatus* SCHULZ, p. 309, Pl. 1, Fig. 3
= 1966 *Zebrasporites sinelineatus* BÓNA, p. 28, Pl. 1, Fig. 1

Diagnosis: Größe: 32 μm. Der eigentliche Sporenkörper ist einer kreisrunden, hyalinen Haut einbeschrieben, die offenbar als Flugorgan fungiert. Der eigentliche Sporenkörper selbst ist ein sehr regelmäßiges Dreieck, mit abgerundeten Ecken und wenig eingebogenen Seitenlinien.

Engl. Translation: Size: 32 μm. The body of the spore is a round circle, enclosed in a hyaline layer, which apparently facilitates flying. The body of the spore itself is a regular triangle, with rounded apices and slightly indented side lines.

Description: Unfortunately, the holotype is uninformative. The spore anatomy is here described based on one perfectly preserved specimen found in Bonenburg (Pl. 6, Fig. 6). The spore is subrounded and consists of a central triangular part with convex sides and rounded apices, deliminating the contact area. In between the apices a cinguli-zona extends from the contact area creating convex sides. The proximal face with a trilete mark whose laesurae are half the spore radius to almost reaching the equator. They are accompanied by a margo that is not always equally well developed. In some specimen (e.g. Pl. 6, Fig. 13) it appears as a bit undefined darkening around the trilete mark, in others it is a margo of almost equal thickness around the laesurae (Pl. 6, Fig. 7) and in others it is narrowing from the center of the spore towards the periphery of the trilete mark (Pl. 6, Fig. 6). The distal side has a perispore that is ornamented with muri (1.5–2 μm thick). 6–7 muri are radially oriented, i.e. perpendicular to each side of the triangular contact area, and in the center merge with those from the opposite side of the triangle. The perispore can be preserved to varying degrees, sometimes giving only a faint impression of the muri. (Pl. 6, Figs. 10, 11, 13–16). The interpretation of a perispore is supported by a fragment that shows only the (poorly preserved) perispore (Pl. 5, Fig. 34).

Remarks: Bóna (1969) erects the new species *Zebrapsorites sinelineatus* based on the supposed absence of thickenings accompanying the trilete mark. When studying Bona's plates however, the same sort of thickening that is visible in *Zebrasporites interscriptus* is visible in *Zebrapsorites sinelineatus* as well. In fact her holotypes very much resembles a specimen with the same kind of margo and preservation de Jersey and Raine (1990a) figured (Pl. 12 Fig. A), which they assigned to *Zebrasporites interscriptus*. Bóna's new species is here considered conspecific with *Zebrasporites interscriptus*, rendering *Zebrapsorites sinelineatus* a junior synonym. Given that Thiergart's diagnosis is not capturing the crucial and distinguishing characteristics (compare also Text-Fig. 12) we propose the following emended description/diagnosis.

Diagnosis *emend*.: Subrounded spore consisting of a triangular spore body and a zona spanning in between the apices. The zona is fromed by a perispore which is ornamented on the distal side. The zona is slightly thickened close to the triangular spore body, the broader this thickening is, the more cingulizonate the spores appear. Proximal face with a trilete mark whose laesurae measure half the spore radius to almost reaching the equator and are accompanied by a margo, that can vary in thickness from specimen to specimen from being almost indistinct to very prominent. The distal side is ornamented with muri of 1.5–2 µm thickness. On each side of the triangle, 6–7 muri are radially oriented, i.e. perpendicular to the respective side of the triangle. These muri merge with those from the opposite side of the triangle. These muri are very straight, which distinguishes the species from *Zebrasporites kahleri*, which has more convolutied muri.

Zebrasporites kahleri KLAUS 1960

Pl. 5, Figs. 36–37

Holotype: *Zebrapsorites kahleri* KLAUS 1960, Geologisches Jahrbuch A, Sonderband 5: 138, Pl. 30, Figs. 18–20 (!, here refigured in Pl.5 Fig. 37 and Pl. 6 Fig. 4)

Preservation of the Holotype: Good. The glycerin gelatin is intact.

Diagnosis: Rundlich-dreieckiger Äquatorumriß mit geraden bis konkaven Rändern der Kontaktareen, welche die Enden der Y-Strahlen am Umriß umgreifen. Y-Strahlen lang, von kräftigen Wülsten begleitet. Proximalseite glatt (Taf. 30, Fig. 20), Distalseite mit dreieckigen, markanten Radialrugae besetzt (Fig. 18, 19), von welchen etwa 6–7 auf je eine Dreieckseite der Spore entfallen). Obwohl die Exine ziemlich dünn ist, erscheint die Spore im Vergleich zu anderen Arten verhältnismäßig massiv. Größe: 42–(48)–50 µm (Klaus, 1960, p. 138).

Engl. Translation: Rounded-triangular outline with straight to concave edges of the contact areas that surround the ends of the Y rays on the outline. Laesurae long, accompanied by strong thickenings. Proximal face smooth (Figs. 30, 20), distal face with triangular, distinct radial rugae [rugulate, best muri] (Figs. 18, 19), from which about 6–7 are at each side of the triangle. Although the exine is quite thin, the spore appears relatively massive compared to other species. Size: 42–(48)–50 µm.

Description: We found one specimen (Pl. 5, Fig. 36) that is conspecific with the holotype of *Zebrasporites kahleri* (Pl. 5, Fig. 37) in Schulz' original material. The specimen is 37 µm in diameter and distinguished from *Zebrasporites interscriptus* by the more convoluted muri (Text-Fig. 12). The zona of the spore appears more thicker than in the other species of *Zebrasporites*.

Remarks: Klaus (1960) described the species from the Carnian, and although its main distribution seems to be in the Carnian, this is one more finding that extends the occurrence till the upper Rhaetian (compare e.g. Bjaerke and Manum, 1977). It was not found in Bonenburg, but in the Rhaetian from Möckern (Schulz original material).

Zebrasporites laevigatus (Schulz 1962) Schulz 1967

Pl. 5, Figs. 10–13, 15–27

Holotype/Basionym: *Thuringiasporites laevigatus* Schulz 1962, Geologie 11: 310, Pl. 1, Fig. 6, X 11181 BGR-S (!, here refigured in Pl. 5. Figs. 11–12)

Preservation of the holotype: Extremely poor. Details on the surface structure imperceivable. We consider it destroyed and suggest designation of a lectotypes from Schulz's original material.

Lectotype: Pl. 5, Fig. 15; NeoMöckern_2_10184_3; EF references: N49/4

Diagnosis: Größe 27–36 μm. Holotypus 35 μm (mit Perispor). Ä-Kontur des Sporenkörpers dreieckig mit gut gerundeten Ecken und konkaven Seiten. Exine etwa 1 μm dick. Y-Marke mehr oder weniger deutlich, r= $^1/_2$–$^4/_5$. Sporenkörper wird von annähernd rundem Perispor umgeben. Perispor glatt (Schulz, 1962, p. 310).

Engl. Translation: Size 27–36 μm. Holotype 35 μm (with Perispore). Equatorial outline of the body of the spore triangular with well-rounded apices and concave sides. Exine ca. 1 μm thick. Trilete mark with more or less clearly visibly, r= $^1/_2$–$^4/_5$. Body of the spore is surrounded of the almost perfectly round perispore. Perispore smooth.

Description: The holotype (Pl. 5, Figs. 10–12) is so poorly preserved, that relocation is difficult. With the help of an overlay (Pl. 5, Fig. 11) the holotype could be reidentified as opposed to other, likewise poorly preserved specimen from the same slide (Pl. 5, Fig. 13). The detailed surface structure is not visible. The spore body has concave sides. A zona spans in between the apices and extends so far that it creates convex sides at the equator. The trilete mark is not visible anymore, but a darkening around it is still perceivable.

Investigation of other original material shows a size range from 22–38 μm. In these specimens it is visible that the zona is darker and more rigid, like a cingulum, where adjacent to the spore body, and is thinning out into a zona towards the equator. The laesurae are about half the radius of the spore, but slightly obstructed by a darkening around the trilete mark.

The specimen from Bonenburg (Pl. 5, Figs. 23–30) are notably darker than specimen from Möckern (Schulz's original material, Pl. 5, marked with "O"). This is surprising as the assemblage in Möckern is comparable to that of the Triletes Beds in Bonenburg. The Bonenburg specimen show a range of spores that are completely laevigate (Pl. 5, Figs. 23–26). It should be noted that specimens are arranged in degrees of perispore preservation (Pl. 5, Figs. 23–28). The better preserved the perispore is, the more becomes a slight regulation visible. The same can be documented from the original material from Schulz with completely laevigate forms with rather poor perispore preservation (Pl. 5, Figs. 15–20) compared to forms that are interpretated as intermediate stages to *Zebrasporites interscriptus*. The better preserved the perispore is, the more regulation is visible (Pl. 5, Figs. 31–33).

Remarks: De Jersey and Raine (1990a) pointed out, that in the material from the southern hemisphere they find many specimen that represent intermediate stages between *Zebrasporites interscriptus* and *Zebrasporites laevigatus*. Although suggesting to synonymise they maintained the separation of the two species "in conformity with the taxonomic procedure of European authors", but pending reinvestigation of the holotypes material. We have documented the same tendencied and by gathering of the holotype material from Thiergart, Schulz and Klaus we have accumulated all material needed for such a reinvestigation. Our observations suggest that the differentiation of the two species heavily relies on the preservation of the perispore. It seems possible that the spore of *Zebrasporites interscriptus* consist of two parts that can separate and preserve unequally well. The proximal part (e.g. Pl. 5, Fig. 15) that when found alone comply with *Zebrasporites laevigatus*, and the distal part with the perispore and rugulate ornamentation typical for *Zebrasporites interscriptus* (which was also found isolated (Pl. 5, Fig. 34). The perispore is very thin and might only be partially preserved which would explain the ample intermediate forms we observed (Pl. 5, Figs. 28–33).

Zhang and Grant-Mackie (2001) point out that the two forms are generally associated when occurring, only *Zebrasporites interscriptus* might be longer-ranging, maybe beyond the Hettangian (Batten & Koppelhus 1996). The ample intermediate forms (especially Pl. 5, Figs. 31–33) make unambiguous classification difficult if not every author draws the same line between the two end-member of morphological variation. Continued separation of the two taxa could be used for a preservational signal, but an ecological signal might be more difficult to argue in view of the presented findings and should probably be avoided for ecological analyses.

Striatella MÄDLER 1964b emend. FILATOFF & PRICE 1988

Type: *Striatella seebergensis* MÄDLER 1964b, Fortschritte in der Geologie von Rheinland und Westfalen 12: 189, Pl. 3, Fig. 8, M318, EK 7, TK-Nr. 3050 LBEG/BGR-H (!, here refigured in Pl. 5, Fig. 1)

Synonymy: = 1977 *Asseretospora* SCHUURMAN, p.197
= 1978 *Rotinella* MALYAVKINA,1949 ex YAROSHENKO, p.60

Diagnosis: Trilete Miosporen von runder oder rundlich-dreieckiger Gestalt. Am Äquator ein bandförmiges Cingulum das an den Enden unterbrochen ist. Proximal begleiten ein oder mehrere ähnliche Bänder kyrtomartig die bis zum Äquator verlaufenden Y-Strahlen. Distal muriartige

Streifen, deren äußere ganzrandig sind und dem Cingulum anliegen, deren inneren in Dreiecksform angeordnete, abstehen und gewellt sind. Das innere Dreieck kann mehrfach weiter geteilt sein (Mädler, 1964b, p. 189).

Engl. Translation: Trilete miospores of round to subtriangular shape. At the equator a ribbon-like cingulum which is interrupted at the end. Proximally, one or more similarly ribbon-like thickenings that are kyrtom-like accompany the laesurae until the equator. Distally, muri-like thickenings, of which the outer ones cling to the cingulum and are more straight, while the inner ones are more protruding, arranged as a triangle with a more undulated outline. The inner triangle can be divided multiple times.

Emended Diagnosis: Spores moderately robust, with low, broad, closely spaced muri and cingulum of similar breadth. Shape plano- to biconvex with the distal face being the more strongly arched; amb convexly subtriangular. Trilete; laesurae normally distinct, simple or with narrow, low lips and extending to inner margin of cingulum. Proximally, a single murus is sited tangentially on each interradial area, adjacent to and paralleling inner margin of cingulum, so that adjoining mural termini tend to coalesce about radial termini of laesurae. Murornate pattern variable distally; at least partially bounded by an outer (disto-equatorial) murus that parallels and is partially superimposed on cingulum. The distal muri may bifurcate, anastomose, or break up into verrucae. Proximal exine laevigate except for verrucae on contact faces of some specimens (Filatoff and Price, 1988, p. 101).

Botanical affinity: Ferns–Polypodiaceae. The given affinity is assumed based on morphology by Balme (1995), Filatoff (1975), Filatoff and Price (1988), Schulz (1967) and is followed here, especially in view of very similar spore morphology of extant *Pteris*.

Remarks: For an elaborate discussion of *Striatella* and related genera the revision of Filatoff & Price (1988) is a much recommended.

Striatella jurassica MÄDLER 1964b

Pl. 5, Fig. 4

Holotype: *Striatella jurassica* MÄDLER 1964b, Fortschritte in der Geologie von Rheinland und Westfalen 12: 189, Pl. 3, Fig. 12, TK-Nr. 3054; N19.4 LBEG/BGR-H (!, here refigured in Pl. 5, Fig. 4)

Preservation of the Holotype: The preservation is mediocre, the glycerin jelly is partially dried, which has transported and lumped organic material together. The prismatic effect and the material are now partially obscuring the outline.

Synonymy: ? = 1958 *Cicatricosisporites dunrobiensis* COUPER, p. 146, Pl. 17, Figs. 13, 14

Diagnosis: Eine Art der Gattung *Striatella* von rundlich-dreieckiger Gestalt mit proximal zwei konzentrischen, bandförmigen Streifen und basal mindestens 7–8 gewellten ebenfalls bandförmigen und knotig verdickten Streifen pro Sektor (Mädler, 1964b, p. 189).

Engl. Translation: A species of the genus *Striatella* of rounded-triangular shape with proximally two concentric, band-shaped stripes [muri] and distally at least 7–8 corrugated stripes per sector, also band-shaped and knobbly.

Remarks: After reinvestigation of the holotype, we can endorse the above given description. Filatoff & Price (1988), after studying a variety of forms described some additional features, eg. the connection of at least some of the muri with the cingulum can also be confirmed. Some other features, like the mostly parallel muri reaching over the distal side either more or less horizontally or at an angle, are not visible, however. Quite the contrary, the muri are a bit meandering and are in between a maze-like pattern than parallel arrangement, but not fully parallel as in the other specimen assigned with this name shown by Filatoff & Price (1988). It is noteworthy, that they already speculate about potential synonym with *Cicatricosisporites dunrobiensis* COUPER 1958, which looks very similar to the here studied holotype and also has more meandering and windy muri. They hesitate to synonymise the latter name based on the potential absence of a cingulum which Couper does not mention. Based on the available photographs, the condition of the cingulum does not appear doubtful to us however, and very similar to the holotype of Mädler, but a final decision is postponed until Couper's holotype is restudied.

Striatella seebergensis MÄDLER 1964b

Pl. 5, Figs. 1–3, 5–9

Holotype: *Striatella seebergensis* MÄDLER 1964b, Fortschritte in der Geologie von Rheinland und Westfalen 12: 189, Pl. 3, Fig. 8, M318, EK 7, TK-Nr. 3050 LBEG/BGR-H (!, here refigured in Pl. 5, Fig. 1)

Preservation of the Holotype: The preservation of the slides is very good, glycerin-jelly completely intact as well as the seal around. Unfortunately, the specimen that Mädler chose is relatively poorly preserved. Slide mount too thick to use oil immersion with a x100.

Synonymy: selected, for a more elaborate list of references (not limited to synonyms however) see Filatoff and Price (1988)

? = 1958 *Cingulatisporites problematicus* COUPER, p. 146, Pl. 24, Figs. 11
? = 1958 *Corrugatisporites scanicus* NILSSON 1958, p. 43, Pl. 2, Fig. 16
= 1965 *Duplexisporites problematicus* (COUPER 1958) PLAYFORD & DETTMANN; p. 140
= 1965 *Duplexisporites scanicus* (NILSSON 1958) PLAYFORD & DETTMANN; p. 140
= 1965 *Duplexisporites gyratus* PLAYFORD & DETTMANN; p. 140, Pl. 13, Figs. 20–22

= 1965 *Contignisporites problematicus* (COUPER 1958) DÖRING; p. 51, Pl. 18, Figs. 6–8

= 1977 *Asseretospora gyrata* (PLAYFORD & DETTMANN 1965) SCHUURMAN, p.198, Pl. 10, figs 5,6.

Diagnosis: Eine Art Gattung *Striatella*, bei der das innere Dreieck der Distalseite noch ein- oder zweimal durch abstehende Muri geteilt ist (Mädler, 1964b, p. 189).

Engl. Translation: A species of the genus *Striatella*, in which the inner triangle of the distal side is divided once or twice by protruding muri.

Description: The cingulum in all our forms is slightly undulating which gives the spores an irregular outline. Our specimen (Pl. 5, Figs. 1–3, 5–9) depict a variety of distal ornamentation. The holotype (Pl. 5, Fig. 1) depicts a cingulum and a disto-equatorial murus which makes a triangular curl towards the center8 of the distal face. The same is visible in other specimens (Pl. 5, Figs. 2, 3, 5, 6) but in other transitionary forms (Pl. 5, Figs. 7–8), the muri are partially “degenerated into discrete circular verrucae” Filatoff and Price (1988), which makes them similar to, but not compliant with their recombined *Striatella parva,* which does not show the same kind of muri. One specimen (Pl. 5, Fig. 9) has particular many verrucae-like reduced muri, probably most similar to the holotype for *Corrugatisporites scanicus* NILSSON 1958 and the paratype for *Cingulatisporites problematicus* COUPER 1958. It is then noteworthy that the paratypes of *Corrugatisporites scanicus* NILSSON 1958 and the holotype for *Cingulatisporites problematicus* COUPER 1958 are more similar to forms with less degenerated muri which are more triangularly curled (Pl. 5, Figs. 5, 6).

Remarks: Observing the variety in our samples and well as the variety within Nilsson’s and Couper’s type material (photographs), these forms are highly variable with one form transitioning into the other. Filatoff and Price (1988) wrote a very thorough review on the genus, but refrain from synonymisation of *Cingulatisporites problematicus* or *Corrugatisporites scanicus* not having investigating the holotypes. They recombine *Cingulatisporites problematicus* with *Crassitudiporites,* arguing it is characterised by a laevigate distal side Filatoff and Price (1988). On the other hand, they recombine *Corrugatisporites scanicus* with *Striatella*. Looking at Couper’s original photograph of the holotype, it appears indistinguishable from Mädler’s holotype. Similarly, Nilsson’s *Corrugatisporites scanicus* is not easily distinguishable from Mädler’s holotype either, except for some variation in the reduction of the distal muri. Assuming that either or even all of these holotypes are be conspecific would imply change of the currently assumed priority of *Striatella seebergensis* following Filatoff and Price's (1988) revision. A final decision should be made based on restudying the holotypes. Such future study will then clarify potential synonymy, which seems likely however, since none of the above studies, although all studying the same time interval and region (Germanic Basin), make use of the other names, but all designate a new name and type for forms that are very likely conspecific.

Subturma Cingulati (POTONIÉ & KLAUS 1954) emend. DETTMANN 1963

Infraturma ***Laevigati*** BURGER 1994

Densosporites (BERRY 1937) POTONIÉ & KREMP 1954

Type: *Densosporites covensis* BERRY 1937, The American Naturalist 18: 159, Fig. 11

Preservation of the Holotype: Potonié and Kremp (1954) already note, that Berry informed them via letter that the holotype is lost. They do not designate a lecto- or neotype for the missing type for the genus however to fill the gap. Potonié (1956) clarifies, that the remaining image of Berry is ambiguous, but speculates that it might be conspecific with *Densosporites faunus*. He then designates the latter, temporarily, as a "Hifstypus", i.e. an epitype. This is problematic in two ways, firstly, because he only mentions the name but no specimen or illustration that shall serve as epitype. Secondly, this action is superfluous, as the epitype is tied to the fate of the holotype (Art. 9.20 Note 8 *Code*). Since it is lost, the epitype has no standing. Therefore, lecto- or neotypification is desirable.

Synonymy:
= 1954 *Anulatisporites* (LOOSE) ex POTONIE & KREMP, p. 159
≡ 1964 *Densisporites* (KONYALI) ex LEVET-CARETTE, p. 273
= 1964 *Cingulatizonites* MÄDLER, p. 184, Pl. 2, Fig. 19

Diagnosis: Characterised by a thick opaque wall, thickness about one-third the diameter of spore; central portion clear, no triradiate split (Berry, 1937 in Jansonius and Hills, 1976; card 3675).

(Latest) emended diagnosis: Spores trilete; outline convexly triangular to subcircular; two-layered; intexine (central body) thin, psilate or faintly roughened, laesurae indistinct, apical papillae sometimes present; proximal surface of outer layer evenly arched on with zona slightly raised above central proximal area; sutural ridges weak to strong, sometimes connected at their extremities to the zonal region; proximal sculpture generally absent or minor except for the central proximal area, and granules, spines, or apiculate on the zona; sculpture of central distal area usually differentiated from distal zonal surface, usually granulose; zona psilate, granulose, spinose, apiculose, verrucose, etc.; internal vacuoles ("rods") rare or absent (Staplin & Jansonius 1964 in Jansonius and Hills, 1976; card 3675).

Botanical affinity: Clubmosses – Lycopodiales. Based on *In situ* finds in Carboniferous lycopsid cone *Sporangiostrobus* which contains triradiate, flanged megaspores and a range of microspores that includes dispersed taxa such as *Densosporites* and *Cingulizonates* (Taylor et al. 2009).

Remarks: Potonié and Kremp (1954) still distinguished *Anulatisporites* based on its lack of ornamentation on the cingulum, yet Potonié himself synonymised them two years later in his *Synopsis* (Potonié 1956), following the emended diagnosis which was quoted above.

Densosporites fissus (REINHARDT 1964) SCHULZ 1967

Pl. 8, Figs. 19–21

Holotype/Basionym: *Densoisporites fissus* REINHARDT Jan/Feb 1964, Monatsberichte der Deutschen Akademie der Wissenschaften zu Berlin 6: 54, Pl. 2, Fig. 1–3, Präp-Nr. 27–36/2

Synonymy: = Dec 1964 *Cingulatizonites rhaeticus* MÄDLER, p. 184, Pl. 2, Fig. 18, 19 (!, here refigured in Pl. 8, Fig. 19)
? = 1958 *Cingulatisporites rigidus* COUPER 1964, p. 147, Pl. 25, figs 1, 2

Diagnosis: Äquatorumriss triangulär. Intexine 1,0–1,5 µm stark. Exoexine geht äquatorial in ein 8–10 µm breites Cingulum über. Intexine und Exoexine z.T. getrennt. Y-Strahlen reichen bis zum Cingulumrand. Größe 44–50 µm (Reinhardt, 1964, p. 54).

Engl. Translation: Equatorial outline triangular. Intexine 1.0–1.5 µm strong. Exoexine turns equatorially into a 8–10 µm wide cingulum. Intexine and Exoexine partially separated. Y-rays extend to the margin of the cingulum. Size 44–50 µm.

Description: The specimen (Pl. 8, Fig. 21) is triangular with very convex sides and a diameter of ca. 38 µm. The spore body diameter is 24 µm, and the cingulum is 7 µm thick. The part of the cingulum adjacent to the spore body is darker in colour. The laesurae reach the equator. The exine is very smooth. Despite the smaller size, the ratio of corpus and cingulum as well as overall appearance comply perfectly with the original description as well as with Reinhardt's holotype (Pl. 8, Fig. 14).

Remarks: Schulz (1967) recombined Reinhardt's taxon with *Densosporites*, which is followed here because *Densoisporites* WEYLAND & KRIEGER 1953 is for spores with an "internally layered flange" which is not the case in the discussed taxon (also see Jansonius and Hills, 1976; card 755). Schulz further argued, that *Cingulatizonites rhaeticus* – MÄDLER is synonymous (Schulz 1967). After studying Mädler's tape material (holotype and paratype; Pl. 5, Figs. 19–20) we agree with Schulz, that Mädler's types (published in December 1964) are conspecific with Reinhardt's holotype, which was published already in Jan/Feb of the same year and therefore has priority. The genus *Cingulizonites* erected together with the new species is subsequently also superfluous. Since Mädler described a species with the epithet "*rhaeticus*" one has to be very careful not to confuse the present taxon with *Aequitriradites rhaeticus* REINHARDT 1961 which was later recombined with *Cingulizonates rhaeticus* (REINHARDT 1961) SCHULZ 1967 and which sounds confusingly similar to the invalid *Cingulatizonites rhaeticus.*

Couper (1958) described the new species *Cingulatisporites rigidus* based on the rigid appearance of the cingulum in comparison to the other species in this genus. The specimen he depicts (Pl. 25, Fig. 1) looks very similar to the specimen that Mädler designated as holotype. Both depict that the spore body is slightly detached from the cingulum. This is interpreted as a preservational effect and given the otherwise compliance with *Densosporites fissus*, *Cingulatisporites rigidus* is likely another junior synonym, but the holotype should be reinvestigated to confirm this interpretation.

Densosporites cf. *foveocingulatus* SCHULZ 1967

Pl. 8, Fig. 16

Holotype/Basionym: *Densosporites foveocingulatus* SCHULZ 1967, Paläontologische Abhandlungen Abteilung B 2: 582, Pl. 12, Fig. 7,8, Möckern 1E–10184/1, X 11324 BGR-S (!)

Preservation of the Holotype: The slide holding the holotype is still available, but the specimen could not be relocated yet.

Diagnosis: Größe 38–50 µm (Holotypus 47 µm). Ä–Kontur dreieckig, Seiten konvex, Ecken gerundet, Exine des Zentralkörpers proximal und distal infragranulat bis glatt, Zentralkörper wird von einem 5–9 µm breiten, foveolaten bis unregelmäßig reticulaten Cingulum umgeben. Foveolae dicht angeordnet, meist radial gestreckt, Größe 1–4 µm. Strahlen der Y-Marke schmal bis bandförmig, an den Enden oft aufgespalten, deutlich bis zum Äquator des Zentralkörpers reichend, meist undeutlich auf das Cingulum übergreifend. Umrißlinie des Cingulums leicht wellenförmig (Schulz, 1967, p. 582).

Engl. Translation: Size 38–50 µm (holotype 47 µm). Amb triangular, sides convex, apices rounded, exine of the central body proximal and distal infragranulate to smooth, the central body is surrounded by a 5–9 µm wide cingulum with foveolate to an irregularly reticulate ornamentation. Foveolae densely arranged, mostly radially elongated, size 1–4 µm. Rays of the Y-mark narrow to ribbon-shaped, often split at the ends, clearly reaching to the equator of the central body, mostly indistinctly extending over the cingulum. Outline of the cingulum slightly undulating.

Description: Our specimen is relatively small (28 µm) and much smaller than indicated in the original diagnosis. Overall, the specimen is very similar to *Densosporites fissus* with the significant differences of smalle foveolae in the cingulum that are arranged circular around the spore body. They are round and very small, i.e. not as elongate as in the holotype, but according to the current phrasing of the *Densosporites foveocingulatus* non-elongate foveolae are included in this taxon. Based on the foveolae the present specimen is most compliant and thus assigned to *Densosporites foveocingulatus.*

Remarks: Given the small site if the specimen it might be possible that it is an immature form of either *Densosporites fissus*, with the currently visible foveolae being closed later or *Densosporites foveocingulatus* with the foveolae growing in length at a later point in time.

Densosporites sp.

Pl. 8, Fig. 23

Description: The specimen measures ca. 37 µm in diameter. The cingulum is ca. 9 µm and darker adjacent to the spore body and lighter and more undulated to the outside. Both the darkening and the cingulum itself have a more undulating edge compared to the holotype or our other specimen of *Densosporites fissus* (Pl. 8, Figs. 14, 21). The trilete mark extends until the equator. The distinguishing characteristics is a tori or possibly a kyrtome on the proximal side that runs in between the laesurae on the area of the spore body. As a singular occurrence and no comparable species known to the author, the specimen remains unassigned to a particular species.

Infraturma ***Apiculati*** BURGER 1994

Cingulizonates (DYBOVA & JACHOWICZ 1957) BUTTERWORTH, JANSONIUS, SMITH & STAPLIN 1964

Type: *Cingulizonates tuberosus* DYBOVA & JACHOVICZ 1957, Oddíl paleontologický 24: 171, Pl. 53, Fig. 1

Diagnosis: Amb rounded triangular to triangular; surface smooth or tuberose or granulose; spores of medium and large size (Dybova and Jachowicz 1957 in Jansonius and Hills, 1976; card 479).

Emended Diagnosis: Spores trilete; outline convexly triangular to subcircular; two-layered; central body (intexine) thin, psilate; outer layer complex, central proximal area thin, minutely sculptured to psilate, sutural ridges or grooves distinct but fine, reaching to the cuesta; cuesta distinctly raised, sometimes internally vacuolate; outer portion of zona much lower than the cuesta, sometimes sculptured; in section, outer portion of zona tapered and relatively thin; sculpture of distal surface of outer layer generally differentiated into two zones, the central distal area (usually granulose or verrucose) and the zona. (Butterworth et. al. 1964 in Jansonius and Hills, 1976; card 479).

Botanical affinity: Clubmosses–Lycopodiales. See details under *Densosporites*.

Cingulizonates rhaeticus (REINHARDT 1961) SCHULZ 1967

Pl. 8, Figs. 24–30

Holotype/Basionym: *Aequitriradites rhaeticus* REINHARDT 1961, Geologie und Mineralogie 3: 709, Pl. 2, Fig. 3, Großer Seeberg bei Gotha

Synonymy: = 1964 *Anulatizonites drawehni* MÄDLER, p. 177, Pl. 2, Fig. 1,2 (!, refigured here in Pl. 8 Fig. 25)
= 1964 *Anulatizonites rotundus* MÄDLER, p. 177, Pl. 2, Fig. 3 (!, refigured here in Pl. 8, Fig. 28)

Diagnosis: Zonabreite zu Sporendurchmesser wie 1/6, proximal unstruiert [unstrukturiert?], glatt, distal negatives Reticulum. Elemente 1–2 µ groß, polygonal, Furchendurchmesser ca. 0,4 µ Y-Marke deutlich, Strahlenverlauf gerade, r = 0,7–0,8 Größe 60–80 µ. (Reinhardt, 1961, p. 709).

Engl. Translation: Zona width to spore diameter like $^1/_6$, proximally not ornamented, smooth, distal negative reticulum. Elements 1–2 µm in size, polygonal, groove diameter approx. 0.4 µ, Y-mark clearly, laesurae straight, r = 0.7–0.8 size 60–80 µ.

Description: The two depicted specimens from Bonenburg (Pl. 8, Figs. 26, 30) are seen from the distal side with the proximal side with the trilete mark weakly shining through. The diameter of the specimens including the zona measure 70 and 46 µm respectively. The cingulum is 6 and 4 µm, the zona is about 10 and 5 µm wide, respectively, i.e. both together make up ca. between 22 and 20% of the overall diameter of the spore. The cingulum is visible as the darkest part of the spore; the zona is more hyaline that the spore body, fragile and a bit folded. The trilete mark seems to reach almost to the outline of the spore body, but not onto the cingulum. The distal side of the spore body appears to be ornamented, but due to the dark preservation of the spore the exact character of the ornamentation is indistinct.

Remarks: Schulz (1967) already suggested that *Anulatizonites drawehni* and *Anulatizonites rotundus* both described by Mädler would be synonymous. The holotypes were reinvestigated here and Schulz' interpretation is confirmed. The variation in width of the cingulum does also not seem to justify separation in two different species as this appears to be part of the intraspecific variety observed in this taxon (compare Pl. 8, Figs. 26, 30). It should also be noted that Mädlers species *Cingulatizonites rhaeticus* is potentially problematic because of its phonetic similarity. As pointed out above however it is conspecific with *Densosporites fissus*, and since it has a cingulum it (as well as the senior synonym *Densosporites fissus*) should not be confused with *Cingulizonates rhaeticus* which possesses a combined cingulum and zona. This feature is not so well visible in Reinhardt's holotype due to the relatively poor photograph, but excellently visible in Mädler's refigured holotype specimen for *Anulatizonites drawehni. Cingulizonates rhaeticus* is a stratigraphically important taxon and its first appearance defines the LR (*Limbosporites lundbladii*

– *Cingulizonates rhaeticus*) Zone in Morbey (1975). Unfortunately, the current diagnosis is not very elaborate and does not even mention the cingulizonate character of the spore, although the recombined name now suggests so. Pending the reinvestigation of the holotype of Reinhardt, so far unavailable for study due to the Covid-19 pandemic, the diagnosis/description should be emended to make distinction of this stratigraphically important taxon clearer.

Kraeuselisporites LESCHIK 1955 emend. SCHEURING 1974

Type: *Kraeuselisporites dentatus* LESCHIK 1955, Schweizerische Paläontologische Abhandlungen 72: 37, Pl. 4 Fig. 21

Synonymy: = 1958 *Styxisporites* COOKSON & DETTMANN, p. 114, Pl. 19, Figs. 3–4
= 1962 *Heliosporites* SCHULZ, p. 311, Pl. 1, Figs. 9–11

Other records: ‘Kraeuselipollenites‘ Corsin, Carette, Danzé & Laveine 1962, p. 3064, nomen nudum

Diagnosis: Mikro- oder Isosporen, deren Zentralkörper mit einer festen Membran abschliesst. Auf diesem stehen dornenartige, zum Teil abgestumpfte Erhebungen bis zu 5 μm. Zentralkörper rundlich bis oval. Zone nicht an allen Stellen gleich breit (Leschik, 1955, p. 37).

Engl. Translation: Microspores or isospores whose central body ends in a solid membrane, which is ornamented with thorny, partially blunted elevations which are up to 5 μm high. Central body round to oval. Zona not equally thick in all places.

Emended Diagnosis: Acavate zonotrilete spores of triangular or subtriangular outline. The exine of the flat or slightly raised proximal face is unsculptured and may show a punctate-infrareticulate structure. The arms of the Y-mark extend to the inner margin of the flange. They are narrow, distinct and may be slightly raised. Lips may or may not be present. On the flange, the arms may change into radially arranged folds or thickenings. The flange may be wide or narrow. It may be smooth, structureless or provided with thinnings or thickenings of variable shape and size, and the outer margin may be entire, dentate or spinose. The proximal side of the zone is unsculptured, but distally, sculptural elements such as echini, coni, grana, etc. may be present. The exoexine of the distal hemisphere is also provided with sculptural elements which are never crowded together. These mainly consist of echini and coni which may vary in shape and size. Some may be reduced to bacula, verrucae or grana. Sculptural elements may be compact or partially hollow and provided with small cavities or tiny perforations. The exoexine may show a punctate-infrareticulate structure (Scheuring, 1974, p. 199).

Botanical affinity: Clubmoss – Sellaginellales. See below.

Remarks: For a more elaborate summary on the discussion as to the narrow or broad interpretation of the genus see Scheuring (1974).

Kraeuselisporites reissingeri (HARRIS 1957) emend. MORBEY 1975

Chapter 3, Fig. 9.2

Holotype: *cf. Selaginella kraussiana* REISSINGER 1950, Palaeontographica Abteilung B 90: 104, Pl. 12, Fig. 28, designated by Harris (1957)

Basionym: *Lycospora reissingeri* HARRIS 1957 Proceedings of the Royal Society of London. Series B, Biological Sciences 147: 305, Fig. 6, a, d.

Synonymy:

= 1962 *Heliosporites altmarkensis* SCHULZ, p. 311, Pl. 1 + 2, Figs. 9–11

= 1965 *Kraeuselisporites altmarkensis* (SCHULZ 1962) LEVET-CARETTE, p. 291, Pl.25, Figs. 5–7

≡ 1969 *Heliosporites reissingeri* (HARRIS 1957) CHALONER 1969.

≡ 1975 *Kraeuselisporites reissingeri* (HARRIS 1957) comb. nov. emend. MORBEY 1975, p. 21, Pl. 8,9, Figs. 10–13

Diagnosis: Trilete spore 40 to 50 μm wide; cingulum equatorial, delicate, up to 5 μm wide, covered with pits 1 to 2 μm wide, margins sometimes forming teeth. Ventral face of spore flattened but triradiate ridges long, prominent, double. Contact facets nearly smooth but showing faint radial striations. Dorsal surface convex, bearing 6 to 10 spines. Spines up to 10 μm long, usually sharply pointed and often hooked, but sometimes shorter and sometimes blunt and straight. Exine thick, especially dorsally. Substance minutely vesicular. An inner thin cutinized wall present, separated from exine by a wider or narrow gap (Harris, 1957, p. 305).

Emended Diagnosis: Miospores trilete, zonali-camerate. Amb triangular to circular, apices rounded, sides convex. Exine two-layered. Intexine laevigate, 1–2 μm thick, rounded-triangular in polar compression, equatorially appressed or separated from the exoexine. Zona ca. 4–10 μm in width. Exoexine of distal surface and proximal surface of zona, punctate, microreticulate or scabrate, 1–2 μm thick. The exoexine is thickened at the proximal base of the zona to form a ridge 1–3 μm in width. The distal surface is ornamented with randomly distributed, broad or narrow based, tapered or parallel sided spinae, which are incurved, recurved, straight, or sinuous in development and possess blunted, bifurcate, trifurcate, and occasionally pointed tips. Processes ca. 3–12 μm in height, ca. 1–2.5 μm in diameter, diameter $^{1}/_{2}$–$^{1}/_{5}$ height, equal or unequal in length per individual. Contact area of proximal surface laevigate or faintly punctate. Suturae simple or labrate, extending to inner margin of zona or rarely indistinctly to the equator. Proximal profile pointed, distal profile convex. Specimens commonly in tetrads (Morbey, 1975, p. 21).

Description: The depicted specimen is subcircular and very small (ca. 20 μm). Its zona is not developed as in the holotype. The small size might hint at an earlier developmental stage of the spore, explaining the not yet developed zona. Morbey's given size range however includes specimens as small as the depicted one. The distal spines are also very small (max. 3.6 μm high). Either they broke of or are not yet developed, their regular conate nature suggests the former as they are neither blunted or furcated, but they could be one of the pointed specimens that Morbey describes. The contact area is rather smooth. The typical distal ornamentation allows assignation to this species.

Botanical affinity: Clubmoss – Sellaginellales. Originally described as *Lycospora reissingeri* Harris 1957, the name already indicates its lycophytic association supported by *in situ* finds (Harris 1957; Balme 1995). The exact morphology of this specimen is very close to *Selaginella selaginoides* (Reissinger 1950), which lead to its assignation to the Sellaginellales by previous authors (Bonis 2010; Kustatscher et al. 2012a).

Remarks: Muir and Van Koijnenberg van Cittert (1970) attempted to emend the diagnosis, which was agreed with by Orbell (1973). Rather than giving an elaborate emendation like Morbey's they refer to Harris' original description and note that he failed to see the striations on the contact faces. When consulting the original diagnosis however, Harris particularly writes "Contact facets nearly smooth but showing faint radial striations" (Harris 1957). We agree with Harris, that the striations, if visible at all, often appear very faint and that apart from this phrasing no emendation as given by Muir and Van Koijnenberg van Cittert (1970) is needed. Scheuring (1974) who restudied *Kraeuselisporites* and related taxa already denoted *Heliosporites* as a junior synonym of *Kraeuselisporites* but did not restudy or emend *Kraeuselisporites reissingeri*. The emendation given by Morbey (1975) however, adds much greater detail and precision to the diagnosis which is followed here.

It is noteworthy, that Leschik's and Jansonius' description of the membranous extension of the spore are rather vague. Leschik speaks of a membrane (1955) when Jansonius refers to it as a "flange" (1962), i.e. a similar non-descript term for membranous equatorial extensions which can be a capsula, cingulum, patina or zona, depending on whether they extend over one or both sides of the spore body, beyond the equatorial area, and on how thick this extension is. Scheuring clarifies this and refers to it as a zona (1974). Morbey likewise uses the term zona, and supports this with a drawing depicting the spore in a sectioned view (1975). What can be seen from that drawing is that the projection indeed is very thin and would thus be considered a zona (rather than a cingulum).

Harris (1957) as well as Morbey, who even includes it as part of the diagnosis in his emendation (1975) already pointed out, that sometimes, *Kraeuselisporites reissingeri* occurs in tetrads of almost spherical form. Where it occurred in Bonenburg, it was mostly found in tetrads, which are easily recognizable by their typical spines on the distal side, or their remains respectively, if the spines are broken probably as a result of transportation. The taxon occurs sporadically in the Rhaetian, Scania (Lindström et al. 2017a), Germanic basin but more abundant from the base of the Jurassic, Germanic Basin (Schulz 1967; Morbey 1975; Lindström et al. 2017a; Gravendyck et al. 2020c)

Infraturma ***Murornati*** BURGER 1994

Limbosporites NILSSON 1958

Type: *Limbosporites lundbladii* NILSSON 1958, Publications from the Institutes of Mineralogy, Paleontology and Quaternary Geology, University of Lund 53: 47–48, Pl. 3, Fig. 7, präp nr. 102, Höganäs

Synonymy: = 1964 *Dentellisporites* MÄDLER, p. 180, Pl. 2, Fig. 13 (!)

Diagnosis: Trilete Miosporen von rundlich eckiger Form. Die Spore im Bereich des Äquators von einem relativ schmalen Randsaum umgeben, der durch die allmähliche Zuschärfung des zentralen Sporenkörpers gebildet wird. Die peripheren Partien des Randsaums mehr oder weniger membranös. Y-Strahlen in den Randsaum hinausragend. Exine im Allgemeinen dick, mit einer groben, oft retikularen Skulptur versehen (Nilsson, 1958, p. 47).

Engl. Translation: Trilete miospores of roundish angular shape. The spore in the area of the equator surrounded by a relatively narrow rim, which is formed by the gradual thinning of the central spore body. Peripheral parts of a hemisphere more or less membranous. Y-rays projecting into the rim. Exine generally thick, with a coarse, often reticulate sculpture.

Botanical affinity: Clubmosses. Tentative assignation based on Bonis (2010).

Remarks: Schulz (1967) already noted that the generic diagnosis of *Limbosporites* and *Semiretisporis* are very similar in regards to the distal sculpture of *Limbosporites*, which can be so dense that it resembles the reticulum of *Semiretisporis.* He stresses however, that Limbosporites does not depict a perfect reticulum on the distal side and possesses a much narrower flange. Later de Jersey (1970) has widened his interpretation of *Semiretisporis* to include species with an imperfect reticulum, which would also solve the problem of validity of *Limbosporites*, which was contested by Potonié (1960) due to the lack of a “Differentialdiagnose” required by PB 6 of the Paris *Code*. De Jersey and coworkers later argued that Potonié’s claim seized effectiveness, since the *Code* would no longer include the requirement that “the name of a monotypic genus of fossil plants published on or after 1st January 1953 must be accompanied by a description or diagnosis of the genus”(de Jersey & Raine 1990a). In fact, Nilsson’s new genus did incorporate such a diagnosis, and on top of that this requirement was not deleted from the revised version of the code as Potonié (1970) discussed himself. What de Jersey and Raine probably meant was, that the requirement in Art. PB 6 that "the name of a monotypic genus […] must be accompanied by a description of the genus indicating its difference from other genera" was deleted in the Leningrad Code. This lack of the "Differentialdiagnose" as Potonié called it therefore does not any more prevent the validity of the genus *Limbosporites*, however on different grounds than previously argued.

Mädler (1964b) describes the new genus *Dentellisporites* characterized through a rounded triangular shape, a flange that he interprets as a cingulum and a typical foveolate distal ornamentation ending with tip-shaped extensions (in French *dentelles*) on the flange which also give the new genus its name. According to Potonié (1970), Mädler himself considers the type of *Dentellisporites* identical with *Limbosporites lundbladiae*. After inspection of Mädler's type and the discussed validity of *Limbosporites*, we consider *Dentellisporites* a juniorsynonym.

Foster (1979), when describing the new *Limbosporites balmei,* mentions that he regards *Semiretisporis* as a juniorsynonym of *Limbosporites* but does not give a justification to back this statement. Later de Jersey and coworkers agree with this opinion given the same view as in the 1970s paper, but now in favour of *Limbosporites* which would have priority if the circumscription indeed comprise a perfect as well as an imperfect reticulum.

When analysing the usage statistics for the species of the two genera (compare chapter 4 and 5), it becomes clear however, that this view was adapted by the minority of authors, while most continue, until today to use the two genera separately for differentiated taxa (chapter 5, Fig. 1).

This view is supported when comparing the original types for the two genera. *Semiretisporis gothae* possesses a distinct and perfect reticulum. The lumen are isodiametric and closed in the area of the corpus. The lumen that extend over the transition from corpus into flange are elongate, with the muri reaching out radially onto the flange. In comparison, the ornamentation of *Limbosporites lundbladiae* is foveolate, which can give the impression of a reticulum depending on the size of the foveolae. The genotype itself depicts foveolae that are about ¼–$^1/_8$ of the size of the lumen created on the flange. The flange itself is much more massive in *Limbosporites* and rather a cingulum than a zona (compare Pl. 8, Figs. 1–8 in comparison to the cingulate and zonate part in cingulizonate spores – Figs. 24–30; and cingulate forms in Figs. 19–23). *Semiretisporis* possess a zona. Although the genotypes for both genera depict an equatorial flange distinct from the spore body and a reticulate-like distal ornamentation, they appear to be sufficiently different to justify a genus distinction, which complies with the continued distinct use of the two genera.

Limbosporites lundbladiae NILSSON 1958

Pl. 8, Figs. 1–3, 5, 8, 9, 13

Holotype: *Limbosporites lundbladii* NILSSON 1958, Publications from the Institutes of Mineralogy, Paleontology and Quaternary Geology, University of Lund 53: 47–48, Pl. 3, Fig. 7, präp nr. 102, KT 35,2/108,2 (Höganäs)

Synonymy:	= 1964	*Dentellisporites achimensis*, MÄDLER, p. 181, Pl. 2, Fig. 13 (!)
	= 1970	*Dentellisporites lundbladii*, POTONIE, p.53
	= 1991	*Canalizonospora regularis*, SHANG & LI, p. 356, Pl. 2, Fig. 8

Diagnosis: Grösse 46-53 μm. (Holotypus 51 μm). Rundlich drei- oder vieleckig. Grösste Breite des Randsaums etwa $^1/_3$ Radius (bis etwa 10 μm). Kontur des Randsaums eben oder etwas unregelmäßig. Exine dick, dunkel gefärbt, auf der distalen Seite eine wechselnde Anzahl (etwa 15–40) membranöser Fenster aufweisend. Form der Fenster kreisförmig oder unregelmässig, ihre Grösse stark wechselnd, meist nicht mehr als 2–3 μm. Fenster bisweilen so dicht liegend, dass eine Retikulation entsteht. Im Randsaum sind die Fenster gewöhnlich grösser als im Zentralkörper und ragen dort oft als mehr oder weniger tiefe, membranöse Buchten von der Peripherie gegen den inneren Rand des Randsaums hinein. Y-Strahlen dünn und, wenn im Präparat nach unten gerichtet, wegen der dickwandigen Distalseite schwer zu sehen (Nilsson, 1958, p. 47–48).

Engl. Translation: Size 46–53 μm. (Holotype 51 μm). Roundish triangular or polygonal. The largest width of the rim is about $^1/_3$ radius (up to 10 μm). The contour of the rim is flat or slightly irregular. Exine thick, dark coloured, on the distal side with an alternating number (about 15–40) of membranous windows. The shape of the windows is circular or irregular, their size varies greatly, usually not more than 2–3 μm. Windows sometimes so close that reticulum occurs. In the rim, the windows are usually larger than in the central body and often protrude there as more or less deep, membranous indentation from the periphery against the inner edge of the rim. Y-rays thin and, if directed to the downward side of the slide, difficult to see because of the thick-walled distal side.

Description: Our typical specimens (Pl. 8, Figs. 1–3) measure between 50–53 μm in diameter. Some are a bit smaller, and also smaller than given in the original diagnosis (32–38 μm, Pl. 8, Figs. 5, 8, 13). These smaller specimens usually originate from the Triletes Beds and are darker. The outline all of the specimens is subtriangular due to the rim being broader in the interradial area and thinner around the apices. The windows are irregular shape in some specimen (Pl. 8, Figs. 1, 3, 5), and very rounded in others (Pl. 8 Fig. 2). Membranous indentation from the periphery against the inner edge of the rim clearly visible, especially on the distal side. The trilete mark reaches the rim and is clearly visible when turned towards the observer (Pl. 8, Fig. 1), and only weakly shining through when turned away (Pl. 8, Fig. 5). The laesurae when visible are straight and without thickening (e.g. margo).

Remarks: Note that specimens figured by Shang and Li (1991, Pl. 3, Fig. 18) and Song et al. (2000, Pl. 84, Figs. 26–28) assigned to *Canalizonospora regularis* are indistinguishable from several from ours (Pl. 8, Figs. 1–2) and the holotype from Nilsson and should be thus treated as synonymous. The size and sha pe of the foveolae can obviously differ (compare Pl. 8, Figs. 1–8) and vary with preservation (compare Pl. 5, Fig. 8). Some forms have however such small foveolae, that they are better assigned to *Limbosporites microfoveatus*; (Pl. 8, Figs. 6–7) see below. In very rare cases, square instead of trilete forms of this taxon occur (Pl. 8, Fig. 9) and are interpreted as aberrant as these changes of forms are also visible in other taxa, e.g. *Perinosporites*, *Deltoidospora* (Lindström et al. 2019; Gravendyck et al. 2020c). It should be noted that, what is here interpreted as, poorly and only half preserved *Semiretisporis* specimen (Pl. 8, Fig. 4) could be mistaken for a *Limbosporites* specimen. We found several of such specimen in the original material from which *Semiretisporis maljavkinae* SCHULZ 1967 was described. In that sample, specimens occurred regularly in this preservation and it appears that underlying the reticulum of *Semiretisporis* these partial thickenings are found which, when seen in isolation can appear similar to *Limbosporites lundbladiae*.

Limbosporites denmeadii (DE JERSEY 1962) DE JERSEY & RAINE 1990 ***emend***.

Pl. 8, Figs. 12, 17–18

Holotype/Basionym: *Callialasporites denmeadi* DE JERSEY 1962, Geological Survey of Queensland Publication 307: 14, Pl. 6, Fig. 2

Synonymy:

≡ 1965 *Lundbladispora denmeadi* (DE JERSEY 1962) PLAYFORD & DETTMANN, pp. 148–149, Pl. 15, Fig. 36 a–c

≡ 1970b *Semiretisporis denmeadi* (DE JERSEY 1962) DE JERSEY 1970b, pp. 12–13, Pl. 4, Figs. 8

Diagnosis: Equatorial contour circular to subcircular. Total diameter (based on 7 measured specimens) 66 to 92 μm. Pollen grain complex, consisting of a subcircular central body (corpus) surrounded distalo-equatorially by a saccus, which is fairly uniform in width. No germinal aperture or tetrad markings observed. Diameter of corpus 48 to 74 μm. Exine of corpus 1 to 2 μm thick, light brownish yellow to dark brown, indistinctly reticulate with lumina 5 to 6 microns in diameter, 1 μm in height and 1 μm in width. Saccus 7 to 20 μm wide, with regularly radiating folds or ridges about 1 μm in width, otherwise smooth, outer margin entire, pale yellow to colourless, 1 μm or less in thickness (de Jersey, 1962, p. 14).

Description: These specimens are between 28–45 μm and are therefore smaller than in the original description. Rather than windows creating a reticulum as in *Limbosporites lundbladii*, these specimens depict a reticulate ornamentation with some free spaces in between. The flange is thicker with radial thickenings that are much more densely packed (although still slightly u-shaped than in *Limbosporites lundbladii.* They thereby depict all the typical characteristics of *Limbosporites denmeadii.*

Remarks: The species was so not yet reported for the Germanic Triassic. It is known from the Carnian to the Jurassic mainly from the Southern hemisphere especially Australia, Tasmania, New Zealand and Antarctica (Playford & Dettmann 1965; de Jersey & Hamilton 1967; de Jersey 1970; Dolby & Balme 1976; Kyle 1977; de Jersey & Raine 1990a; Lindström & McLoughlin 2007); but also from the Middle East and Asia including Russia (Martini et al. 2004; Ilyina 2006; Ilyina & Egorov 2008; Ghavidel-Syooki et al. 2015; Hashemi-Yazdi & Bashiri 2020). In the Germanic Triassic *Limbosporites lundbladiae* is stratigraphically a very important taxon, and due to its abundance some of the variation that complies with the description of *Limbosporites denmeadii* might have been overlooked or obscured in the past. Future studies will be needed to further document the presence or absence of this taxon in the Germanic Basin.

The epithet *denmeadii* was recombined several times (see also chapter 5). Although *Semiretisporis denmeadii* is the more frequently used name, *Limbosporites denmeadii* is the most established named (Text-Fig. 13), which is applied here. Taxonomically, specimens of this form have a flange that is too thick and lacks a reticulum for assignation to *Semiretisporis*. Given that the scientific community seems to have rightfully accepted this there is no need for rejection or conservation.

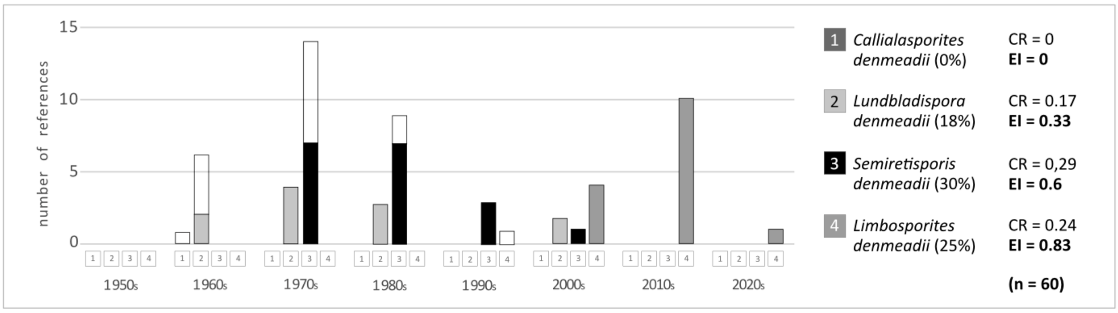


Fig. 13. Name usage of different recombinations of the epithet denmeadii. Partial reprint from chapter 5. CR=Citation rate; EI=Establishment Index.

It should be further noted, that neither de Jersey (1970) nor de Jersey and Raine (1990) formally emend the species, additionally to recombining it. This is particularly unfortunate because there is a large discrepancy between the originally interpreted characters unique to pollen (e.g. saccus) and because de Jersey (1970) already provided an elaborate new description, which was however not indicated to serve as an emendation. Therfore the following emended description from de Jersey is proposed to serve as formal emendation in the future. For a more elaborate discussion of the taxon consult de Jersey (1970) and de Jersey and Raine (1990).

Description *emend.*: Trilete miospores. Amb convexly subtriangular to subcircular. Full diameter 48 to 92 μm; diameter of the spore body 25 to 74 μm. Laesurae distinct to imperceptible, where evident straight, length about half to three-quarters of the spore radius, not extending over the spore body. Slight development of a margo can be visible. Exine two-layered, consisting of an inner homogeneous layer that, apart from proximal attachment, is separated from a structured exoexine. Exoexine consisting of an inner region and an equatorial region, which is 5 to 12 μm in width, with radially developed ridges, about 1.5 μm in width, that bifurcate towards the equator. Inner region of distal exoexine with murornate sculpture, consisting of low, irregular rugulae about 1.5 to 3 μm wide, forming a reticulum imperfectum with lumina from 2 to 10 μm. Distal rugulae anastomosing or freely terminating. Inner layer smooth, thin (less than 1 μm), in well preserved specimens exhibits 3 low, proximally situated, interradial polar thickenings (papillae) (slightly altered after de Jersey, 1970).

Limbosporites microfoveatus (ZHANG 1979) BAI et al. 1983

Pl. 8, Figs. 6–7

Holotype/Basionym: *Camarozonosporites microfoveatus* ZHANG 1979, p. 470, Pl. 129, Figs. 18, 19

Synonymy:	= 1979	*Camarozonosporites kuzhuqiavensis* ZHANG 1979, p. 470, Pl. 129, Fig. 20
	? = 1991	*Trizonites venustus* SHANG & LI, pp. 348, 356, Pl. 2, Figs. 18–20

Description: Our specimens (Pl. 8, Figs. 6–7) comply very much with the description of Limbosporites lundbladiae, except for having significantly smaller foveolae and much more regular u-shaped thickenings that extend from the spore body onto the fringe.

Remarks: Although transitionary forms (e.g. Pl. 8, Figs. 3, 5) are visible between *Limbosporites lundbladiae* and *Limbosporites microfoveatus* the latter seems to be the end of morphological variation and is kept separate pending further investigation of infraspecific variation in *Limbosporites lundbladiae*. This taxon, aside *Ricciisporites tuberculatus*, currently encompasses much more variation than in most other taxa which, rendering them almost the exclusive and predominant names used for forms found in the Germanic Triassic. Observing greater detail in morphological variation, quantifying the abundance of the respective morphs together with aberrations might harbour a so far unrecognised ecological signal that is worth further investigations in the future.

Cf. *Limbosporites* sp. A

Pl. 8, Figs. 11, 15

Description: This specimen (Pl. 8, Fig. 11) measures only 45 μm. The trilete mark seems to have a margo, which is not present in *Limbosporites lundbladiae.* The distal ornamentation is such a dense reticulum that it depicts only very few, very small rounded (ca. 1 μm) windows. The membranous indentation from the periphery against the inner edge of the rim appear more elongate than in *Limbosporites lundbladiae* and similar to those of *Limbosporites denmeadii*. Given the overall similarity with the genus it is tentatively assigned to *Limbosporites*, but no further assignation is possible.

Cf. *Limbosporites* sp.

Pl. 8, Fig. 10

Description: This is a very small and very poorly preserved specimen, representative of some that are hard to assign to a particular taxon. The flange is less well developed than in typical *Limbosporites* specimens, but the overall ornamentation and organiisation of the spore suggests tentative assignation to this genus.

Semiretisporis REINHARDT 1961 ***emend***.

Type: *Semiretisporis gothae* REINHARDT 1961, Geologie und Mineralogie 3: 709, Pl. 2, Figs. 5, 6; sample nr. 27; 36/3

Diagnosis: Trilet, Äquatorumriss triangular bis subtriangular. Körper mit einer dünnen Haut bedeckt, die am Äquator flanschförmig, zonaartig vorspringt. Zentralkörper: distal grobmaschiges Reticulum, Muri ragen stäbchenförmig radial in die zonaartige Exinendifferenzierung (Reinhardt, 1961, p. 709).

Engl. Translation*:* Trilete, equatorial outline triangular to subtriangular. Body of the spore covered with a thin layer which protrudes flange-shaped, zona-like at the equator. Spore-body: distally with a coarse meshed reticulum. Muri protrude radially and rod-like into the zona-like part of the exine.

Botanical affinity: Schulz (1967) tentatively assigned this taxon to the Bryophytes and some authors assign similar spores from the Carboniferous (*Sagenotetradites*) to liverworts (Satterthwait & Playford 1986), while others have tentatively assigned them to lycophytes, which can also show similar ornamentation (Paterson et al. 2016). Others have refrained from further assignation (Bonis 2010), which is followed here, due to opposing possibilities of two major groups

Remarks: *Semiretisporis* encompasses currently 10 formally described species according to palynodata and the JWIP: (1) *Semiretisporis gothae* REINHARD 1961, (2) *Semiretisporis achimensis* MÄDLER 1964*,* (3) *Semiretisporis maljavkinae* SCHULZ 1967, and (4) *Semiretisporis ornatus* ORLOVSKA-ZWOLINSKA 1966 and (5) *Semiretisporis wielichoviensis* ORLOVSKA-ZWOLINSKA 1966 are limited to the TJ–transition*.* (6) *Semiretisporis lycopodioides,* seems to be limited to the same time interval in China, but is mentioned in only two studies Bai et al. 1983 and Shan et al. 1991 (7) *Semiretisporis reticulatus* MÄDLER 1964 has a similar distribution (8) *Semiretisporis taiwanensis* HUANG ET AL. 1984 is reported from the Pliocene of Taiwan, but a flange is missing in this taxon which probably should be assigned to another taxon, e.g. *Reticulatisporites*. (9) *Semiretisporis flaccida* SHANG & LI 1991 described from China and in two publications only, in the early Norian and Cretaceous (10) *Semiretisporis antiquus* DE JERSEY 1964, was later recombined to *Limbosporites antiquus* (DE JERSEY 1964) DE JERSEY & RAINE 1990, as well as (11) *Semiretisporis denmeadii* DE JERSEY 1964 as *Limbosporites denmeadii* (DE JERSEY 1964) DE JERSEY & RAINE 1990. (12) *Semiretisporis hochuli* PATERSON et al. 2019 is a zonate spore, but without distal reticulum, probably assignable to another genus (possibly Kraeuselisporites) and is not considered here. Apart from *Semiretisporis flaccida* the remaining species (1–7) of *Semiretisporis* are limited to the late Triassic or early Jurassic and are thus of high stratigraphic value. Several of them are here interpreted to be conspecific and are revised below, based on reevaluation of the original holotypes and studying infraspecific variation in samples from Bonenburg,

It should be noted that the original genus description is rather short and ambiguous. Especially, the term flange, as an indefinite term for equatorial extensions is ambiguous and has led to numerous different uses in the following species descriptions. We find that the flange is closest to a zona, *sensu* Punt et al. (2007). The term describes a thin outer structure of a spore that projects at the equator (Text-Fig. 8), problematic is, that it – per definition does not extend over the distal or proximal face. There is no other term that covers cases where the perispore extends also over the distal phase, i.e. a hyaline analogue to a patina (Text-Fig. 9). In case of *Semiretisporis* the perispore does cover the entire distal face additionally to the equatorial extension. Reinhardt (1961) to referred to it as “zona-like”, probably owed to the almost, but not quite fitting definition of “zona” for the given case. Since the term is very well known for equatorial extension of particular hyaline character, we propose to use the term *sensu lato*, to also include spores like in the present genus without coining yet another term.

Shang and Li (1991) emended the diagnosis (in Chinese) to also include forms without the radial muri that occur in other species of *Semiretisporis*, which would otherwise be excluded (Jansonius and Hills, 1976; card 5244). To update and disambiguate the terminology we propose the following emended genus description.

Description *emend.*: Triangular or subrounded spores with a perispore that extends at the equator in a zona and shows a distinct hetero- or homobrochate reticulation on the distal face. Proximal face without ornamentation. Spore body darker, often not fully preserved, trilete mark thus not always visible. Laesurae $^1/_2$–$^2/_3$ of the radius of the spore body.

Distinction: Similar to but usually larger than *Limbosporites*. *Limbosporites* is distinguished by a cingulizonate flange with less hyaline zona.

Semiretisporis gothae REINHARD 1961

Pl. 6, Figs. 18–25

Holotype: *Semiretisporis gothae* REINHARDT 1961, Geologie und Mineralogie 3: 709, Pl. 2, Figs. 5, 6; sample nr. 27; 36/3

Synonymy: = 1962 *Perinotriletes reticulatus* ORLOWSKA-ZWOLINSKA, p. 729

= 1964 *Semiretisporis achimensis* MÄDLER, Pl. 2, Fig. 16, M116, EK 1, TK-Nr. 3140 (!, here refigured in Pl. 24)

Diagnosis: Flanschbreite 12–16 µm, an den Ecken breiter. Distale Sporenwand mit Reticulum bedeckt, Lumina polygonal, 4–8 µm weit, Muri 1–2 µm breit, Anzahl der Lumen distal 15–23, Anzahl der radialen Stäbchen 14–16. Y-Marke zart, r= 0,7–0,9. Größe 55–80 µm (Reinhardt, 1961, p. 709).

Engl. Translation: Width of the flange 12–16 µm, wider at the apices. Distal spore wall covered with a reticulum. Lumen polygonal, 4–8 µm wide, muri 1–2 µm thick, number of the lumen distal 15–23, number of radial rods 14–16. Trilete mark fine, r=0.7–0.9. Size 55–80 µm.

Description: Our spores are more or less triangular (Pl. 6, Figs. 18, 19, 21–23), with some rather small specimens around 40–50 µm in diameter (Pl. 6, Figs. 18, 19) and some bigger specimen 60–

70 μm (Pl. 6, Figs. 21–23). In the larger specimen the flange makes up ca. 30% of the entire spore diameter, in the smaller specimens only about 15%. Characteristically different from other species of the genus is the distal distinctly heterobrochate reticulum. On the surface of the spore body it depicts a honeycomb-like structure, but the outermost brochi covering the spore body have an open end, extending onto the zona. Therefore, the zona is ornamented by radially arranged muri that extend from the reticulum. This feature is not present in the other species of *Semiretisporis* from the Rhaetian discussed below, but visible in the holotype, as well as in the holotype of *Semiretisporis achimensis* MÄDLER 1964 (Pl. 6, Fig. 24), which is thus synonymised here.

Remarks: *Semiretisporis gothae* is the most commonly species of *Semiretisporis*. It seems questionable though, whether this is the result of a rather dubious distinction between the various described species of *Semiretisporis* (but compare new clarified distinction in Text-Fig. 15).

Semiretisporis reticulatus MÄDLER 1964b

Pl. 7, Fig. 5

Holotype: *Semiretisporis reticulatus* MÄDLER 1964b, Fortschritte in der Geologie von Rheinland und Westfalen 12: 178, Pl. 2 Fig. 5, M703/III, TK-Nr. 3129, LBEG/BGR-H (!, here refigured in Pl. 7, Fig. 5)

Preservation of the Holotype: very good, glycerin-jelly completely intact as well as the seal around. The spore itself chosen as the holotype is a rather poorly preserved.

Diagnosis: Eine Art der Gattung *Semiretisporis* mit stärker ausgeprägter Netzstruktur des Perispors als beim Genotypus (Mädler, 1964b, p. 178).

Engl. Translation: A species from the genus *Semiretisporis* with stronger developed reticulum of the perispore compared to the type specimen.

Description: Interestingly the holotype for *Semiretisporis reticulatus* MÄDLER 1964b (Pl. 7, Fig. 5) looks very similar to a semi-preserved form (Pl. 7, Fig, 7) found in Schulz' original material. The holotype shows a special form of preservation with the distal side preserved with a reticulum, but much more like "skeleton" in comparison to other specimens. The spore is triangular, 75 μm in diameter. Part of the spore body is also preserved, 40 μm diameter. The organiisation of the reticulum is not clearly visible, because of the poor preservation of the reticulum on the flange. In the lower half of the spore it looks homobrochate, in the area of the top apex it appears to have more elongate brochi, similar to those in species of *Semiretisporis gothae.*

It is noteworthy, that we found a specimen in Mädler's original material (Pl. 7, Fig. 3), which is also similar to *Semiretisporis reticulatus,* but much more comparable to the other specimens assigned to *Semiretisporis wielichoviensis* based on its homobrochate reticulum.

Remarks: A final judgment of the relation of this form with other taxa is difficult. Size and shape put it closer to *Semiretisporis gothae,* but if one interprets the reticulum as homobrochate, this would put it closer to *Semiretisporis maljavkinae* and *Semiretisporis wielichoviensis.* Given its singular occurrence and scarce use by later authors (CR=0.08), the name is best limited to the holotype, to ensure taxonomic stability.

Semiretisporis ornatus ORŁOWSKA-ZWOLIŃSKA 1966

Pl. 6, Figs. 26, 27

Holotype: *Semiretisporis ornatus* ORLOWSKA-ZWOLINSKA 1966, Geological Quarterly 52: 1012, Pl. 5, Figs. 24, 25

Description: Some of our specimens (Pl. 6, Figs. 26, 27) are relatively small (40–57μm) and are stand out by their very narrow zona (ca. 6 μm, i.e. between 10–15% of the spore diameter). The reticulation is homobrochate, i.e. the brochi are all more or less the size, including those extending on the zona (in contrast to *Semiretisporis gothae* where the brochi extend on the zona being bigger and more elongate). The specimens only have one line of brochi (in contrast to the multiple lines in *Semiretisporis wielichoviensis* ORLOWSKA-ZWOLINSKA 1966). Thereby they comply best with the holotype of *Semiretisporis ornatus* ORLOWSKA-ZWOLINSKA 1966, although being a bit smaller than the diagnosed size range (60–85 μm).

Semiretisporis wielichovinsis ORŁOWSKA-ZWOLIŃSKA 1966 ***emend***.

Pl. 7, Figs. 1–4, 6–8

Holotype: *Semiretisporis wielichoviensis* ORLOWSKA-ZWOLINSKA 1966, Geological Quarterly 52: 1012, Pl. 4 Fig. 23

Synonymy: = 1967 *Semiretisporis maljavkinae* SCHULZ, p. 578, Pl. 10, Fig. 6, Pl. 11, Fig. 3 (!, here refigured in Pl. 7, Fig. 6)

Description: Only ¾ of our first studied specimen is preserved (Pl. 7, Fig.1). The specimen is seen from the distal side, the spore body itself is almost not preserved which makes it impossible to observe a trilete mark. It is however visible that the spore body was much darker in colour and measured ca. 62 μm. The overall size including the flange measures ca. 107 μm. The flange itself has a thickness of 20–24μm. The entire distal side is covered by a reticulum with more or less isodiametric brochi of more or less equal size. The lumina are roughly pentamers of 7–12 μm in diameter. There are multiple lines of brochi on the zona (2–3) which distinguished the specimen from *Semiretisporis gothae* which has large and elongate brochi extending on the flange. The studied specimen is almost subcircular. It is particularly noteworthy, that at the base of the muri of the reticulum, a darker shade of yellow is visible, which appears to be a very thin thickening at the base of the reticulum.

When studying a poorly preserved specimen (Pl. 7, Fig. 2) from Schulz' original material from which *Semiretisporis maljavkinae* was described, we can see only this faint thickening, which was visible in the first studied specimen. The patter of this thickening is reminiscent of the ornamentation in *Limbosporites lundbladiae* (compare also Pl. 8, Figs. 3, 4), but in contrast to *Limbosporites*, only present on the base of the reticulum; such a reticulum is not present in *Limbosporites.* Size and shape of this specimen comply with the first, but only the distal side is preserved. More such specimen with only the distal side preserved were found with varying degrees of preservation (Pl.7, Fig. 7; Pl. 8, Fig. 4). All of them are similar to, but larger than *Limbosporites lundbladiae* and should not be mistaken for it, as the preservation can be misleading.

Some specimens in Bonenburg are a bit smaller (70–80 μm total diameter) (Pl. 1, Fig. 4), but otherwise comply with the description of the first specimen of this morphotype (Pl. 7. Fig. 1).

All of the previous described forms appear conspecific with the holotype for *Semiretisporis maljavkinae* SCHULZ 1967 (Pl. 7, Fig. 6). The holotype is ca. 130 μm in diameter, the spore body is ca. 90 μm, and the zona 20 μm wide. The distal face of the spore is covered with a homobranchiate reticulum that has more than one line of brochi on the zona. The outline of the spore body is thickened. Trilete mark is distinct, length of the laeusura is less than half of the spore's radius. Proximal face without reticulum, partial damage of the zona can give the impression of foveolae but appears to be a secondary effect of preservation. In the original material of Schulz from which this form was described we found partially preserved specimen with either the distal face preserved as was discussed above, but also with only the proximal face preserved (Pl. 7, Fig. 8), which supports the interpretation of lack of ornamentation on the proximal face as well as the cingulizonate character of the spores, however with a much more hyaline zona than in *Limbosporites* for example.

Remarks: Unfortunately, the holotype for *Semiretisporis wielichovinsis* was not available for study. Based on the original diagnosis and depicted holotype, we consider the form to be conspecific with the above discussed specimen and conspecific with the holotype for *Semiretisporis maljavkinae* SCHULZ 1967 in particular. According to Orłowska-Zwolińska (1966) *Semiretisporis* *wielichovinsis* differs from *Semiretisporis gothae* by larger size, rounder outline, a narrower perispore beyond the body of the spore in relation to the diameter of the spore-body, and a denser and more compact reticulum. These similar distinguishing characteristics that Schulz (1967) describes for *Semiretisporis maljavkina,* which further supports synonymisation of the two taxa.

Orłowska-Zwolińska (1966) described the new taxon before Schulz (1967), wherefore the name *Semiretisporis wielichovinsis* should be adopted. Although less cited and less established (Text-Fig. 14), we hope that the name will be adopted more frequently, after emendation of the taxon, i.e. making a new diagnosis available in English. We propose the following preliminary emendation, which (in revised form) shall take effect upon effective publication of our results after investigating the holotype for *Semiretisporis wielichovinsis.*

Description *emend.*: Triangular-Convex to subrounded spores with a perispore. Total diameter between 70–160 μm. Spore body $^{1}/_{2}$–$^{2}/_{3}$ of the overall spore diameter. Perispore partially thickened at the outline of the spore body, but then homogeneously hyaline in the area of the zona. Width of the zona between 10–15% of the overall spore diameter. Proximal face without ornamentation with a trilete mark (not always visible), with laesurae $^{1}/_{2}$–$^{2}/_{3}$ of the diameter of the spore body. Distal face with a pronounced more or less homobrochate reticulum. Reticulum covering the spore body with hexamerous brochi, giving the impression of a honeycomb. Brochi more variable in the area of the zona, but not elongate, and in 2–3 rows.

Distinction: *Semiretisporis wielichovinsis* differs from *Semiretisporis gothae* by larger size, rounder outline, a homobrochate reticulum. *Semiretisporis wielichovinsis* is larger and has more than one line of brochi on the zona in comparison to *Semiretisporis ornatus* (Text-Fig. 15).

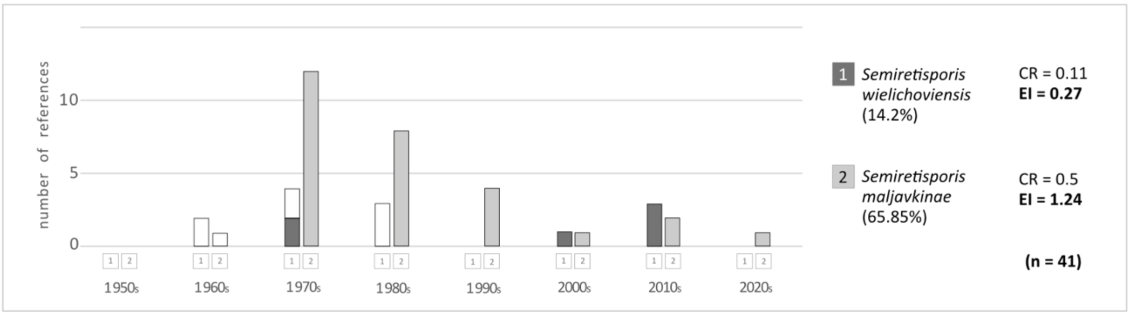
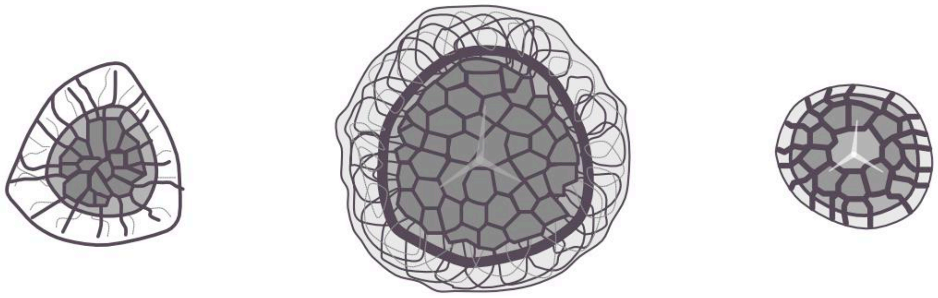


Fig. 14. Name usage of *Semiretisporis wielichoviensis* and *Semiretisporis maljavkinae* in comparison. Partial reprint from chapter 5. CR=Citation rate; EI=Establishment Index.



S. gothae
more triangular
heterobrochate
one line of brochi on zona

S. wielichoviensis
more rounded
homobrochate
multiple lines of brochi on zona

S. ornatus
more rounded
homobrochate
one line of brochi on zona

Fig. 15. Comparison and characteristics of Rhaetian *Semiretisporis* species.

Suprasubturma **PERINOTRILETES** (Erdtman 1947) emend. Dettmann 1963

Subturma **AZONOPEROTRILETES** Burger 1994

Infraturma ***Laevigati*** Burger 1994

Cornutisporites Schulz 1962

Type: *Cornutisporites seebergensis* Schulz 1962, Geologie 11: 310, Pl. I, Figs. 7–8, Seeberg 13/1, X 11182 BGR-S (!)

Diagnosis: Trianguläre, trilete Mikrosporen mit ungefähr bis an den Äquator reichender Dehiszenzmarke. Eine als Perispor gedeutete hüllartige äußere Wandschicht hat die Gestalt eines dreifachen T-Ankers mit stark konkaven Einbuchtungen an den Seiten. Die Ankerspitzen treten stark in die Kontur (Schulz, 1962, p. 310).

Engl. Translation: Triangular, trilete microspore with the laesurae of the trilete mark almost reaching the equator. An exterior, as perispor interpreted wall layer, in the shape of a threefold T-anchor with strongly concave invaginations at the sides. The cross-bars of the anchors strongly protrude in the equatorial outline. (altered after Jansonius and Hills (1976), card 604)

Botanical affinity: Ferns–Filicales. Schulz (1967) makes this assignation based on the similarity with extant species, but no *in situ* finds, yet.

Remarks: The genus has great resemblance with *Triancoraesporites*, especially because of the concave invaginations and the anchor shaped apices. They are supposed to differ however in the perispore present in *Cornutisporites*. It should be noted however, that some specimen in *Triancoraesporites ancorae* depict the beginning of a similar differentiation (e.g. Pl. 3, Fig. 23, arrowhead) and its questionable, whether the latter are simply an earlier maturation stage of spores of the same mother plant, especially as they are generally smaller than *Cornutisporites*. The thicker and unevenly thick exine typical in *Cornutisporites* (compare especially Pl. 3, Fig. 17), and the laesurae reaching the equator might also only develop later.

Cornutisporites seebergensis SCHULZ 1962

Pl. 3, Figs. 11–15

Holotype: *Cornutisporites seebergensis* SCHULZ 1962, Geologie 11: 310, Pl. I, Figs. 7-8, Seeberg 13/1, X 11182 BGR-S (!)

Preservation of the Holotype: The slide is available but in very poor condition (glycerin jelly strongly desiccated) and the specimen could not be relocated yet.

Diagnosis: Holotypus 45 µm (ohne Perispor). Ä-Kontur des Sporenkörpers dreieckig mit abgerundeten Ecken und geraden bis schwach konkaven Seiten. Die Y-Marke ist deutlich ausgebildet, r= $^5/_6$ – $^6/_6$. Die Exine ist glatt und weniger als 1 µm dick. Der Sporenkörper wird von einer Hülle umgeben, die der Gestalt eines extremen dreifachen T-Ankers sehr nahe kommt. Proximal und distal sind seitlich stark konkave Einbuchtungen vorhanden. An den Ecken dagegen ist dieselbe gerade bis schwach konvex und schmiegt sich am Scheitelpunkt der Ecken fast an die Exine des Sporenkörpers an. Durch die starke laterale Einbuchtung und die schwache Abrundung an den Ecken entstehen hornartig vorspringende Gebilde (Schulz, 1962, pp. 310–311).

Engl. Translation: Holotype 45 µm (without perispore). Equatorial outline of the body of the spore triangular with rounded apices and straight to slightly concave sides. The trilete mark is clearly visible, r= $^5/_6$ – $^6/_6$. The exine is smooth and less than 1 µm thick. The body of the spore is surrounded by an additional layer, which is very similar to an extreme trimerous T-anchor. Proximally and distally there are strongly concave invaginations present. At the apices on the other hand, they are straighter or even convex and cling close to the exine of the spore body at the peak of the apices. Due to the strong lateral invaginations and the weak rounding at the apices, this results in horn-shaped protrusions.

Description/Remarks: Many of our specimens are similarly poorly preserved as the holotype (Pl. 3, Figs. 13–15), but even where the preservation is rather poor the distinct shape and spore body and perispore shape make recognition still rather easy. There are also intermediate specimens that are in between forms assignable to *Triancoraesporites ancorae* and *Cornutisporites seebergensis* (Pl. 3, Figs. 11–12). Their laesurae are too long and exine too thick to comply with *Triancoraesporites ancorae,* but the perispore is not as well developed as typical for *Cornutisporites seebergensis.* Together with the beginning perispore differentiation observed in

Triancoraesporites ancorae this could support an interpretation of different maturity stages of the same mother plant.

Cornutisporites rugulatus SCHULZ 1967

Pl. 3, Figs. 16–20

Holotype: *Cornutisporites rugulatus* SCHULZ 1967, Paläontologische Abhandlungen Abteilung B 2: 580. Pl. 11, Figs. 8–9, Möckern 1E 10184/3, X 11320 BGR-S (!)

Preservation of the Holotype: The slide is available but in very poor condition (glycerin jelly strongly desiccated) and the specimen could not be relocated yet.

Diagnosis: Größe 38–40 µm. Trilete Mikrosporen, Ä-Kontur dreieckig-konkav. Strahlen der Y-Marke gerade oder schwach wellenförmig, deutlich, r = $^{5}/_{6}$ – $^{6}/_{6}$. Sporenkörper wird distal und äquatorial von einer pseudoreticulaten bis rugulaten Hüllschicht umgeben, die die Form eines extremen dreifachen T-Ankers hat (Schulz, 1967, p. 580).

Engl. Translation: Size 38–40 µm. Trilete microspores, amb triangular-concave. Rays of the Y-mark straight or slightly undulating, distinct, r = $^{5}/_{6}$ – $^{6}/_{6}$. Spore body is surrounded distally and equatorially by a pseudoreticulate to rugulate “covering layer” [perispore], which has the shape of an extreme threefold T-anchor.

Description/Remarks: Our first specimen (Pl. 3, Fig. 17) is very similar to a specimen assigned to *Cornutisporites seebergensis* (Pl. 3, Fig. 11). The former specimen however shows a more distinct rugulate ornamentation on the distal side (which is not only an effect of the little air bubbles in the mounting medium, which appear more prominent in the photograph). More hyaline specimens originate from the last sample of the Contorta Beds (Pl. 3, Figs. 18–19). We can also document a very arcane hybrids specimen that depicts characteristics of both *Cornutisporites rugulatus* and *Perinosporites thuringiacus* (Pl. 3, Fig. 20). They share a rugulate perispore, which is more developed on the righthand side and without the typical invaginations which are visible on the lefthandside of the specimen. It does not depict however the tori or kyrtomes typical for *Perinosporites thuringiacus* and is in its overall appearance more similar to *Cornutisporites rugulatus.* This is an interesting example of aberration, but also shows the plasticity of the discussed characteristics.

Perinosporites SCHULZ 1962 ***emend***.

Type: *Perinosporites thuringiacus* SCHULZ 1962, Geologie 11: 309, Pl. 1, Figs. 1–2 Möckern 1E, E46/1, X 11178 BGR-S (! here refigured in Pl. 9, Fig.1)

Synonymy: = 1964 *Trizonites* MÄDLER 1964, p. 185, Pl. 3, Fig. 1

Diagnosis: Trilete Mikrosporen mit vorwiegend auf die Distalseite beschränktem zartem Perispor, Sporenkörper triangulär mit konkaven Seiten und bis an den Äquator reichender Dehiszenzmarke. Perispor hat annähernd gleiche Gestalt wie der Sporenkörper (Schulz, 1962, p. 309).

Engl. Translation: Trilete microspores with a delicate perispore which is mainly limited to the distal side. Body of the spore triangular with convex sides and the laesurae reaching the equator. Perispore has almost the same shape as the spore body.

Remarks: Mädler (1964b) erects the new genus *Trizonites*, with two new species *Trizonites cerebralis* and *Trizonites rugulatus* choosing the former as the type for the genus. In the species description he clarifies that the type of the genus differs from *Perinosporites thuringiacus* by having a perispore rather than a zona. Upon comparison of the two types, we consider this rather a semantic misunderstanding, as the two types are considered conspecific. The problem with Mädler's type is, that only the distal half is preserved, in fact only the part that Schulz interprets as the perispore. Except for a minor semantic difference, the two authors are describing the same thing. The hyaline and delicate half, which constituted the remaining parts of the taxon preserved in Mädler's type is the perispore, yet at the equator this perispore extends into a zona. The interpretation that Mädler's specimen is only a part of intact specimen is supported by the fact that his other described species of thus genus, *Trizonites reticulatus*, consists of an additional proximal side, and complies perfectly with *Perinosporites thuringiacus* except for a difference in ornamentation that suggests distinction on a species level. Consequently, *Trizonites cerebralis* in *Perinosporites thuringiacus* are synonymised in the following and *Trizonites rugulatus* is recombined with the senior genus name *Perinosporites*. After studying Schulz's and Mädler's holotype material we also incorporate our observations in emended genus and species diagnoses.

Diagnosis *emend*.: Trilete microspores with a delicate perispore which is mainly limited to the distal side. Perispore protrudes over the body of the spore in a zona, less so at the apices and more so at the sides, but mirroring the triangular shape of the spore body. Sides of the spore slightly concave to slightly convex. On the proximal side, a kyrtome, i.e. a connected interradial band, encloses the laesurae which reach the equator. The kyrtome, often shining through the perispore, forms a concave triangle with club shaped apices. The distal side hamulate, i.e. ornamented with winding muri that delimit a maze-like pattern similar to the gyri of a brain.

Distinction: Despite possessing a kyrtome, this spore is differentiated from *Kyrtomisporis* through its possession of a perispore. *Zebrasporites*, although possessing a perispore differs in shape: *Zebrasporites* possesses a rounder outline and *Perinosporites* is more triangular. Moreover, *Perinosporites* possesses a kyrtome, while *Zebrasporites* possess maximum a thickened exine or tori.

Perinosporites thuringiacus SCHULZ 1962 ***emend***.

Pl. 9, Figs. 1–8, 15, 17, 29

Holotype: *Perinosporites thuringiacus* SCHULZ 1962, Geologie 11: 309, Pl. 1, Figs. 1–2 Möckern 1E, E46/1, X 11178 BGR-S (! here refigured in Pl. 9, Fig.1)

Preservation of the Holotype: rather bad, the glycerin jelly is dried out, the framing Canada balm is cracked in multiple place and even the cover slip is cracked. Without the embedding medium the details, especially on the proximal side are hard to discern. We thus propose lectotypification from Schulz' original material, which has plenty of suitable specimens.

Synonymy: = 1964 *Trizonites cerebralis* MÄDLER; p. 185, Fig. 1, TK.-Nr. 3144; M24/1 (!, here refigured, Pl. 9, Fig. 5)

Diagnosis: Größe 31–43 μm (Holotypus 42 μm). Ä-Kontur des Sporenkörpers dreieckig mit geraden oder nur schwach gerundeten Ecken und mehr oder weniger unregelmäßig konkaven Seiten. Y-Marke mehr oder weniger deutlich sichtbar und bis zum Äquator reichend. Perispor distal unregelmäßig verfaltet, greift meistens gleichmäßig mit etwa 6 μm über den Äquatorrand der Spore hinweg. An den Ecken des Sporenkörpers liegt das Perispor meist an (Schulz, 1962, p. 309).

Engl. Translation: Size 31–43 μm (holotype 42 μm). Equatorial outline of the spore body triangular with straight or only slightly rounded apices and more or less irregularly concave sides. Trilete mark more or less clearly visible and reaching the equator. Perispore on the distal side irregularly folded, reaching mostly regularly with ca. 6 μm beyond the equatorial outline of the spore body. At the apices the perispore mostly clings to the spore body.

Description: Our specimens (Pl. 9, Figs. 1–8) measure between 32–56 μm. Interestingly the holotype (Pl. 9, Fig. 1) was measured as 46 μm and it remains questionable, whether this is a primary measuring difference or secondary alteration of the specimen, which is known from glycerin jelly embedding (Neuhaus et al. 2017). Similar to the holotype, most of specimen show the typical, rather straight apices, which form a straight line perpendicular to the inserting laesurae. Some of them can have more rounded apices than others however (e.g. Pl. 9, Figs. 3 and 8). The kyrtome shows varying degrees of concaveness. The irregular foldings (muri) on the distal side are a bit variable in thickness and ca. 1.5–2.5 μm thick. From some specimens only these muri are preserved (Pl. 9, Fig. 19) provide a clear view on the ornamentation.

Preservation can be quite variable, mainly because of the inherent nature of the delicate perispore which damages easily and thus is not always preserved (Punt et al. 2007). In fact, most poorly preserved specimen of *Perinosporites* specimens (Pl. 9 Figs. 13–26) who different degrees of damage to the perispore. Sometimes it is damaged only at the apices (Pl. 9, Figs. 13, 18–19) or damage of the equatorial extension (Pl. 9, Figs. 14–17, 20–26) which gives the spore a very different look. If only the distal side is preserved (Pl. 1, Figs. 5, 20, 29) this makes identification much harder, as Mädler has proven, but it is a bit easier when the proximal kyrtome is imprinted in some faint thickenings at least (Pl. 9, Figs. 15–17). When the perispore is damaged at the sides but not the apices (Pl. 9, Fig. 26), specimens resemble *Cornutisporites rugulatus*, but the kyrtomes and thickenings differ. Some specimens have neither the proximal nor the distal side perfectly preserved, but show varying degradation of either (Pl. 9, Figs. 28–31) which also makes identification much more difficult, on the other hand these specimens give a good skeleton-like impression that help imagine the morphological features on either side of the spore.

Diagnosis *emend.*: Size 31–56 μm (holotype 46 μm). Equatorial outline of the spore body triangular with straight or only slightly rounded apices and more or less irregularly concave sides. Trilete mark more or less clearly visible and reaching the equator; accompanied by a kyrtome i.e. interradial thickening, of varying degrees of concaveness, sometimes forming a broader club shaped end towards the apex. Perispore on the distal side covered with muri that end openly at the equator, where the perispore forms a zona, that can be thickened where attaching to the triangular spore body. The distal side hamulate, i.e. ornamented with winding muri that are 1.5–2.5 μm thick.

Perinosporites rugulatus MÄDLER 1964 **nov. comb. et *emend.***

Pl. 9, Figs. 9–12, 14

Holotype: *Trizonates rugulatus* MÄDLER 1964, Fortschritte in der Geologie von Rheinland und Westfalen 12: 189–190, Pl. 3, Fig. 9; TK.-Nr. 3151, K26/1, LBEG-BGR-H (! here refigured in Pl. 9, Fig. 9)

Preservation of the Holotype: While the specimen itself was primarily not ideally preserved the preservation of the mount is still good.

Diagnosis: Eine Art der Gattung *Trizonites* mit proximal verdicktem Teil der an den Ecken T-förmig verbreitert ist und sich an den Seiten in konkaven Kurven in die Winkel der Y-Marke einschmiegt. Die Y-Strahlen verlaufen bis zur engsten Stelle des verdickten Teiles, zwischen dessen konkaven Seiten eine dreifach unterbrochene Zona ausgespannt ist, die über den Äquator der Spore hinausragt. Distale Exine mit dichtstehenden, geschlängelten Rugae besetzt (Mädler, 1964b, pp. 189–190).

Engl. Translation: A species of the genus *Trizonites* with a proximally thickened part that is widened in a T-shape at the corners and nestles in concave curves in the angles of the Y-mark. The Y-rays run up to the narrowest point of the thickened part, between its concave sides a triple interrupted zona is spanned, which protrudes over the equator of the spore. Distal exine ornamented with tightly packed, gyrose rugae.

Description: Our specimens measure 32–56 μm. Most of the specimens have a less constricted kyrtome near the apex compared to the holotype (Pl. 9, Fig. 9). The degree of concaveness of the kyrtome is variable (Pl. 9, Figs. 9–11). The ornamentation is distinctly finer than in *Perinosporites thuringiacus*. In addition to the triangular forms, we also found square specimens with four laesurae (Pl. 9, Fig. 12), which is interpreted as an aberrant spore, probably resulting from a tetrad with more than four spores. Other specimens appear as hybrids between *Perinosporites rugulatus* nov. comb and *Cornutisporites seebergensis*. Interestingly, these variations that we interpret as aberration seem to appear mostly in *Perinosporites rugulatus* nov. comb and not in *Perinosporites thuringiacus.*

Remarks: We find that Mädler's description is quite complicated and phrased a bit ominous in places. When comparing the holotype with that of *Perinosporites thuringiacus*, the morphology of the proximal side is identical. The kyrtome is more concave in the holotype of *Trizonites rugulatus*, but seen the infraspecific and interspecific variation of this characteristic, it falls within the variation also observed within *Perinosporites thuringiacus*. The striking difference however is the much smaller ornamentation consisting of thinner muri only about half (i.e. ca. 1 μm) the thickness observable in *Perinosporites thuringiacus* with more intertwined muri forming a more sinuous reticulum that allows distinction.

Diagnosis *emend.*: Like *Perinosporites thuringiacus*, but with smaller narrower muri (under 1.5 μm thick) and thereby having a finer maze-like pattern on the distal side of the spore.

Fig. 16. Pollen colour alteration throughout the detailed sampling I. D–1 to D–5 from the black Contorta Beds, D–10 from the grey layer in between the Contorta and the Triletes Beds. In several samples specimens of varying colour/preservation occur.

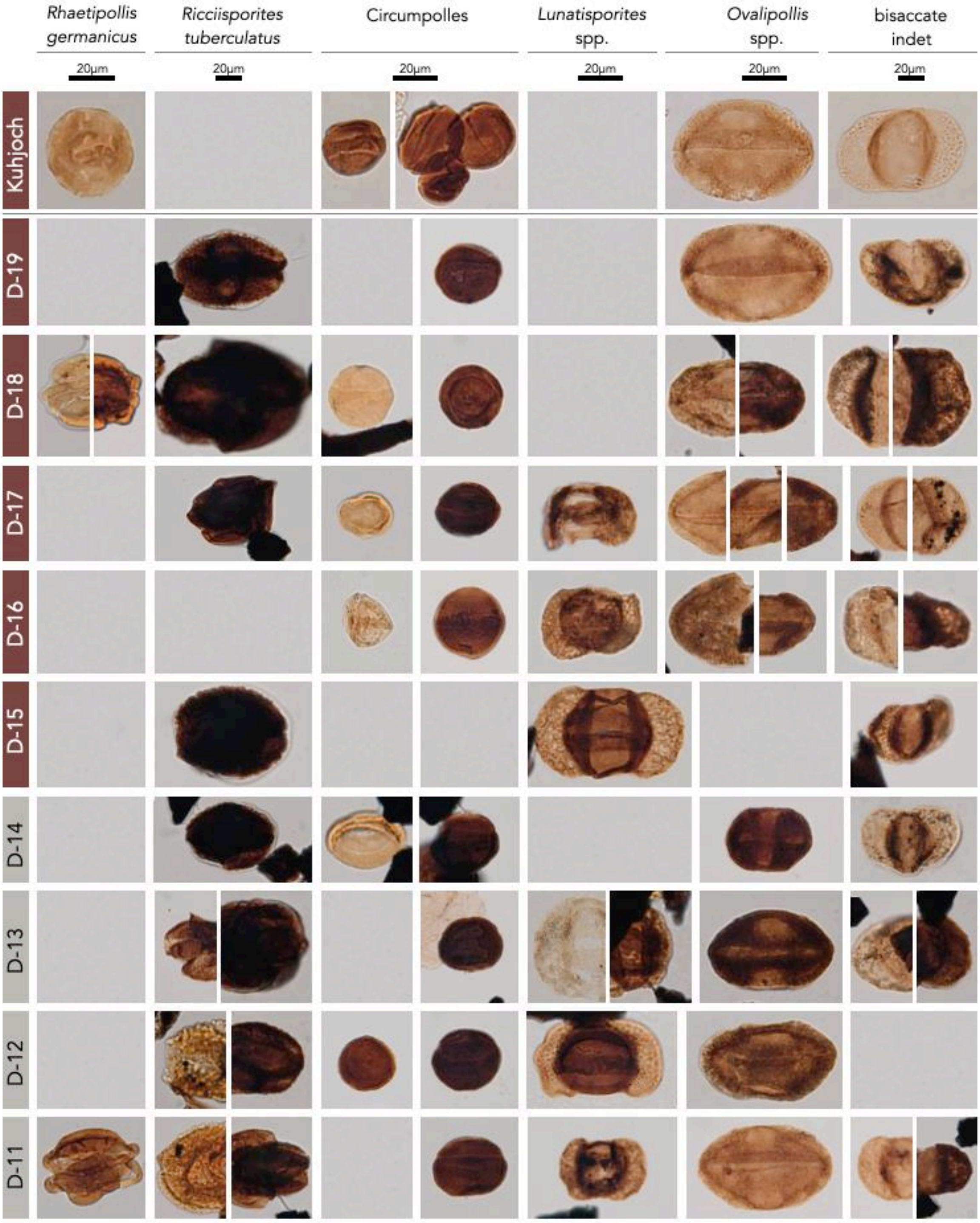


Fig. 17. Pollen colour alteration throughout the detailed sampling II. D–11 to D–14 from the grey layer in between the Contorta and the Triletes Beds. D–15 to D–19 from the reddish Triletes Beds. One sample from Kuhjoch from the Schattwald Beds in comparison. In several samples specimen of varying colour/preservation occur.

Anteturma **POLLENITES** POTONIÉ 1931

Turma **SACCITES** ERDTMAN 1947

Subturma **MONOSACCITES** (CHITALEY 1951) POTONIÉ & KREMP 1954

Infraturma ***Inaperturati*** BURGER 1994

Enzonalasporites (LESCHIK 1955) emend. SCHEURING 1970

Type: *Enzonalasporites vigens* LESCHIK 1955, Schweizerische Paläontologische Abhandlungen 72: 44, Pl. 5, Fig. 24, B51/1b

Diagnosis: Kontur oval bis kreisförmig. Die Zone ist aus kurzen gewundenen Leistchen zusammengesetzt. Die gleichen Skulpturelemente liegen auf dem Sporenkörper. Sporenkörper und Zona werden durch eine meist deutliche Membran getrennt. Formen, deren Gesamtdurchmesser 40 μm niemals überschreitet und deren Randkrause bis zu 5 μm breit ist (Leschik, 1955, p. 44).

Engl. Translation: Amb oval to circular. The zone is composed of short, twisted small “laths” (Leiste). The same sculpture elements lie on the spore body. Spore body and zona are separated by a mostly distinct membrane. Species whose overall diameter never exceeds 40 μm and whose rims are up to 5 μm wide.

Emended Diagnosis: Suboblate bis oblate, in Polansicht angenähert runde Mikrosporen. Der Corpus ist – abgesehen von der evtl. vorhandenen distalen Keimarea – von einer dicken, retikulat – bis rugulaten, zuweilen auch wellig, faltig oder lappig ornamentierten Ectexine bedeckt. Ein angenähert runder, scharf oder unscharf begrenzter distaler Germinalapparat kann vorhanden sein. Eine schwache, gegen die Äquatorregion zu kontinuierliche Verdickung der Ectexine oder der sie verzierenden Skulpturelemente ist möglich, doch kennt die Gattung keine zonaten oder saccaten Exinendifferenzierungen am Äquator (Scheuring, 1970, p. 84).

Engl. Translation of emended Diagnosis: Suboblate to oblate, in polar view approximately round microspores. The corpus is – apart from the distal germinal area that may be present – covered by a thick, reticulate to rugulate, sometimes wavy, wrinkled or lobed ornamented ectexine. An approximately round, sharply or indistinctly delimited distal germinal “apparatus” can be present. A weak thickening of the ectexine or its sculptural elements, which may extend to the equatorial region, is possible, although the genus lacks a zonate or saccate exine differentiations at the equator (altered after Jansonius and Hills (1976), card 937).

Botanical affinity: Gymnosperms – Voltziales. Due to the morphological resemblance to *Patinasporites* (Balme 1995; Lindström et al. 2016) assigned to the same plant group. Patinasporites was found in situ in the Voltzialean *Glyptolepis* sp. (Balme, 1995 and citation therein). The family assignation is a bit problematic (see discussion in Taylor et al., 2009) and is thus not assigned here.

Remarks: Several authors provided emendations of the genus (Schulz 1967; Jansonius & Hills 1976). Schulz (1967) provides a relatively general discussion, tentatively synonymising *Vallasporites*, *Zonalasporites* pro parte and *Undulatisporites*. He does not restudy the holotype material like Scheuring (1970) does. The more elaborate and detailed study and emendation of Scheuring (1970) is followed here, and said publication can be consulted for detailed study and justification to keep *Vallasporites* and *Zonalasporites* as separate genera, additional to the newly erected genus *Pseudoenzonalasporites* (which is baculate not rugulate like *Enzonalasporites*).

Enzonalasporites vigens LESCHIK 1955

Chapter 3, Fig. 6.14

Holotype: *Enzonalasporites vigens* LESCHIK 1955, Schweizerische Paläontologische Abhandlungen 72: 44, Pl. 5, Fig. 24, B51/1b

Diagnosis: Kontur oval bis kreisförmig. Die 3,5 µm breite „Randkrause" besteht im wesentlichen aus feinen radiär gestellten Stäbchen. (Unterschied zu den bisher besprochenen [*E. tenuis*] Formen!) Skulptur der Zentralfläche: Sehr kurze Leisten bis Körner. Farbe: Dunkler als vorige [*E. tenuis*] (Leschik, 1955, p. 44).

Engl. Translation: Contour oval to circular. The 3.5 µm wide "Rim" consists essentially of fine radially placed rods (in contrast to the previously discussed [*E. tenuis*] species!) Sculpture of the central surface: very short laths or grains. Colour: darker than previous [*E. tenuis*].

Description: Our specimen is slightly broken, but the subcircular to slightly oval amb is still recognizable. The depicted specimen measure 32 µm in diameter with a rim of 3.6 µm. The rim depicts the typical rods which are radially oriented. The rim is darker in colour than the corpus, which seems to be preserved only in part. A trilete mark is not visible. The corpus is covered with regulate ornamentation.

Remarks: Stratigraphically, this species is very important in the Germanic Basin, as it is one of the defining palynomorphs of the *Classopollis*–*Enzonalasporites* Zone at the Norian–Rhaetian transition and of the *Enzonalasporites–Conbaculatisporites* sub–zone in the Lower Rhaetian (Lund 1977; Beutler et al. 2005; Barth et al. 2018; Schobben et al. 2019).

Subturma **DISACCITES** COOKSON 1947 emend. POTONIÉ & KREMP 1954

Infraturma ***Murornati–Costati*** BURGER 1994

Lunatisporites (LESCHIK 1955) emend. SCHEURING 1970

Type: *Lunatisporites acutus* LESCHIK 1955, Schweizerische Paläontologische Abhandlungen 72: 56–57, Pl.7, Fig. 24, B51/1a

Synonymy: = 1956 *Taeniaesporites* LESCHIK, p. 58, Pl. 8, Fig. 1
= 1964a *Striatisaccus* MÄDLER, p. 56, Pl. 2, Fig. 14
= 1966 *Taeniaepollenites* VISSCHER, p. 360, Pl. 18, Fig. 1

Diagnosis: Der Sporenkörper ist in einzelne Streifen zerlegt. An den beiden Stellen, auf denen das Flügelnetz liegt, erscheint der Körper dunkelbraun bis schwarz. Dort ist mit einer Verdickung des Exospors zu rechnen. Dadurch entsteht eine dünnere Exosporstelle in der Mitte des Körpers, die vertikal verläuft (Leschik, 1955, pp. 56–57).

Engl. Translation: The microspore body is divided by taeniae. At both places where the sacci attach to the corpus, the corpus appears dark brown to black. There one should expect a thickening of the exospore. As a result, there is a thinner exspore area in the centre of the corpus, which runs vertically.

Emended Diagnosis: Bisaccate Pollenkörner mit breiten fein reticulierten Ectexinenstreifen (Taeniae) die den Corpus in Längsrichtung bedecken und mitunter Auf- und Abspaltungen aufweisen; einer (zumindest am Proximalpol) breit aufklaffenden zentralen Ectexinenläsur, welche die Kalotte längs der Longitudinalachse in zwei Streifenpackete teilt; einer durch diese Läsur entstandende ectexinenfreien Zone am Proximalpol („Zentralstrasse“), in deren Zentrum sich eine kurze, längsgerichtete Intexinenläsur befindet; einem, zwei (oder auch völlig fehlenden) Taeniarudiment(-en) welche die Enden der Zentralstrasse bedecken können; einem Sulcus zwischen den distalen Luftsackansätzen (Scheuring 1970, p. 51).

Engl. Translation of Emended Diagnosis: Bisaccate Pollen Grain with broad finely reticulate ectexine strips (taeniae), which cover the corpus horizontally and sometimes depict cleavages or broken-off parts; a (at least at the proximal pole) broadly gaping central ectexine-cleavage, which separates the corpus in two strip packages along a longitudinal axis; a ectexine free area at the proximal pole as a result of the central ectexine-cleavage ("main street"); one, two (or even completely missing) taeniae rudiment(s) which can cover the ends of the "main street"; a sulcus between the distal insertions of the sacci.

Botanical affinity: Gymnosperms, Peltaspermales (Looy et al. 2001).

Remarks: The genus and associated genera were emended and recombined with each other several times in different ways, and a comprehensive literature review about the genus and its synonymy can be found in Scheuring (1970). Scheuring also studied the holotype material of Leschik (1955) to support his synonymy and emendation which is followed here.

Lunatisporites cf. acutus LESCHIK 1955 emend. SCHEURING 1970

Pl. 10, Fig. 11

Holotype: *Lunatisporites acutus* LESCHIK 1955, Schweizerische Paläontologische Abhandlungen 72: 56–57, Pl. 7, Fig. 24, B51/1a

Synonymy: = 1955 *Lunatisporites impervius* LESCHIK, p. 57, Pl. 7, Fig. 21
= 1955 *Taeniaesporites kräuseli* LESCHIK, p. 59, Pl. 8, Fig. 1

Diagnosis: Kontur des Körpers oval, teilweise mit zugespitzten Polen an den Enden der longitudinalen Achse. Farbe dunkelbraun. Exine kräftig, bis 2 µm dick, zum Teil wulstartig. Streifung parallel der longitudinalen Achse. Die Spalten sind geschlossen. Maximale Breite der Streifen an den Schnittpunkten der transversalen Achse und longitudinalen Achse 10 µm. Die Ansatzlinie der Luftsäcke ist konkav eingebogen. Breiteste Stelle in der Gegend der longitudinalen Achse zwischen den Ansatzlinien 11 µm. Durch das sehr dichte Netzwerk der Luftsäcke erscheint der überdeckte Teil des Pollenkörpers schwarzbraun (Leschik, 1955, pp. 56–57).

Engl. Translation: The contour of the body is oval, sometimes with pointed poles at the ends of the longitudinal axis. Colour dark brown. Exine strong, up to 2 µm thick, partly thickened. Striations parallel to the longitudinal axis. Striae are closed. Maximum width of the striae at the intersections of the transversal to longitudinal axis 10 µm. The line of attachment of the air sacs is concave. Widest distance on in the area of the longitudinal axis is 11 µm in between the striae. Due to the very dense reticulum on the sacci, the covered part of the pollen body appears black-brown.

Emended Diagnosis: Eine Art von *Lunatisporites* mit: (1) einem angenähert runden (zuweilen leicht längs- oder querovalen) Zentralkörper, (2) zwei haploxylonoiden oder leicht diploxylonoiden lateral genäherten Luftsäcken von halbkreisförmigem bis etwas überhalbkreisförmigem Habitus, (3) vier (bei der Mehrzahl der Funde) oder < 4 längsgerichteten, fein infraretikulaten Streifen (Taeniae) auf der Proximalhemisphäre, die zuweilen (auf ihrer ganzen Länge oder bloss schräg, bruchstückhaft) in weitere Streifen oder Streifenfragmente aufgespalten sind, (4) einer – im Gegensatz zu den Parietalläsuren – breit aus einanderklaffenden Zentralstrasse, die die Intexine am Proximalpol freilegt und einen keil- oder spindelförmigen Habitus besitzt, (5) einer längsgerichteten, monoleten Intexinenläsur am Proximalpol von der ungefähren Länge eines Drittels des Zentralkörpers. (6) Die Enden der Zentralstrasse können – je nach Varietät – von einem, zwei oder auch keinem Taeniarudiment bedeckt sein (Scheuring 1970, p. 51).

Engl. Translation of Emended Diagnosis: A species of *Lunatisporites* with: (1) approximately rounds (sometimes slightly longitudinal or transversally oval) central body, (2) two sacci of the haploxylon-type or slightly diploxylonoid that laterally are closer together. Sacci semicircular to slightly more than semicircular (3) four (in the majority of cases or <4 longitudinal, finely infrareticulate stripes (taeniae) on the proximal side, which are sometimes split into smaller stripes or stripe fragments (over the whole length or only skewed or fragmented), (4) one – in contrast to the "Pariettalläsuren" – a wide "central road" which exposes the intexine at the proximal pole and which is wedge-shaped or spindle-shaped, (5) a longitudinal, monolete intexine laesura at the proximal pole, approximate length of the laesurae is a third of the central body. (6) The ends of the "central road" can – depending on the variety – be covered by one, two or no taeniaete rudiment.

Description: Although the majority of specimens of *Lunatisporites* found in Bonenburg comply with the circumscription of *Lunatisporites rhaeticus*, one specimen was strikingly different because of a taeniate rudiment. With only one "broken" taeniae it not comparable with *Striatoabieites aytugii* (Pl. 10, Fig. 17), which has several of these broken taeniae. Since this element is a distinguishing characteristic of *Lunatisporites acutus,* it complies best with the circumscription of the latter, although it is typically known from the Lower and Middle Keuper. Therefore, the specimen might be reworked, but it is noteworthy that it is in excellent condition with the corpus still attached and no other damage either which might be expected in case of reworking.

Remarks: Scheuring (1970) restudied Leschik's material after which he pointed out, that a crucial characteristics of this species is the additional half taeniae, which is also present in *Taeniaesporites kraeuseli* and *Lunatisporites impervius*, which, in addition to the general conformity of the two holotypes, lead to synonymising the three taxa.

Lunatisporites rhaeticus (SCHULZ 1967) WARRINGTON 1974

Pl. 10, Figs. 1–10, 12–15

Holotype/Basionym: *Taeniaesporites rhaeticus* SCHULZ 1967, Paläontologische Abhandlungen Abteilung B 2: 597–598, Pl. 18, Figs. 3,4; Möckern 1E, 10184/1; X11353 BGR-S (!, here refigured in Pl. 10, Fig. 1)

Preservation of the holotype: The glycerin jelly around the holotype is completely dried out, leaving a very unclear view on the specimen. Although the number of taenia and overall shape is still visible, any ornament details (e.g., infrareticulatum) on the sacci are not visible. On top of that, the taeniae are now weirdly shaped, which was not the case in the original microphotograph and is probably a result of desiccation. To be able to identify the finer ornamentation it might be necessary to designate a lectotype, material for this is available as documented in plate. 9, figures 2 and 3.

Diagnosis: Gesamtbreite 55– 71 µm (Holotypus 65 µm). Zentralkörper oval, stets breiter als lang, auf der proximalen Seite durch drei, selten vier Striemen geteilt. Exine des Zentralkörpers fein infrareticulat, Lumina bis 1 µm Durchmesser. Keimspalt auf der Proximalseite meist sichtbar. Luftsäcke überhalbkugelig, selten halbkugelig, nach distal versetzt, Maschen des Infrareticulums deutlich radial gestreckt, Lumina 1,5–3 µm groß (Schulz, 1967, pp. 597–598).

Engl. Translation: Overall width 55–71 µm (Holotype 65 µm). Corpus oval, always wider than long. On the proximal side the corpus is divided by three, seldom four long taeniae. Exine of the corpus finely infrareticulate, lumen up to 1 µm in diameter. Germination slit on the proximal side most of the time visible. Sacci more than half-round, seldom half-round, and shifted distally, lumen of their infrareticulum clearly radially stretched, lumen 1.5–3 µm in size.

Description: Specimens from Bonenburg come in a variety of colours or thermal maturation. At the very top of the Contorta Beds specimen are very hyaline Pl. 10, Figs. 4, 7, 10 ,13) and increasingly dark, and then generally dark in the grey-layer in between the Contorta Beds and Triletes Beds and throughout the latter (overview in Text-Fig. 16 and 17). Rarely specimen of two preservations occur in one sample (Text-Fig. 16, D–13). This is interesting because other bisaccates vary very much in colour (Text-Figs. 16 and 17)

It regularly occurs that only the distal side, i.e., the sacci and taeniae are preserved only (Pl. 10, Figs. 4, 5, 7, 8, 10), which was also observed from the original material from Schulz (1967) (Pl. 10, Fig. 2). In other cases, one finds the corpus still attached (Pl. 10, Figs. 3, 6, 9, 12–15). It is possible that some rounded elements that represent the corpi of those specimens without, might be regarded as undetermined algae or other palynomorphs that are counted as “indet”, when the remaining characteristics are inconclusive. It should be noted that individuals of this taxon are usually directed with the distal side to the viewer. This is probably a result of the preparation technique, where the residue is dried on the coverslip before mounting. Therefore, the proximal view with the broad "germination slit" is rarer to be seen (exception in Pl. 10, Fig. 6). In this specimen the thickening along the area where the sacci attach to the corpus are well visible. Overall, the Bonenburg specimens compare well with the holotype, one notable difference is the generally bigger size of the holotype the original material (Pl. 10, Figs. 1–3). This might be an effect of the storage in glycerin jelly that is known to cause this effect (Sluyter 1997; Meltsov et al. 2008; Neuhaus et al. 2017)

Remarks: While *Lunatisporites rhaeticus* is a typical marker for the Rhaetian as the name suggests, taeniate forms with more than four taeniae, e.g. assignable to *Protohaploxypinus* (Pl. 10 Fig. 16) or *Striatoabieites* (Pl. 10, Figs. 17–19) are likely reworked from the Lower or Middle Keuper, but found together with Rhaetian forms.

Ovalipollis KRUTZSCH 1955 emend. SCHEURING 1970

Type: *Ovalipollis ovalis* KRUTZSCH 1955, Geologie 4: 70, Pl. 1, Fig. 2

Synonymy: = 1955 *Unatextisporites* LESCHIK, p. 59, Pl. 8, fig, 8

Botanical affinity: Gymnosperms–Voltziales. Grauvogel-Stamm and Grauvogel (1975) found microspores in a male cone of *Voltzia* sp., which looks very similar to *Illinites*. Likewise, Balme (1995) found spores similar to *Illinites* in another conifer cone of *Aethophyllum stipulare* in the Upper Bunter (Triassic) of France. Due to the morphological similarity between *Ovalipollis* and *Illinites* Scheuring (1970) argues in favor of *Ovalipollis* being of coniferous origin.

Remarks: Scheuring (1970) provides a very elaborate study of the genus and should be consulted further detail.

Ovalipollis pseudoalatus (THIERGART 1949) SCHUURMAN 1976

Pl. 11 Figs. 1–24

Holotype/Basionym: *Pollenites pseudoalatus* THIERGART 1949, Palaeontographica Abteilung B 89: 9, Pl. 1, Fig. 15

Preservation of the holotype: The slide that should hold the holotype is lost, so is the holotype and since no original material that would be suitable is available, neotypification is necessary (but see discussion on current limitations, section 1.4.3).

Diagnosis: Größe 60 µ. Der Pollenkörper samt Flügel bildet ein sehr regelmäßiges Ovaloid, ohne daß ein Übergang des Pollenkörpers in die Flügel festzustellen ist. Die Flügel lassen zwischen sich nur einen schmalen Raum für die Keimfalte frei (Thiergart, 1949, p. 9).

Engl. Translation: Size: 60 µm. The pollen corpus including the "wings" forms a very regular ovaloid, without any perceivable transition of the "wings" into the corpus. The "wings" leave only a narrow space between them for the germinal fold.

Emended Diagnosis: Bilaterally symmetrical pollen, generally with elliptical outline in both polar and lateral view. Thin nexine constituting a central body with elliptical to rhombic outline in polar view. Nexine surrounded by differentially thickened sexine; sexine fused to the nexine. Presumed proximal sexine relatively thin with fine infrapunctate structure in plan view, rectum smooth. Presumed distal sexine relatively thick with a complex infrastructure composed of a three-dimensional network of sexinous elements, appearing as an infrapunctate, infrareticulate or infrarugulate pattern in plan view; rectum ornamented by irregular ridges. Longitudinal furrow in the presumed proximal area. Two lateral, elliptical, fusiform or rounded-triangular tenuitates in the presumed distal area. No transverse aperture in the presumed distal area (Schuurman, 1976, p. 250).

Description: In samples from Bonenburg we observe a large variation from very small and square forms (Pl. 11, Fig. 6) to extremely elongate and oval forms (Pl. 11 Fig. 19) and more standardly oval forms most similar to the holotype *Pollenites pseudoalatus* (compare Pl. 11 Figs. 4 and 9). All of these forms are connected through intermediate forms (Pl. 11 Figs. 5–8, 9–24). Colour variation ranges from very light and hyaline specimens in the Contorta Beds (Text-Fig. 16, D–1 to D–5), with forms of increasing darkness in the grey layer of the detailed sampling (Text-Fig. 16, D–7 and D–8) which in the first samples however co-occur with hyaline forms (Text-Fig. 16, D–7 and D–8). In the samples from the Triletes Beds specimens have a wide range of colours co-occuring in one sample, but without very hyaline forms present (Text-Fig. 19, D–16 to D–18). The lightest forms of this darker colour palette comply with forms found in a studies Kuhjoch sample from the Schattwald Beds.

Remarks: Although the genus shows a wide range of variation (Pl. 11) we follow the "inclusive" approach of Schuurman (1976) without further splitting, since all forms seems to be seamlessly connected by hundreds of gradational forms that connect morphological end-members of: (1) very small and more square forms (Pl. 11, right column) to (2) more elongate and oval forms (Pl. 11, middle and left column) that include the holotypes of *Ovalipollis pseudoalatus* THIERGART 1949 (Pl. 11, Fig. 4) *Ovalipollis lunzensis* KLAUS 1960 (Pl. 11, Fig. 2) and large (i.e. around 100 µm and larger) specimens similar to the holotype of *Ovalipollis rarus* KLAUS 1960 (Pl. 11, Fig. 1).

Infraturma *Sulcati* BURGER 1994

Pinuspollenites RAATZ 1937

Lectotype: *Pollenites labdacus* RAATZ 1937, Abhandlungen der Preußischen Geologischen Landesanstalt 183: 16, Präp. IV 31a (in Krefeld)

Preservation of the Lectotype: Since all material from the Beisselsgrube is considered to be lost after inquiry at the Geological Survey in Krefeld, the lectotype designated by Potonié (1958) is probably also lost. Alongside his lectotypification he cites a specimen from the Grube Marga. Since this material is available from Thiergart (1937) and which might serve as original material for lectotypification for several other "lost" types (see chapter 8), the same might be considered here.

(Monotypic Species) Diagnosis: Bei vierseitig symmetrischer Lage gehen die Luftsäcke über eine einfach ovale Umrandung hinaus. Sie sind im Gegensatz zu *Pollenites alatus* über halbkreisförmig (Potonié and Venitz, 1934, p. 20).

Engl. Translation: If the position is symmetrical on four sides, the sacci protrude beyond the outline. In contrast to *Pollenites alatus*, they are a bit larger than semicircular

(Genus) Diagnosis: Die Gattung unterscheidet sich von *Abiespollenites* und *Piceaepollenites* durch oft relativ größere, z.T. mehr als halbkugelförmige Sacci, deren proximaler Ansatzrand sich näher dem proximalen Pol befindet als bei den beiden anderen Gattungen. Dies ist im Meridian-Schnitt erkennbar (Fig. 76). Distal streben die Sacci beiderseits der Keimregion deutlich vor. Im Äquatorschnitt erscheinen die Sacci meist so weit aufgebläht, daß der Äquator-Schnitt als ganzes nicht oval erscheint wie bei *Piceaepollenites*, sondern beiderseits durch die Sacci angeschwollen. Der „Kamm" ist weniger kräftig als bei *Abies*- und *Piceaepollenites* (Potonié, 1958, p. 62).

Engl. Translation: The genus differs from *Abiespollenites* and *Piceaepollenites* by the often larger, sometimes more than semicircular sacci, their proximal attachment is closer to the proximal pole than in the two other genera. This can be seen in side-view (Fig. 76). Distally, the sacci clearly protrude on both sides of the germinal region. In polar view, the sacci usually appear so inflated that the outline does not appear oval as in *Piceaepollenites*, but rather swollen on both sides by the sacci. The "ridge" [cappa] is less thick than in *Abies*- and *Piceapollenites* (altered after Jansonius and Hills (1976, card 2012).

Botanical affinity: Gymnosperms–Pinaceae (Balme 1995; Bonis 2010).

Remarks: Jansonius and Hills (1976, card 2012) indicate, that they consider the genus not validly published until 1958 as they do for other monotypic genera published in the same publication from Raatz (1937) (e.g. *Sciadopityspollenites*). Potonié (1958) rightly disagrees since Art. 38.5

Code for monotypic genera only demands a description/diagnosis for either the species or the genus for both to be validly published. This criterion is fulfilled, wherefore the genus was validly published as of 1937. The full genus description was then added by Potonié in 1958.

Pinuspollenites minimus (COUPER 1958) KREMP 1970

Chapter 3, Fig. 9.16

Holotype: *Abietinaepollenites minimus* COUPER 1958, Palaeontographica Abteilung B 103: 153, Pl. 28, Fig. 14, 15, slide C 128/10, specimen K 5097 CGE (!)

Preservation of the Holotype: Although the slide holing the holotype is full with specimens of this taxon, the holotype itself could not be relocated and has to be considered "lost". There is ample material to choose a potential lectotype from, but it should be noted, that the overall preservation is fairly poor and one should invest some time, to find a suitable specimen for lectotypification.

Diagnosis: As for *A. microalatus* [Grains disaccate, rarely trisaccate; body of the grain broader than long, rarely circular to longer than broad, exine of the proximal cap …scabrate to sub-foveolate …bladders large of the haploxylon type…exine of the distal furrow thin and more or less smooth], except that the exine of the proximal cap is thinner (1 to 2 µm) and the mesh of the bladder reticulum is from 3 to 5 µm across (Couper, 1958, p. 153).

Description: Our specimens are all very badly preserved and it is hardly possible to distinguish more than overall sizes and orientation of the sacci. Due to lack of other known similar looking species at this time interval our specimens are tentatively assigned to this species. The depicted specimen is particularly small with an overall length (including sacci) of 20 µm, with the sacci of a maximum extension of about 10 µm.

Quadraeculina MALJAVKINA 1949 emend. SRIVASTAVA 1987

Type: *Quadraeculina anellaeformis* MALJAVKINA 1949, Trudy VNIGRI 33: 110, Pl. 39, Fig. 3 (designated by Potonié, 1960)

Diagnosis: The outline of the pollen grain is rectangular. The air sacs are large, and the body is large, semi-free or semi-enclosed. The dorsal distance is less than $^1/_2$ of the body ($^2/_5$ of it), the ventral distance about $^2/_3$. In species with a semi-free body the segments are indistinct, whereas in species with a semi-enclosed body they are large, well delineated, irregular in outline (Maljavkina (1949) in Jansonius and Hills (1976), card 4507).

Emended Diagnosis: Pollen, rectangular to subcircular shape, bisaccate, sacs pendulous on one side of the body (distal?), each sac with a large thin semicircular area (tenuitas) subequatorially adjacent to body margin, outer pendulous margins of both sacs form a distal “sulcus” with auriculate terminal ends in the centre of the body (Srivastava, 1987a, p. 39).

Botanical affinity: Gymnosperms – Pinales – ?Podocarpaceae (Boulter & Windle 1993). Gymnosperms – Voltziales? See discussion below.

Remarks: Jansonius and Hills (1976, card 4507) argue that the name was not validly published by Maljavkina lacking a genus diagnosis, when only a dichotomous key was available. It should be noted, that such a key provides the same information as a diagnosis, only in a different format. The *Code* only specifies that such information has to be given, not in which form (confirmed interpretation by Turland, personal communication, 2021). The genus is therefore considered to be validly published as of 1949. Therefore, *Quadraeculina annelaeformis* has priority over *Pityopollenites bitorosus* REISSINGER 1950.

Quadraeculina annelaeformis MALJAVKINA 1949

Pl. 12 Figs. 1–11

Holotype: *Quadraeculina anellaeformis* MALJAVKINA 1949, Trudy VNIGRI 33: 110, Pl. 39, Fig. 3

Preservation of the holotype: “Lost” (Vakhramev in Srivastava, 1976). Lecto- or neotypification needed.

Synonymy:
= 1950 *Quadraeculina limbata* MALJAVKINA, p. 110, Pl. 39, Fig. 2
= 1950 *Pityopollenites bitorosus* REISSINGER, p. 116, 125, Pl. 17, Fig. 25–30
= 1958 *Parvisaccites enigmatus* COUPER, p. 154, Pl. 30, Fig. 3–4
= 1958 *Chasmatosporites radiatus* NILSSON, p. 58, Pl. 4, Fig. 9
= 1969 *Ovalipollis limbata* (MALYAVKINA 1949), POCOCK & JANSONIUS, p. 161, Fig. 21
= 1969 *Ovalipollis enigmatus* (COUPER 1958), POCOCK & JANSONIUS, p. 161, Fig. 21
= 1974 *Ovalipollis bitorosa* (REISSINGER 1950), POCOCK, p. 94, Pl. 20, Figs. 4,5
= 1974 *Ovalipollis canadensis* POCOCK, p. 95, Pl.20, Figs. 6, 7
= 1974 *Pocockipites limbata* (MALYAVKINA 1949), BHARADWAJ, p. 18
= 1974 *Pocockipites bitorosa* (REISSINGER 1950), BHARADWAJ, p. 18

Description: The specimens are bisaccate pollen which have an elongate rectangle and show transitionary forms that are squarer in shape. Corpus as well as the sacci with reticulate ornamentation. The specimens are variable in size (35–57 µm wide and 30–50 µm long) and depict a broad sulcus. The outline of the specimens is accompanied by radial foldings. Lateral tenuitas adjacent to the air sacs clearly identify the specimens as belonging to this taxon.

Remarks: Stratigraphic range reaches from the Upper Triassic (Rhaetian) to the middle Jurassic (Tralau & Artursson 1972). Schulz (1967) notes that the forms occur more regularly and abundantly in the Lowest Jurassic compared to the Upper Triassic.

It is noteworthy, that *Quadraeculina* has a lot of similarities with *Ovalipollis*. Pocock (1970) even synonymised *Parvisaccites enigmaticus* which is considered conspecific with *Quadraeculina annelaeformis* with *Ovalipollis*. *Ovalipollis* as representative of the Voltziales is one of the few declining taxa after the TJ–transition (Gravendyck et al. 2020c). If we assume that not only the pollen of *Ovalipollis* and *Quadraeculina,* but also the parent plants are closely related, it could be possible, that the increasing abundance of *Quadraeculina* is a result of the parent plant taking the freed niche of the parent plant of *Ovalipollis*.

Some authors distinguish also the form *Quadraeculina limbata* (Malyavkina 1949; Pocock 1970; Srivastava 1987) by the more "wide-rectangular" shape and wider body compared to the only "rectangular" *annelaeformis* with narrower body. Others, like Schulz (1967), synonymise them, however. Unfortunately, the two mentioned criteria go hand in hand and are very hard to judge, because it is strongly influenced by secondary folding, compression and the position of the pollen, which can give a squarer or more elongate outline. Lacking other distinctive characteristics, the two forms are here considered conspecific.

It is noteworthy, that few other forms were so often described independently under other names (see Reissinger 1950, Couper, 1958, Nilsson 1958, and see synonym list). We believe that no more than two forms (*Quadraeculina anellaeformis* and *Quadraeculina limbata*) can be distinguished even if one does not synonymise squarer and more elongate forms; see subsequent synonymy in Srivastava (1987). Additionally, erected forms like *Pityopollenites bitorosus* REISSINGER 1950, *Parvisaccites enigmatus* COUPER 1958, *Chasmatosporites radiatus,* NILSSON 1958 *Ovalipollis canadensis* POCOCK are superfluous either way. The holotype material cannot be consulted any more to confirm synonymisation or separation of the two names, because it is "lost" (Vakhramev in Srivastava, 1976). A wider study of intraspecific variation and potentially different stratigraphic ranges are needed, to evaluate separation or synonymisation of *Quadraeculina anellaeformis* and *Quadraeculina limbata*, without the holotype material available. Lectotypification is impossible due to assumed lack of original material. Therefore, neotypification is needed, but currently not available (see discussion).

Vesicaspora (SCHEMEL 1951) WILSON & VENKETACHALA 1963

Type: *Vesicaspora wilsonii* SCHEMEL 1951, American Midland Naturalist 46: 749, Fig. 1,3

Botanical affinity: Gymnosperms – Cordaitales/Callistophytales (Balme 1995; Taylor et al. 2009; Zavattieri et al. 2018).

Vesicaspora fuscus (PAUTSCH 1958) emend. MORBEY 1975

Chapter 3, Fig. 6.28

Holotype: *Picea-Pollenites fuscus* PAUTSCH 1958, Micropalaeontology 4: 323, Pl. 1, Fig. 1

Synonymy: ? = 1964a *Sulcatisporites kraeuseli* MÄDLER, p. 65, Pl. 4, fig, 3–4

Other records: Protoconiferae Rogalska 1956, p. 27, Pl. 12, Figs. 1, 2

Diagnosis: Pollen dark brown, with only poorly developed bladders in equatorial view. In polar view a narrow slit is clearly visible between the bladders. Secondary folds are frequent. Size varies between 60 and 90 µm (Pautsch, 1958, p. 323).

Emended Diagnosis: Miospores disaccate, haploxylonoid, variable in preservation. In polar view, overall outline oval, circular, or quadrangular. Central body oval or circular, vaguely defined. Sacci and central body with a finely punctate or vermiculate sculpture, dense or sparse in development, occasionally completely absent (? preservation); exo- and intexine consequently laevigate, scabrate, often irregularly corroded. Sacci almost semi-circular, distally pendent, compressed upon and enclosing central body in polar view. Ventral saccus roots delimited often by thin transverse folds following compression of exoexine. Saccus detachment ca. 1–15 µm, sulcus laevigate. Distal saccus overlap generally more or less complete. Dorsal saccus roots vague, equatorial (Morbey, 1975, p. 29).

Description: The depicted specimen is 70 x 66 µm with the outline slightly oval. The two sacci are clearly visible but lay close to the corpus. Sacci with a very fine reticulum with lumen smaller than 0.5 µm. The pollen is broken at the narrow slit between the sacci.

Vitreisporites LESCHIK 1955 emend. DE JERSEY 1964

Type: *Vitreisporites signatus* LESCHIK 1955, Schweizerische Paläontologische Abhandlungen 72: 53, Pl. 8, Fig. 10

Synonymy:
= 1958 *Caytonipollenites* COUPER p. 149, Pl. 26, Figs. 7,8
≡ 1963 *Vitreipollenites* DANZÉ-CORSIN & LAVEINE, p. 93
= 1973 *Diaphanisporites* PAUTSCH, p. 137, Pl. 4, Fig. 6
non 1958 *Caytonipollenites* PAUTSCH, p. 328, Pl. 1, Fig. 4 (lacking type, not validly published)

Diagnosis: Sporenkörper oval bis rundlich, sehr hell und durchsichtig. Ausbildung eines Wulstes an den Ansatzstellen der Luftsäcke. Am proximalen Pol ist eine schwache Y-Marke zu beobachten. Grösse des Sporenkörpers unter 20 µm (Leschik, 1955, p. 53).

Engl. Translation: Microspore body oval to round, very light in colour and hyaline. Develops a thickening at the insertion of the sacci. Trilete mark is weakly visible at the proximal pole. Size of the spore body below 20 µm.

Emended Diagnosis: Bisaccate grains, central body subcircular, bladders with fine reticulation, faintly roughened, or smooth, proximally attached at equator, distally reaching almost to distal pole leaving a narrow straight germinal area uncovered, distal bladder base distinct; proximal face without infrareticulate exoexine: whole spore characteristically pale and thin walled, but proximal bladder base often with some folding, size small for a bisaccate pollen (de Jersey, 1964, p. 9).

Botanical affinity: Gymnosperms–Caytoniales. *Found in situ in *Caytonanthus* and *Salpingocarpus* from the Caytoniales from the Permian till the Cretaceous from around the world (Balme, 1995).

Vitreisporites bjuvensis NILSSON 1955

Chapter 3, Fig. 6.24

Holotype: *Vitreisporites bjuvensis* NILSSON 1958, Publications from the Institutes of Mineralogy, Paleontology and Quaternary Geology, University of Lund 53: 79, Pl. 7, Fig. 11, Präp. Nr. 129, KT 28,9/113,1

Diagnosis: Zentralteil: longitudinale Achse 15 µm (Holotypus), transversale Achse 28 µm (Holotypus). Luftsäcke: longitudinale Achse 10–18 µm (Holotypus 18 µm), transversale Achse 17–28 µm (Holotypus 28 µm). Gesamtlänge: 27–36 µm (Holotypus 36 µm). Verhältnis Länge zur transversalen Breite = etwa 1.4. Unterscheidet sich von *V. pallidus* durch größere relative Breite, schmalere Enden, gröbere intraretikulierte Struktur an den Luftsäcken (Lumina oft über 1 µm) und nur angedeutete radiale Anordnung der Strukturelemente; Zentralteil ziemlich schmal, Germinalfurche eng (Nilsson, 1958, p.79).

Engl. Translation: Corpus: longitudinal axis 15 µm (Holotype), transversal axis 28 µm (Holotype). Sacci: longitudinal axis 10–18 µm (holotype 18 µm), transversal axis 17–18 µm (holotype 28 µm). Overall length: 27–36 µm (Holotype 36 µm). Relation of overall length to transversal width = ca. 1.4. Distinguishable from *V. pallidus* by the bigger relative width, narrower ends, rougher intrareticulate structure on the sacci (lumen often bigger than 1 µm) with the radial orientation of the structural elements is less apparent; corpus rather narrow with small germinal furrow.

Description: Our specimen measures 39 x 25 µm, but it is more unfolded than the depicted holotype by Nilsson, which might explain the relative bigger size. The corpus measures 25 x 16 µm and depicts the typical appearance of longer than wide. The inserting area of the sacci is very dark and thickened, as mentioned in the genus diagnosis.

Vitreisporites pallidus (REISSINGER 1950) NILSSON 1955

Chapter 3, Fig. 6.24

Holotype: *Pityosporites pallidus* REISSINGER 1950, Palaeontographica Abteilung B 90: 109, Pl. 15, Figs. 1–5

Preservation of the Holotype: "Destroyed"; just like all other original material according to Reissinger (1950). Neotypification necessary.

Synonymy:
≡ 1950 *Pityopollenites pallidus* REISSINGER, p. 109, Pl. 15, Figs. 1–5
≡ 1958 *Caytonipollenites pallidus* COUPER, p. 150, Pl. 26, Figs. 7,8

Diagnosis: Geflügelter Pollen. Die Größe varriiert etwa zwischen 18 und 34 µm in der Länge. Der Gesamtpollen mit seinen Flügeln scheint stark abgeflacht zu sein. Die Flügel besitzen die schon erwähnte, noch genauer zu besprechende Netzstruktur, die den Pollen von dem Pinaceentypus entscheiden abrückt (Reissinger, 1950, p. 109).

Engl. Translation: Winged pollen. The size varies between 18 and 34 µm in length. The pollen with its wings seems to be strongly flattened. The wings have the already mentioned network structure, to be discussed in more detail, which distinguishes the pollen from the Pinacea type.

Description: Our specimen is not very hyaline, but the typical shape clearly identifies it as *V. pallidus*. The overall measurements are 37 x 20 µm, with the corpus 19.5 x 10 µm in size. The corpus of the specimen is not very well preserved, and the dirt obstructs the view. Nevertheless, the radial orientation of the lumen in the reticulum of the sacci is visible.

Remarks: The species was first mentioned as *Pityosporites pallidus* in Reissinger (1939), it was not however validly published, as it was missing the necessary illustration or reference to such (Art. 43.2 *Code*). Later Reissinger (1950) published an accompanying illustration and provided a more elaborate description. Although Reissinger does not clearly indicate it as validating publication, in fact he does not seem to be aware of the fact, the name was the earliest validly published from 1950 onwards. Unfortunately the type specimen for the name, was already lost at the time of this validating descriptionn as he explains in several places of his 1950 publication. Neither Couper, nor Nilsson designate a lecto- or neotype. Since all of the original material is lost neotypification is necessary but currently not available. See section 1.4.2 for further discussion on the current problem with neotypifications.

Turma **ALETES – INAPERTURATES** IBRAHIM 1933

Suprasubturma **ACAVATALETES** BURGER 1994

Subturma **AZONALETES** (LUBER 1935) POTONIÉ & KREMP 1954

Infraturma ***Apiculati*** BURGER 1994

Araucariacites COOKSON 1947 ex COUPER 1953

Type: *Araucariacites australis* COOKSON, 1947, B.A.N.Z. Antarctica Research Expedition Report 2: 130, Pl. 13, Fig. 3

Diagnosis: This designation characterizes spherical non-aperturate grains with granular exines of the type met with amongst recent members of the Araucariaceae (Cookson, 1947, p. 130).

Botanical affinity: Gymnosperms – Araucariaceae. Pollen of this type were found in situ in a number of araucariaceous fossils: *Agathis yallournensis* Cookson et Duigan 1951, *Araucaria lignitica* Cookson et Duigan 1951 (Oligocene), in a number of *Brachyphyllum* species (Jurassic–Cretaceous), *Dammarites coriaceae* Barale 1992 (Cretaceous), and a number of *Masculostrobus* species (Jurassic) (Balme 1995 and citations therein). This is supported by ultrastructural similarities with extant pollen from the Araucariaceae (Batten & Dutta 1997).

Remarks: Jansonius and Hills (1976, card 151) argue, that the name was not validly published, because Cookson uses the trinomial “coenotype” system: *Granuloapites (Araucariacites) australis*. They further explain that although Cookson & Duigan 1951 use the binomial *Araucariacites australis*, they do not formally validate the name. The name was then validated by Couper (1953).

Araucariacites australis COOKSON 1947 ex COUPER 1953

Chapter 3, Fig. 8.6

Holotype: *Araucariacites australis* COOKSON, 1947, B.A.N.Z. Antarctica Research Expedition Report 2: 130, Pl. 13, Fig. 3 (designated in Potonié, 1958)

Diagnosis: Pollen grains large, usually flattened and crumpled, when fully expanded circular in outline, from 39–93 µm in diameter and averaging about 70 µm , Exine thin, finely and closely granular, the “furrow-rim“ described by Wodehouse (1935) as occurring in *A. imbricata* Pav. not indicated (Cookson, 1947, p. 130).

Description: Our specimen is ca. 63 µm in diameter and depicts the typical "pancake" shape and fine granulation typical for the species. It thus complies well with the description and compares well with Cookson's illustrations.

Remarks: Cookson herself, after studying extant specimens of *Agathis* and *Araucaria*, clarifies that an association of *Araucariacites* is not trivial. She states that the discriminating factor would be size, rendering *Araucariacites* more similar to *Araucaria* due to the typically bigger size of pollen in this genus. Cookson further argues that despite the vast size range of *Araucariacites*, the pollen could still originate from one mother plant, since the extant pollen of *Araucaria bidwilli* show a similarly large size range (Cookson 1947).

It should be noted that Cookson (1947) provides illustrations for the name later validated by Couper (1953), but she does not indicate in any way, which specimen she illustrated. When Couper later designates the lectotype, he chose Cookson's illustration as type, but since the type always has to be a specimen (Art. 8.5 *Code*) and since Cookson's publication does not provide the necessary information to identify the type specimen, new lecto- or neotypification is needed. Recovery of the original material doubtful and probably lost, but currently the only option as neotypification is currently not available. See section 1.4.3 for further discussion on the current problem with neotypifications.

Turma **MONOSULCATES** Burger 1994

Chasmatosporites (Nilsson 1958) Pocock & Jansonius 1969

Type: *Chasmatosporites major* Nilsson 1958, Publications from the Institutes of Mineralogy, Paleontology and Quaternary Geology, University of Lund 53: 54, Pl. 3, Fig. 12

Diagnosis: Monolete Sporen, die in geschlossenem Zustand die Gestalt eines Kugelquadranten haben, in aufgeplatztem Zustand abgeflacht, kreisförmig oder länglich oval sind. Enden bei geschlossenen Sporen im Äquatorumriss abgerundet oder stumpfwinklig, die flachen Seiten halbmondförmig, Proximalkante gerade oder schwach eingebuchtet. Monolete Marke im geschlossenem Zustand gerade oder konkav, in aufgeplatztem Zustand mehr oder weniger weit geöffnet; Öffnung lanzettförmig mit spitzen Enden, oval oder kreisförmig. Exine dünn oder verdickt (bis etwa 3 µm), mit mehr oder weniger grober, intraretikularer Struktur versehen. Umrisslinie eben oder rauh (Nilsson, 1958, p. 53).

Engl. Translation: Monolete spores, which, when closed, have the shape of a spherical quadrant, and which, when opened, are flattened, circular or oblong oval. Ends of closed spores rounded or obtuse-angled in the equatorial outline; the flat sides crescent-shaped, proximal edge straight or slightly indented. Monolete mark straight or concave when closed, more or less open when opened; Opening lanceolate with pointed ends, oval or circular. Exine thin or thickened (up to about 3 u), with a more or less coarse, intrareticulate structure. Outline smooth or coarse.

Emended Diagnosis: Monosulcoid pollen of subspherical or ovoid shape; amb subcircular to oval, smooth; in compressed state lenticular, sometimes the distal side flattened or slightly concave. Exine proportionally thick, distinctly two-layered; sexine thick, with pronounced internal zone of collumeallae; collumeallae arranged in short muri, leaving between them short sinuous canali that form a more or less vermiculate pattern (similar to that in *Classopollis*) or an irregular infrareticulum; sexine appressed to nexine, which is thinner but distinct underneath the collumellae layer. The exinal pattern is coarse on the proximal side, the distal side shows a more or less distinctly delineated circular to oval area of approximately one-half to three-fourths of the total diameter, in which the exine is noticeably thinner and with much finer pattern, representing a leptoma or sulcoid area; a pore or sulcus not developed. Size range ca. 30–80 µm (Pocock and Jansonius, 1969, p. 155).

Botanical affinity: Gymnosperms – Cycadopsida/Ginkgopsida – Cycadales/Ginkgoales/Gnetales. Pollen complying with this taxon were found *in situ* in *Androstrobus* (Cycadales), but an affinity with Ginkgoales and Gnetales is also put forward (Balme 1995) as a result of morphological similarity with extant Ginkgo pollen (especially *Chasmatosporites apertus*) which would also be possible in view of ultrastructural similarities (Batten and Dutta, 1997). For now, a more precise association remains unresolved.

Remarks: Nilsson (1958) erected the genus to separate specimens similar to *Monosulcites magnolioides* ERDTMAN 1947 and distinguishing them from other species retained in *Monosulcites* described by COOKSON and DELCOURT & SPRUMONT. He also recombined a species already described by Rogalska but despite her interpretation of the microspore as a pollen, noting a resemblance with cycadean pollen (1954), Nilsson (1958) regarded his new genus as monolete spore of lycophytic origin. Later on Schulz, 1967a) suggested a gymnospermous origin which lead to a minor emendation by Pocock and Jansonius (1969) which mainly translated the original diagnosis and reinterpreted it as a pollen and rephrasing the subsequently necessary terms.

Chasmatosporites apertus (Rogalska 1954) Nilsson 1958

Pl. 12, Figs. 12–15

Holotype/Basionym: *Pollenites apertus* Rogalska 1954, Instytut Geologiczny Biulletin 89: 45, Pl. 12, Figs. 13, 15 (designated by Nilsson 1958)

Synonymy:
≡ 1958 *Chasmatosporites apertus* (Rogalska 1954) Nilsson 1958: p. 56, Pl. 4, Figs. 5, 6.
= 1958 *Chasmatosporites crassus* Nilsson 1958: p. 57, Pl. 5, Fig. 3.
= 1958 *Chasmatosporites flavus* Nilsson 1958: p. 57, Pl. 5, Fig. 4.
≡ 1962 *Verrucipollenites apertus* (Rogalska 1954) Bona, p. 23, Pl. 2, Fig. 2.

Other Records:
1956 *Pollenites apertus* Rogalska, p. 44, Pl. 32, Figs. 1, 2
1969 *Chasmatosporits* sp. Pocock & Jansonius, p.165, Pl. 2 Figs. 46,47, 49,50

Diagnosis: Form 34–50 µm. Circular or oval in outline. Membrane coarse-grained, margin slightly undulating with a rim 3 µm broad. In the middle a large aperture, either circular or oval, depending on the shape of the pollen. Margin of the aperture also undulating. The pollen grain looks as if it were open, hence the name. The oval specimens (Phot. 14) resemble the pollen of the Genus *Cycas*. Photo 15 shows this pollen from the distal side. Dark yellow in colour (Rogalska, 1954, p. 54).

Emended Diagnosis: Diameter 32–50 µ. Äquatorumriss annähernd kreisrund (bisweilen mehr oval oder abgerundet dreieckig). Proximalseite flach. Monolete Marke weit geöffnet (oval oder kreisförmig). Streifen zwischen Peripherie und Rand der Öffnung annähernd gleich breit, $^{1}/_{3}$ – $^{1}/_{2}$ Radius. Exine dick, etwa 2–3, zweigeteilt (innere Schicht dünn), diffus und fein intraretikuliert (Lumina etwa 0,5 µ). Umrisslinie rauh, wellig, bisweilen fast granuliert (Nilsson, 1958, p. 56).

Engl. Translation of Emended Diagnosis: Diameter 32–50 µm. Equatorial outline almost circular (sometimes more oval or rounded triangular). Proximal side flat. Monolete mark broadly opened (oval or circular). Strips between periphery and edge of the opening approximately same width, $^{1}/_{3}$ – $^{1}/_{2}$ of the radius. Exine thick, ca. 2–3 µm, two-layered (inner layer thin), diffuse and finely intrareticulate (lumina ca. 0.5 µm). Equatorial outline rough, undulate, to finely granulate.

Description: Our specimens are between 32–40 µm long, i.e. rather on the smaller side of the spectrum. They clearly stand out by their typically thick exine and round sulcus area. They vary in colour depending on preservation from very light colour (Pl. 12, Figs. 13–15, Contorta Beds) to relatively dark specimen (Pl. 12, Fig. 12, Triletes Beds).

Remarks: Stratigraphic range from the Upper Triassic (Rhaetien) to Middle Jurassic (Schulz 1967). This paper agrees with Schulz (1967), that a separation of *Chasmatosporites crassus* and

Chasmatosporites flavus based on their slightly less pronounced ornamentation in comparison to *Chasmatosporites apertus* appears unnecessary, especially as there is no difference in stratigraphic range. Furthermore, the minute differences might be just as well a result of varying preservation. The overall difference of shape appears to be the result of compression.

Chasmatosporites elegans NILSSON 1958

Pl. 12, Figs. 25–26

Holotype: *Chasmatosporites elegans* NILSSON 1958, Publications from the Institutes of Mineralogy, Paleontology and Quaternary Geology, University of Lund 54: 58, Pl. 4, Figs. 11–12

Diagnosis: Länge 32–48 (Holotypus 47 µ), Breite (Äquatorialumriss) 30–43 µ. (Holotypus 39 µ). Äquatorumriss kreisförmig oder oval. Monolete Marke mehr oder weniger breit offen, Öffnung oft breit oval. Im Übrigen mit *C. minor* übereinstimmend (Nilsson, 1958, p. 58).

Engl. Translation: Length 32–48 (holotype 47 µm), width (equatorial outline) 30–43 µm. (Holotype 39 µm). Equatorial outline circular or oval. Monolete mark more or less wide open, opening often wide oval. Otherwise identical to *C. minor*.

Description: The specimens assigned to *Chasmatosporites elegans* best comply with the holotype for *Chasmatosporites elegans*, even though the original diagnosis does not provide much information to distinguish these forms of other species. The here presented specimens differ in a more regularly shapes sulcus, that is equally wide along the hole length of the pollen grain and narrower than in *Chasmatosporites hians*.

Remarks: When Pocock & Jansonius (1969) revised the genus to fit the interpretation of a pollen rather than a spore, they only revised the species *Chasmatosporites major*, but none of the others. Assignations amongst different authors to different species is relatively inconsistent (compare for example Lund, 1977; Nilsson, 1958; Schulz, 1967) and for stratigraphic and taxonomic purposes a thorough revision would be beneficial. Pending study of the available holotype material especially from Nilsson, we refrain from emendation here.

Chasmatosporites hians NILSSON 1958

Pl. 12, Figs. 16–20, 23

Holotype: *Chasmatosporites hians* NILSSON 1958, Publications from the Institutes of Mineralogy, Paleontology and Quaternary Geology, University of Lund 54: 55, Pl. 4, Figs. 3–4

Diagnosis: Länge 51–72 µ (Holotypus 51 µ), Breite (Äquatorialumriss) 48–58 µ (Holotypus 50 µ). Äquatorialumriss annähernd kreisförmig. Proximalseite flach. Monolete Marke weit geöffnet; Öffnung oft fast kreisförmig, ihre Enden mehr oder weniger weit vom Aussenrande der Spore entfernt. Exine verhältnismässig dünn, meist unter 1 µ, deutlich intraretikuliert; Form der Maschen sehr wechselnd, mehr oder weniger unregelmässig, bisweilen schlängelnd (Lumina meist etwa 1, Muri relativ schmal. Umrisslinie fast eben (Nilsson, 1958, p. 55).

Engl. Translation: Length 51–72 µm (holotype 51 µm), width (equatorial outline) 48–58 µm (holotype 50 µm). Equatorial outline approximately circular. Proximal side flat. Monolete mark wide open; Opening often almost circular, its ends more or less far from the outer edge of the spore. Exine relatively thin, mostly less than 1 µm, clearly intrareticulated; The shape of the brochi is very variable, more or less irregular, sometimes meandering (lumina usually around 1, muri relatively narrow). Outline almost flat.

Description: The specimens assigned to this taxon are characterised by a sulcus area that is wider than in *Chasmatosporites elegans*, and on top op of the narrower on one of the two sides of the sulcus area.

Chasmatosporites major NILSSON 1958 emend. POCOCK & JANSONIUS 1969

Pl. 12, Figs. 21–22

Holotype: *Chasmatosporites major* NILSSON 1958, Publications from the Institutes of Mineralogy, Paleontology and Quaternary Geology, University of Lund 54: 54, Pl. 3, Figs. 10–15

Synonymy: = 1958 *Chasmatosporites rimatus* NILSSON p. 55, Pl. 4, Figs. 1–2

Diagnosis: Länge 67 - 89 µm (Holotypus 77 µm), Breite (Äquatorialumriss) 43 - 56 µm (Holotypus 49 µm). Äquatorumriss mehr oder weniger breit oval, Enden mehr oder weniger stumpfwinklig, bisweilen abgerundet. Proximalkante in Seitenansicht gerade oder eingebuchtet. Enden gewöhnlich etwas hervorstehend, Distalseite stark konvex. Monolete Marke geschlossen. Exine in der Regel dick, 1 - 3 µm (meist 1,5 - 2 µm), ziemlich fein intraretikuliert (Lumina 0,5 - 1 µm meist etwa 0,5 µm, Muri relativ dick). Eine ziemlich schwache Columellarstruktur oft sichtbar. Umrisslinie eben oder annähernd eben (ausnahmsweise ein wenig rauh) (Nilsson, 1958, p. 54).

Engl. Translation: Length 67–89 µm (Holotype 77 µm), Width (Equatorial Outline) 43–56 µm (Holotype 49 µm). Equatorial outline more or less broad oval, ends more or less obtuse-angled, sometimes rounded. Proximal edge in lateral view straight or concave. Ends usually standing out, distal side strongly convex. Monolete mark closed. Exine generally thick. 1–3 µm (most often 1.5–

2 µm), very finely intrareticulate (lumina 0.5–1 µm, mostly 0.5 µm, muri relatively thick). Often a very weak columellar structure is visible. Amb smooth or almost smooth (seldom slightly rough).

Emended Diagnosis: Pollen, approximately 65–90 x 45–55 µm (holotype 77x49 µm), of more or less broadly oval outline, commonly with a few large longitudinal tapered folds, causing the prominent longitudinal ends of the pollen grain to appear angular. Exine 1–3 µm thick (usually 1.5–2 µm), with a rather fine infrareticulation (lumina usually 0.5 µm, but up to 1 µm) with relatively wide muri. Usually more or less well-developed columellar structure of the exine can be observed in the optical cross section. The outline is essentially smoot, but occasionally slightly roughened (Pocock & Jansonius 1969).

Description: As the name suggests, these are the largest specimens, ranging between 93 and 73 µm in length, that otherwise depict the typical exine infrareticulation and sulcus area.

Remarks: Stratigraphic distribution from the Upper Triassic (Rhaetien) to Middle Jurassic, with an abundant occurrence in the Lower Liassic (Schulz 1967).

Ricciisporites LUNDBLAD 1954 emend. LUNDBLAD 1959

Type: *Ricciisporites tuberculatus* LUNDBLAD 1954, Särtyck ur Botaniska Notiser 48: 401, Pl. 4 Figs. 8–9

Synonymy: non 1954 “*Tetradosulcites*”, Erdtman 1954 Särtyck ur Botaniska Notiser 48: (not validly published)

Diagnosis: Spores of roundish-tetrahedral shape, permanently united into tetrads. Distal surface strongly tuberculate showing a reticulate perinium (Lundblad, 1954, p. 400).

Diagnosis: Spores more or less roundish, permanently united into tetrads. Distal surface provided with a sulcus. Free exine surface clavate with densely spaced strong processes of varying size (appearing as a reticulum at certain adjustments of the microscope) (Lundblad, 1959, p. 83). [Lundblad clarifies, that the term “spore” is here used in the wider sense (i.e pollen, spore or both) (Erdtman 1952; Lundblad 1959)]

Botanical affinity: Gymnosperms (Lundblad 1959; Mander et al. 2012; Kürschner et al. 2014).

Remark: Lundblad formally described pollen of this form in 1954 although, they had been retrieved and figured before, e.g. adherent to a variety of plant cuticles (Lundblad 1954). Due to the association of these tetrads with hepatic macrofossils of *Ricciopsis*, hence the name *Ricciisporites* which is to refer to *Riccia*, which Lundblad claims is similar to the present palynomorph which she thus assigned to liverworts (Lundblad 1954).

Ironically, Erdtman described and identical palynomorph as *Tetradosculcites* in the same issue as Lundblad, however without designating a holotype nor a diagnosis, wherefore

Ricciisporites should have priority as Lundblad (1959) points out. In fact Lundblad expresses that it "is regrettable that Erdtman's generic name *Tetradosulcites* cannot be conserved here" as would become evident from her identification of a sulcus in her holotype after restudying leading to her emended diagnosis which incorporates "sulcus" in the generic as well as specific diagnoses (Lundblad 1959). Accordingly, she also took back her association of the taxon as a liverwort. Still unfortunate was her choice of words, however, describing the specimen as "spores". Although she clarifies herself that she means the term "spore" in the wider sense, i.e. meaning "meiospores", some authors have mistaken the word "spore" to suggest a cryptogam affinity. Although this interpretations stands in stark contrast to the emended interpretation of a sulcus (clearly suggesting a gymnosperm affinity) the unfortunate term "spore" has still lead to confusion in the coming years despite her changed diagnosis and despite her expressed interpretation of a gymnosperm (e.g. Balme, 1995). This was clarified though ultrastructural studies, which confirmed the presence of a sulcus and potential Benettitelian affinity due to the particular characteristics of the sulcus (Mander et al. 2012)

Ricciisporites tuberculatus (LUNDBLAD 1954) LUNDBLAD 1959 ***emend***.

Pl. 11, Figs. 9, 10 and Pl. 12, Figs. 9, 11–13

Holotype: *Ricciisporites tuberculatus* LUNDBLAD 1954, Särtyck ur Botaniska Notiser 108: 401, Pl. 4 Figs. 8–9

Diagnosis: Spore tetrad with a diameter of about 108 µm, consisting of spores approximately 50 µ in diameter. The surface of the spore has very strong tubercles, about 6 µm wide (three measurements), and a reticulum with areolae about 5 µm wide (4–7 µm; three measurements) (Lundblad, 1954, p. 401).

Emended Diagnosis: Spore tetrad with a diameter of about 108 µm, consisting of spores approximately 50 µm in diameter. Free spore surface clavate with very strong processes ("tubercles") with a maximum width of about 6 µm (three measurements). The sculpture of the exine may at certain adjustments of the microscope appear as a reticulum with lumina about 5 µm wide (4–7 µm; three measurements). A distal sulcus is present in the spores (Lundblad, 1959, p. 83).

Description: Pollen of this kind typically occurs almost obligatory in tetrads (Pl. 13). Only very rarely single grains are found (Pl. 14, Figs. 9, 11–13). The grains typically depict a clavate ornamentation (Pl. 14, Fig. 10). It should be noted, that one regularly encounters laevigate or supposedly laevigate grains. These are not primarily laevigate, but as a result of detached outer layer of the exine with the characteristic ornamentation (see such a fragment in Pl. 14, Fig. 10), which leaves the grains only with its inner, non-ornamented layer, with the occasional clavate remains (Pl. 13, Figs. 2–4, arrow heads).

While tetrads occur in a typical orange-yellow colour in the Triletes Beds (Text-Fig. 16) they occur in two different colours, orange as well as darker brown specimens in the grey layer (Text-Figs. 16 and 17) and then only dark specimens in the Triletes Beds (Text-Fig. 17, Pl. 13, Fig. 12 and Pl. 14, Figs. 6, 12).

It is very interesting, that the tetrads in Bonenburg but also in Schulz' original material depict quite a large variety of variation in the size and type of sculptural elements, which go beyond the scope of those depicted by Lundblad. The typical grain compliant with those in Lundblad has sculptural elements of ca. 4–6 µm wide, with some variation observable in the grains (compare Pl. 13, Figs. 9, 10) and occasional smaller sculptural elements below 4 µm, which are only observable in fluorescence light or SEM images (Pl. 13, Figs. 10a–c). It is noteworthy that in many specimens we observe some bigger sculptural elements around the sulcus and in between the four pollen where they are adjacent to each other in the tetrad (Pl. 13, Figs. 1, 10 and Pl. 14, Fig. 2). Again this is feature is most of the time only visible with fluorescence light, but is occasionally also visible in tetrads (Pl. 14, Fig. 4) or single grains, because of variations in the outline (Pl. 14, Figs. 11–12).

In addition to this typical ornamentation we observed specimens ornamented with plates rather than a tuberculate ornamentation. These plates are covering the grain in various shapes and sizes that are close to each other and very much resemble the scutes in a turtle shell (Pl. 13, Fig. 11). On top of that we found a single specimen with exorbitant large projections in Schulz' original material (Pl. 13 Fig. 13). The sculptural elements in this specimen are highly variable and show big spaces in between them. Thirdly we found a specimen that have relatively homogenously small verrucae (Pl. 13, Figs. 5, 6 and Pl. 14, Figs. 1–4, 7, 8, 10) that are on average much smaller than those visible in the holotype of *Ricciisporites tuberculatus* and other material depicted by Lundblad.

Interestingly we found aberrant tetrads comparable to those aberrant tetrad types observed in *Classopollis* (Gravendyck et al., 2020b; Kürschner et al., 2013; and see below). These aberrant tetrads were mostly observed in those *Ricciisporites* with the smallest sculptural elements so far. We found tetrads with one aborted grain in several samples Bonenburg (BB1000, BB1012, BB-D-05) as well as in Möckern (Schulz material) (Pl. 14, Figs. 1–4). A tetrad with two aborted grains was found only once in Möckern so far (Pl. 14, Fig. 7). Tetrads with three aborted grains were not observed in either of the two sites. It should be noted that tetrads some quite dramatic size differences. The standard tetrads measure between (70)–90–(110) µm in lenght (compare Pl. 13-14), but some are less than 60 µm (Pl. 14, Figs. 5, 6, 8). Most of them also have an underdeveloped ornamentation and resemble grains that can be easily identified as aberrant due to their variation within the tetrad. Therefore, these smaller tetrads are interpreted as aberrant and therefore comparable to those tetrads of four aberrant grains in *Classopollis*.

It is worth emphasizing, that aberration in *Ricciisporites* does not seem to be as abundant as in *Classopollis* since we had to study at least five times the amount of pollen specimens of the former genus to find aberrant tetrads in comparisons to *Classopollis*, although the samples are full with this pollen. In this context its also noteworthy, that we could not yet find tetrads with three aberrant grains although we especially looked for them. This suggests that they are much rarer than in *Classopollis*, but quantitative data will be needed to further investigate this.

Remarks: It is very noteworthy that *Ricciisporites tuberculatus* is almost the only name used to describe the variety of forms we find in the genus. According to Palynodata a total 10 species names/designations of *Ricciisporites* are designated: (1) *R. tuberculatus* LUNDBLAD 1954 emend. LUNDBLAD 1959; (2) *R. convolutus* POCOCK 1962; (3) *R. umbonatus* FELIX & BURBRIDGE 1977 (4) *R. luquanensis* LEI 1978; (5) *R. solidus* LEI 1978; (6) *R. yunnanensis* LEI 1978 (7) *R. sinensis* BAI et al. 1983 (8) *R. spatiosus* BAI et al. 1983 (9) *R. tenuis* BAI et al. 1983 (10) *R. psilosus* OUYANG 1988.

(2) Reinvestigating the illustration of the holotype in Pocock (1962), reveals that it is not actually a pollen tetrad, with the typical sulcus directed at the viewer, but rather a spore tetrad of possible lycophyte affinity. The original discussion and comparison with tetrads of modern *Riccia* in Lundblad (1954) that look similar to Pocock's tetrads might have caused this confusion. (7–9) are not in fact validly published, because Bai et al. (1983) do not provide the type designation necessary after 1958 (Art. 40.1 *Code*). This is unfortunate, because the forms describe the variety we observed above. (4–6, 10) are also lacking non-author citations and are dubious in their distinction and should be probably best limited to the holotypes, lacking verifiability. This leaves only the names *Ricciisporites tuberculatus* LUNDBLAD 1954 emend. LUNDBLAD 1959 and *Ricciisporites umbonatus* FELIX & BURBRIDGE 1977 available to describe the variety of forms assignable to the genus. The latter is a pre-Rhaetian taxon and occurs as single grains rather than tetrads and with very spherical and scattered sculptural elements (Text-Fig. 19) and does not comply with any of our forms from the Rhaetian. Although we acknowledge some intraspecific variation in the size of the "tubercules" in *Ricciisporites tuberculatus*, we believe that forms with very large sculptural elements with much bigger spaces in between these elements, with plate-like sculptural elements that resemble a turtle shell, and those with significantly smaller sculptural

elements than the name "*tuberculatus"* suggests should be addressed separately with bespoke names that will be described below.

It is surprising, that the variety observed in *Ricciisporites* has not caused more descriptions, as many other taxa have been differentiated for much smaller differences. Given the dominance of the taxon which occurs to have interchangeable abundances with the diversified group of Circumpolles (i.e. *Classopollis meyeriana*, *Classopollis classoides*, *Geopollis zwolinskae* and *Granuloperculatipollis rudis*) in Bonenburg (Gravendyck et al. 2020c) also makes it questionable whether it is not a variety of closely related mother plants.

In the following we emend the diagnosis of *Ricciisporites tuberculatus* and describe the most distinctive other forms as new species. Abundance data is not yet available, but it would be very interesting in the future, whether the different forms correlate with differences in their assumed environmental conditions like it is assumed for *Classopollis classoides* and *Classopollis meyeriana* (Kürschner et al. 2007; Bonis et al. 2009; Bonis & Kürschner 2012).

The alternative patterns of abundance between two domineering species *Classopollis* and *Ricciisporites* are conspicuous and could have explained by ecological exclusion of the two taxa (Kürschner et al. 2014).

Diagnosis *emend*.: Sulcate pollen occurring regularly in tetrads, rarely as single grains. Tetrads of a diameter of 70–110 µm consisting of pollen of approximately 50-70 µm in diameter. Ornamented with heterogeneously sized clava ("tubercles") of a maximum width of about 6 µm.

Ricciisporites megaturberculatus (sp. nov.?)

Pl. 11 Fig. 13

Holotype: To be determined upon effective publication.

Diagnosis: Specimens that occur in a tetrad with large and very irregularly shaped sculptural elements. They are between 6-25 µm in width and between 6-13 µm high. The spaces in between these elements are large and would permit the placement of an additional element in between two others. While the overall impression of the species is somewhat reminiscent of Ricciisporites umbonatus, the sculptural elements in the latter are more rounded and homogenous. Also, Ricciisporites umbonatus usually occurs as single grains and not in tetrads. The other Ricciisporites species can be easily distinguished by their very different and generally smaller sculptural elements (compare Text-Fig. 18).

Derivatio Nominis: after the extremely large sculptural elements in comparison to *Ricciisporites tuberculatus*.

Remarks: *Ricciisporites umbonatus* is typical for Upper Triassic, but pre-Rhaetian strata (Felix & Burbridge 1977) and was not observed in this study. This is a singular occurrence of the taxon in the slide holding the holotype of *Cerebropollenites thiergartii* SCHULZ 1967 and is presumed to derive from the base of the Hettangian due to its palynofloral assemblage. In Bonenburg and other European section there have been reports from reworked material in the Triletes Beds as well as at the base of the Jurassic, although possibly to a minor degree in the Jurassic (van de Schootbrugge et al. 2020; Gravendyck et al. 2020c). It is thus possible that the specimen is a reworked specimen possibly from the Norian or Carnian. Despite some similarities with *Ricciisporites umbonatus*, the observed differences rather suggest, that this might be a taxon derived from it. Final erection of this new species will pend the documentation of additional specimens complying with this description beyond the one isolated tetrad that was described above.

Ricciisporites cataphractes sp. nov.

Pl. 11 Figs. 11, 12

Holotype: tentatively *Ricciisporites cataphractes,* BB1042_3; F27/1; to be determined upon effective publication.

Diagnosis: Specimens ornamented with areolate ornamentation, with polygonal plates that are variable in size and shape, which are slightly domed and which are separated by grooves which form a negative reticulum.

Differentiation: Is distinguished from other species of the genus by the much more flattened sculptural elements, while the other species are more clavate with sculptural elements in different sizes, the sculptural elements in this species cover a much larger surface are not as elevated.

Derivatio Nominis: From Latin "cataphractus" for armoured or armour-plated which alludes to the plated appearance of the areola that resemble the ornamentation of the shell of a turtle.

Ricciisporites lundbladiae sp. nov.

Pl. 11 Figs. 5,6 and Pl. 12 Figs. 1–4, 7–10

Holotype: To be determined upon effective publication.

Description: Specimens ornamented with very small clava which are on average less than 4 µm in diameter. Clava are heterogeneous in size, significantly larger clava (5 µm and more) especially occur where grains are adjacent to each other in the tetrad, nevertheless the average size of the clava are much smaller than in *Ricciisporites tuberculatus* or other species of *Ricciisporites*.

Derivatio Nominis: From the variety of forms we describe here, these are the closest to those described by Britta Lundblad. The name honours her contribution to the genus.

R. umbonatus

R. lundbladiae sp. nov.

R. tuberculatus

R. cataphractes sp. nov.

R. megatuberculatus (sp. nov. ?)

Fig. 7.18. Comparison of *Ricciisporites* species.

Turma **ZONO–ANNULICOLPATES** Burger 1994

Classopollis Pflug 1953 emend. Pocock & Jansonius 1961

Holotype: *Classopollis classoides* Pflug 1953, Palaeontographica Abteilung B 95: 91, Pl. 16, Figs. 29–13

For discussion concerning the valid type for the genus and opposing possibilities compare Pocock and Jansonius (1961) and Traverse (2004).

Synonymy: ≡ 1963 *Classopollenites* Briché, Danzé-Corzin, Laveine, p. 105

Diagnosis: Tricolporat, seltener tetracolporat. Mit deutlicher Rimula. Germinalien klaffen. Pole nicht oder höchstens angenähert gleichgestaltet (Pflug, 1953, p. 91).

Engl. Translation: Tricolpate, rarely tetracolpate. Rimula well developed, germinales gaping. Poles never quite identical in appearance (Pocock & Jansonius 1961).

Emended Diagnosis: Pollen grains; distally monoporate; ovoid spherical, or flatly acorn-shaped; exine two-layered; exoexine absent or much reduced over a circular area surrounding the distal pole, and absent or reduced over a triangular area with its center at the proximal pole; intexine frequently bearing a reduced trilete scar, which has no germinal function, at the proximal pole;

exine always ornamented by striations in a band or girdle surrounding the equator and interrupted (if at all) at only one point; the band usually, but not always, marking a zone of exinal thickening (Pocock and Jansonius, 1961, p. 443).

Botanical affinity: Gymnosperms – Cheirolepidiaceae. Being very distinct and well-studied, there is a well-established association with the Cheirolepidiaceae based on many in situ finds e.g. from *Brachyphyllum*, *Classostrobus*, *Frenelopsis*, *Hirmeriella* and others ranging from the TJ-boundary till the Cretaceous from around the world with many finds originating from England and Germany (see further discussion in e.g. Alvin, 1982; Balme, 1995; Taylor et al., 2009; Watson, 1988).

Description: Typical for the genus is the distal pore and proximal triangle (Pl. 15, Figs. 1-3 and 8, arrow heads), which is filled with hair (Pl. 15, Fig. 31; Pl. 17, Fig. 13). In all *Classopollis* species we observed a wide array of malformations (overview in chapter 3 Fig. 13 and details in Pl. 16 in this chapter) and appear to be independent from species association, but quantitative data is still needed to evaluate potential variation in abundance in between species.

The most obvious aberrant grains are those that are significantly smaller (mostly below 20 µm), darker in colour and have a thicker exine, no infrastructural characteristics and underdeveloped pore, triangle and rimula (Pl. 15, Figs. 24, 25). When found alone they might easily be mistaken for a separate species i.e. *Classopollis simplex* (see discussion therein). Due to their occurrence in tetrads of otherwise normal grains (Pl. 16, Figs. 3–7, 9–13), these grains can be identified as aberrant grains, however. Various coordinations with one to 4 four aberrant grains in one tetrad occur (Pl. 16, Figs. 3, 6, 20, 22–25), but often only remains thereof are encountered (Pl. 16, Figs. 13–17).

Sometimes *Classopollis* or related species like Geopollis are found in larger accumulations (Pl. 16, Figs. 29-30 and Pl. 17 Figs. 1-6). These clusters alone are not as such interpreted as aberrant, as they might have been deposited originally in the microsporangium and/or closer to the source and were thus not as likely separated by transportation. Usually, these clusters show grains of equal size and development, and even when clusters of aberrant looking grains are found (Pl. 16, Fig. 29 and Pl. 17, Fig. 12) these could also be immature grains. More rarely, grains in such clusters show variable sizes (Pl. 17, Fig. 4, arrow heads indicate smaller grains), which are therefore more comparable to the aberrant grains in tetrads.

It should be noted that aberrant grains are not always smaller and darker in colour. Sometimes significant size differences (ca. $^1/_3$ smaller than other grains in the tetrad or clusters) might indicate aberration however. Additionally, different types of preservation, i.e. more hyaline (Pl. 16, Figs. 2, 7, 18 arrow heads) could also indicate aberration, although this kind is harder to distinguish, and might sometimes simply be a taphonomic rather than a biological effect (e.g. in Pl. 17, Fig 9).

Lastly, some grains which are much more wrinkled and lack the distal pore, equatorial rimula and proximal triangle might also be considered as aberrant (compare Pl. 16, Fig. 26 with direct juxtaposition of normal on the right and aberrant on the left). These are mostly found in tetrads (Pl. 16, Figs. 27-28) and are interpreted as *Classopollis*, due to some transitionary forms found in clusters, with "normal" *Classopollis* grains (Pl. 16, Fig. 30).

Study of aberrant grains in different sections revealed that aberrant Classopollis occurs also outside of Bonenburg. Especially St. Audrey's Bay shows a variety, and even more kinds of aberrations (e.g. hyaline and wrinkled grains) (Pl. 16, images indicated with an "S"). Yet also in samples from Camin, Marnitz and Gr. Seeberg bei Gotha from Schulz (1967) aberrant Classopollis were encounted after only a few minutes of looking at the slides (Pl. 16, images indicated with an "O"). In Kuhjoch we also observed these aberrations (Pl. 16, Fig. 12). Although throurough abundance data on such occurrences is still lacking, the time it needs to encounter such finds suggests, that abundance of aberrant grains is highly variable.

Preliminary abundance data on the occurrence of aberrant *Classopollis* grains in the Bonenburg section (Text-Fig. 19 A) suggests, that abundance of *Classopollis* alone cannot explain potential variation in the frequency in which aberrant grains occur. Very interesting is some variation in the abundance of the different tetrad coordinations (Text-Fig.19 B). Tetrads that contain at least one aberrant grain compared to normal ones are more frequent in the Contorta Beds than in the Lowest Jurassic. Tetrads with three aberrant grains are the rarest coordination type based on preliminary counts. However, one sample in the middle of the Contorta Beds shows very high percentages of tetrads with three aberrant grains (Text-Fig. 19 B). More abundance data for aberrant grains in tetrads or as individual grains is needed to complement and interpret these preliminary observations.

Remarks: The history of this genus is a good example for the divide that language and regional separation can cause in taxonomic literature during the golden age of taxonomical literature during the 50–80s. Originally Malyavkina (1949) described the genera *Corollina* and *Circulina* from the Mesozoic. Unfortunately, her publication was illustrated rather poorly, and the generic diagnosis had to be collected by going through a classification key. Four years later, apparently unaware of this publication, Pflug (1953) described the genus *Classopollis* from the Lower Jurassic of Germany and subsequent literary discussion has agreed, that Malyavkina and Pflug describe an identical genus (Traverse 2004).

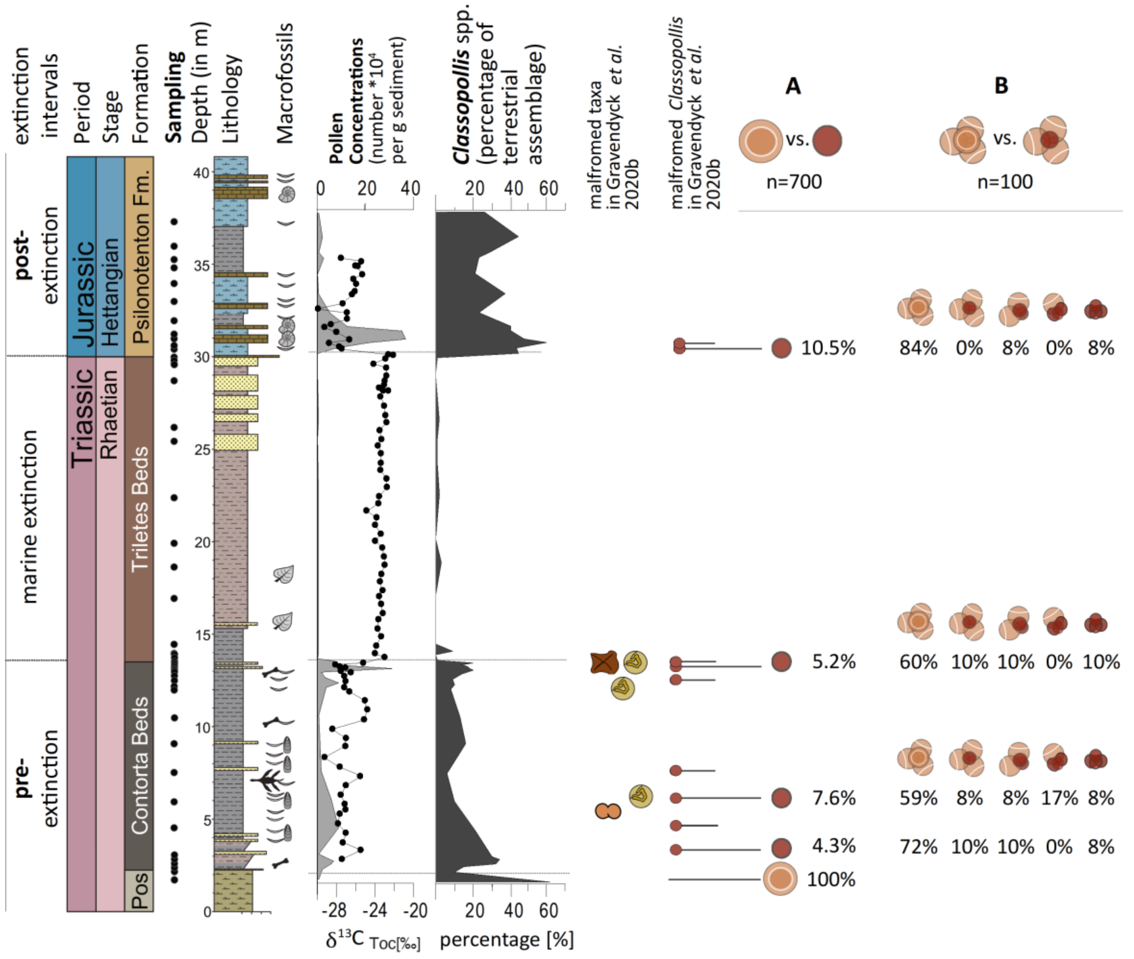


Fig. 19. Abundance of aberrant *Classopollis* grains and tetrads from selected Bonenburg samples. A. Relative abundance of normal sized *Classopollis* grains (dark yellow) in comparison to abnormally small grains (<20 μm) (dark red); all grains, i.e. single and in tetrads or remains thereof were counted alike. **B.** Relative abundance of normal versus tetrads with 1-4 malformed grains. Extinction phases after (Lindström et al. 2017b). Chronostratigraphy, isotopes, pollen concentrations and abundances from (Schobben et al. 2019; Gravendyck et al. 2020c). Previously recorded aberrant *Classopollis* occurrences were detected during standard palynological counting of 200 terrestrial palynomorphs.

In the years following these two diagnoses and elaborate discussion evolved. While *Corollina/Circulina* enjoys priority over *Classopollis*, many people regarded Malyavkina's illustration and diagnosis as inadequate and have therefore adapted Pflug's *Classopollis* (Traverse 2004). As a result, the latter has been widely adapted, especially in Cretaceous literature, while *Corollina/Circulina* was more widely used in Triassic and Jurassic literature (Cornet & Waanders 2006). Cornet and Waanders (2006) calculated that after 1975 the use of *Classopollis* became significantly more widespread, with an estimate of only 15% of publications still using *Corollina/Circulina* (2006). There is hardly a taxonomic work up to the end 1990s, that does not touch upon this discussion, with continuously contrary viewpoints (Traverse 2004). Traverse aimed to resolve the situation by *Classopollis* for conservation (Traverse 2004), which was accepted at the International Botanical Congress in Vienna in 2005 (Skog 2005). For a more detailed summary of the discourse see (Pocock & Jansonius 1961; Cornet & Traverse 1975; Traverse 2004).

Apart from the complication about the name for the genus, Pocock and Jansonius (1961) further complicated the argument by claiming that the standing of type for the genus depends on the potentially synonymy with *Pollenites reclusus* THIERGART 1949 and *Pollenites torosus* REISSINGER 1950. This is a problematic argument, because it is confusing the terms "name" and "type" (see chapter 4). Nevertheless, this seems to have been a more common misconception, as Mädler (1963) designates the holotype for *Pollenites reclusus* THIERGART 1949 as a new type for the genus, claiming it would have priority. Here it is important to differentiate, that names have priority, types are only the specimens that serve as specimens for this name. Unless one can show them to be taxonomically different, there is no need nor grounds to effectively designate a

Accordingly, Traverse (2004) clarified that the designated type for the genus remains the same irespective of whether earlier names are considered synonymous with the name *Classopollis classoides* and should be given priority or not. It however illustrates, that the potential synonymy of these names is problematic. Unfortunately, the preservation of the different holotypes is bad, which makes a final resolution of this problem impossible. For further discussion see information on the individual taxa below.

It should be noted, that the genus has a hardly comprehensibal and understandable number of species. At least 118 formally described species are registered on palynodata, many of which have none or few non-author citations. For example, alone for species names beginning with the letter "a" (n= 9), four of them (*C. albicintus*, *C. amplectiformis*, *C. anchowensis*, *C. assez*) have a citation rate of zero.

For the Rhatian Palynodata gives at last more than 20 different species that have been reported to occur at this time interval: *C. corniculatus* (CR=0), *C. corrodes* (CR=0.02), *C. declassis* (CR=0.1), *C. harrisii* (CR=0.26), *C. hausmanioides* (CR=0), *C. ituensis* (CR=0.7), *C. jingguensis* (CR=0), *C. jardinei* (CR= 0.3), *C. kieseri* (CR=0.2), *C. martinottii* (CR= 0.26), *C. muralis* (C=0.02), *C. monostriatus* (CR=0.13), *C. obidosensis* (CR=0.4), *C. pujoli* (CR=0.06), *C. quezeli* (CR=0.08), *C. rarus* (CR= 0.1), *C. rimula* (CR= 0.02), *C. striatus* (CR=0.12), *C. tristriatus* (CR=0.11), *C. visscherii* (CR=0). These values are all really low and might be still overestimations as the references were not checked for adequacy. The more commonly used, but potentially synonymous *C. classoides* (CR=11.4) and C. torosus (CR=8.1) are much more common. *C. reclusus* on the other hand has a very low citation rate, too (CR=0.3). The citation low citation rates for many of these taxa already indicate, that there might be many synonymous names. The following revision is a first attempt to untangle the sheer mass of names in the genus.

Table 7.3: Overview of (potential) synonymy of names for taxa believed to be conspecific with *Classopollis classoides*

basionym	Author	Non-Author citations of the epithet	CR	EI	Synonymous according to this study and:
Pollenites reclusus	Thiergart 1949	22	0.3	<0.1	Mädler (1963), Couper (1958); ? Pocock and Jansonius, 1961; ? Traverse, (2004)
Pollenites torosus	Reissinger 1950	569	8.1	0.5	Cornet & Traverse (1975); Couper (1958); Mädler (1963); Pocock and Jansonius (1961); Traverse (2004);
Classopollis classoides	**Pflug 1953**	**768**	**11.4**	**0.76**	Cornet & Traverse (1975); Couper (1958); Mädler (1963); Pocock and Jansonius, 1961; Traverse, (2004)
Classopollis declassis	Pflug 1953	7	0.1	<0.1	Couper (1958); Mädler (1963)
Classopollis rimula	Pflug 1953	2	0.02	<0.1	Couper (1958); Mädler (1963)
Circumpollis phariseaus	Pflug 1953	6	0.08	<0.1	Couper (1958); Mädler (1963)
Circumpollis philosophus	Pflug 1953	11	0.16	<0.1	Couper (1958); Mädler (1963)
Classopollis chateaunovi	Reyre 1970	14	0.28	<0.1	Lund (1977)
Classopollis kieseri	Reyre 1970	9	0.18	<0.1	Lund (1977)
Corollina murphy	Cornet & Traverse 1975	72	1.6	<0.1	Lund (1977)
Total		1480			

Classopollis classoides PFLUG 1953

Holotype: *Classopollis classoides* PFLUG 1953, Palaeontographica Abteilung B 95: 91, Pl. 16, Figs. 29–13

Synonymy: ≡ 1963 *Classopollenites classoides* BRICHE, DANZE-CORZIN, LAVEINE, p. 105

= 1953 *Classopollis declasses* PFLUG, p. 92, Pl. 16, Figs. 16–19

Diagnosis: ca. 30 µm. Figura breit bis schmal ellipsoidisch. Breiten–Längen–Index über 1. Porus meridional gestreckt. Cavernae und Rimulae verlaufen von Pol zu Pol. Sehr kräftige, ca. intrareticulate Exine (Pflug, 1953, p. 91).

Engl. Translation of the Diagnosis: Circa 30 µm. Figura broad to narrow elliptic. Latitude-longitude index higher than 1. Porus is stretched meridionally. Cavernae and rimulae run from pole to pole. Very solid, approximately intrareticulate exine.

Description: Specimens with sub-equatorial stria are assigned to this taxon. The number of striae varies from one specimen to the other even within one tetrad and is mostly between 6-10 (same number is indicated by (Cornet and Traverse, 1975). Above and below these striae specimen are ornamented with extremely small verrucae or microverrucae and microconi according to (Cornet and Traverse, 1975). These form a negative reticulum, which is best visible in specimen where the outer layer of the exine has detached from the rest of the pollen grain (Pl. 15, Fig. 30). It should be noted that we find the degree to which this characteristic is visible depend also on how well the specimen is incubated with the embedding medium. Having used the relatively fast drying Entellan®, this feature is especially visible in less well incubated specimens (in additional to the natural variability of this feature) (Pl. 15, Figs. 8, 14). Some specimen, although posessing the typical striae, do however have somesimtes a smoother exine (Pl. 15, Figs. 11, 29) with less distinct microverrucae. This makes distinction of these specimen harder when they lay in polar view position.

Remarks: While probably the youngest name for specimens of this form it is probably the most verifyable one in comparison to the names *Classopollis reclusus* (THIERGART 1949) MÄDLER 1963 and *Classopollis torosus* (DANZÉ-CORSIN & LAVEINE 1963) CORNET & TRAVERSE 1975 whose types are lost or uninformative to highly ambiguous (see additional discussion for the respective names below). Because there is no material that would help to support unambiguous application of these older names, it might be best to use only the verifiable *name Classopollis classoides* for the sake of taxonomic stability. Since this name is the most commonly used and most established name (EI=0.76) for taxa that are most likely all synonymous (see also discussion in Pocock and Jansonius, 1961; Traverse, 2004) this would also be the least disruptive approach. Since the name *Classopollis torosus* is also quite frequently used and quite well, although less, established (EI=0.5) in comparison to the competing names we will propose the name *Classopollis classoides* for conservation against the other competing names, especially *Classopollis torosus* which is threatening (comparing the name usage indices in Table 3).

It should be noted that there is a series of other potentially synonymous names (especially those described parallel with *Classopollis classoides.* The different positions of the grains can give particular impression of the palynomorphs which likely lead Pflug to describe these additional forms. In retrospect and considering the variation in preservation and position observable in the taxon however strongly suggests, that these are all conspecific forms which was already proposed by Couper (1958) and Mädler (1963) (Table 7.3). Later authors (Reyre 1970; Cornet & Traverse 1975) also erected new species, based on minute differences, that are very hard (to impossible) to comprehend based on reexamination of the illustrations of the respective holotypes. Accordingly, Lund (1977) synonymises them and we concur with this interpretation (Table 7.3).

Although the species *Classopollis classoides* seems to show some variation as to the thickness of the subrimulate striae and infrastructural ornamentation (from smooth to more infrapunctate to (pseudo)infrareticulate) we believe this to be part of the infraspecific variation, which is on top of that influenced by and only discernable in excellent preservation. Species splitting based on only infrastructural characters is therefore doubtful and rather impractical and has probably led to an over-separation of species which explains the currently incomprehensive mass of potentially synonymous names.

Classopollis meyeriana (KLAUS 1960) VENKATACHALA & GOCZAN 1964

Pl. 15, Figs. 1, 6; Pl. 17, Figs. 3, 7 and 13

Holotype: *Circulina meyeriana* KLAUS 1960, Geologisches Jahrbuch A, Sonderband 5: 165, Pl. 36, Fig. 58

Synonymy: ≡ 1964 *Corollina meyeriana* (KLAUS) VENKATACHALA & GOÇZÁN, p. 217, Pl. 3, Figs. 1–15.
≡ 1966 *Gliscopollis meyeriana* (KLAUS) VENKATACHALA, p. 93.

Diagnosis: Glatte bis undeutlich und fein infrapunktierte Form mit allgemein der Gattungsdiagnose entsprechenden Eigenschaften. Das proximale Dehiszenzdreieck hat gerade bis schwach konkav gebogene Seiten, deren Länge etwa $^2/_3$ bis $^1/_1$ des Sporenradius mißt. Die schmale Ringtenuitas liegt in Polansicht ziemlich nahe dem Äquatorumriß. Der Abstand beträgt etwa 4–5 µm bei mittelgroßen Körnern. Die Distaltenuitas besitzt eine ± unregelmäßige kreisförmige Kontur. Durchmesser etwa $^1/_2$ Sporenradius. Eine schwach polygonale Verformung kommt vor (Klaus, 1960, p. 165).

Engl. Translation of the Diagnosis: Smooth to indistinct and finely infrapunctate form with properties generally corresponding to the generic diagnosis. The proximal dehiscence triangle has straight to slightly concave sides, the length of which measures circa $^2/_3$ bis $^1/_1$ of the spore radius. The narrow ring-tenuitas lies fairly close to the outline of the equator in polar view. The distance measures about 4–5 µm for medium-sized grains. The distal tenuitas has an irregular circular contour. Diameter about $^1/_2$ of the spore radius. A weak polygonal deformation can occur.

Description: Specimens assignable to this taxon are characterised by their very smooth exine (Pl. 15 Fig. 6). Sometimes they look a bit more infrapunctate, which can be heightened by poor preservation (e.g. Pl. 16, Figs. 2–3, Pl. 17, Fig. 13).

Classopollis reclusus (THIERGART 1949) MÄDLER 1963

Pl. 15, Fig. 12

Lectotype (Mädler 1963): *Pollenites reclusus* THIERGART 1949, p. 11, Pl. 2, Fig. 16 (here refigured in Pl. 15, Fig. 12)

Preservation Lectotype: Out of the four syntypes that Thiergart described, Mädler (1963) luckily chose the very same specimen as lectotype, which is now the only remaining of Thiergart's syntypes. Unfortunately, the specimen is in such poor condition and without embedding, that it is utterly informative as to the details of the ornamentation. Species characteristics ambiguous due to this preservation.

Diagnosis: 33 µ. Die Gestalt ist ein ziemlich regelmäßiges Ovaloid, ein 5 µ breiter, wie mit Perlen besetzter Rand umgibt das ganze Pollenkorn. Diese Exinenstruktur fehlt auf einer von Pol zu Pol verlaufenden Falte, der charakteristischen Cycasfalte, die sich auch bei anderen Gymnospermen und später bei verschiedenen Monokotylenfamilien, Magnoliaceen u. a. in ähnlicher Ausbildung wiederfindet. Hier liegt jedenfalls ein Pollen aus der Cycadeen- oder Ginkgoverwandtschaft vor. Eine nähere systematische Bestimmung ist vorerst noch unmöglich (Thiergart, 1949, p. 11).

Engl. Translation: Size: 33 µm. The shape is a fairly regular oval, a 5 µm wide rim, as if ornamented with pearls, surrounds the whole pollen grain. This exine structure is missing on a fold running from pole to pole, the characteristic Cycas fold, which is also found in other gymnosperms and later is found in similar form in various monocot families, Magnoliacea and others. In any case, this is a pollen from the cycad or ginkgo affinity. A more detailed systematic determination is not yet possible.

Remarks: Given the poor preservation of the lectotype (and only remaining syntype) is further complicated by its position. In general, the polar view in which the specimen is lying, already obscures the particular expression of the ornamentation around the ring-furrow which is mostly used for distinction for different *Classopollis* species as most of the other features are the same. Although we consider the grain typical and compliant with other such grains assignable to *Classopollis classoides*, a final judgment is impossible, due to the unfavourable preservation and position. Due to this unresolvable ambiguity, we propose that the name should be limited to the lectotype. Since the name is hardly used and in comparison to the (potentially) competing names the least established name (EI=0.0005), this will not disrupt current taxonomic practice.

Classopollis simplex (Danze-Corsin & Laveine 1963) Cornet & Traverse 1975

Pl. 15, Figs. 24, 25

Holotype/Basionym: *Classopollenites simplex* Danze-Corsin & Laveine 1963, Microflore 13: 106, Pl. 11, Fig. 7 a and b

Diganosis: Grains de pollen de contour équatorial circulaire, en forme de gland en vue méridienne. Exine formée de deux couches: (1) intexine mince (environ 1 µ d'épaisseur), lisse, continue sur toute la surface du grain et portant du côté proximal une aire triangulaire équilatérale de 8 µ de côté et correspondant à la trace d 'accolement dans la tétrade; (2) ectexine formée de deux parties: un anneau équatorial continu large de 6 à 8 µ et portant une ou deux rangées de perforations internes plus ou moins régulières, inférieures à 0,5 µ de diamètre, une zone annulaire plus distale large de 5 à 6 µ et laissant libre un pore germinal de 10 à 15 µ de diamètre. Exine en dehors des perforations de l'anneau équatorial complètement lisse à infraponctuée. Teinte tirant sur le brun clair. Taille comprise entre 20 et 40 µ (Danzé-Corsin and Laveine, 1963, p. 106).

Remarks: It should be noted that Reyre (1970) designated "*Classopollis simplex*" based on a different type. it is thus a later homonym (Art. 53 *Code*) and since Reyre only referred to an illustration but did not indicate which specimen serves as holotype (Art. Art. 40. 1 and Art. 8.5 *Code*). Therefore, the designation was not validly published and remains a designation only.

The holotype for the earlier validly published name *Classopollis simplex* is rather small, but still shows the typical, although reduced infrastructure compared to other 'normal' *Classopollis classoides* specimens for example. Nevertheless, we concur with Cornet and Traverse (1975) who remark that *Classopollis simplex* is not a natural species as it was found as anomalous grains in tetrads of both *Classopollis meyeriana* and *Classopollis torosus*. It is also noteworty, that Reissinger (1950), when erecting *Classopollis torosus*, already depicted an aberrant tetrad of an "unknown species" (Reissinger 1950, Pl. 14, Fig. 17) that occurs coeval with the new taxon and which complies with the underdeveloped grains which could be called *Classopollis simplex*. Cornet and Traverse (1975) point out that *Classopollis simplex* grades into forms of *Classopollis meyeriana* with a slightly thickened equatorial band, as well as into small compact forms of *Classopollis torosus*. They also point out however, that this does not preclude use of the concept of *Classopollis simplex* (Cornet & Traverse 1975). This is nomenclaturally correct, but we suggest that the name should be limited to the type, and grains complying with this taxon should be referred to as aberrant grains in order to not overlook their ecological and biological significance.

Classopollis torosus (REISSINGER 1950) COUPER 1958

Holotype: *Pollenites torosus* REISSINGER 1950, Palaeontographica Abteilung B 90: 115, Pl. 14, Fig. 10–15, 18–28

Preservation of the holotype: Lost already at the time of its description as Reissinger explains himself.

Diagnosis: Hiervon abweichend, mit auffallenden Wülsten versehen (Reissinger, 1950, p. 115).

Engl. Translation: Distinguished from these forms [acorn shaped pollen that regularly occur in tetrads] by their conspicuous thickenings.

Remarks: Traverse (2004) objects, that the name torosus was not validly published lacking a species diagnosis. In fact, the description that Reissinger (1950) provides is very short and not very helpful, but technically it suffices the minimum demands for these criteria (Turland, personal communication in 2019). Thus, the name has to be considered validly published. Since this new species can never be unambiguously synonymised or separated from *Classopollis reclusus* and *Classopollis classoides* (see also discussion in Pocock and Jansonius, 1961; Traverse, 2004), because of lost and ambiguous types, we propose that the name *Pollenites torosus*, and all subsequent recombinations thereof should be limited to the holotype. Note that we studied the holotypes and conducted this revision after Gravendyck et al. (2020b) where *Classopollis torosus* is still used. In all future studies this new recommendation to not use *Classopollis reclusus* or *Classopollis torosus* will be followed.

Geopollis BRENNER 1986

Type: *Corollina zwolinskai* LUND 1977, Geological Survey of Denmark II 109: 70, Pl. 7, Fig. 5; Single Grain slide R 1930 SG 20

Diagnosis: Fossile Pollenkörner kugeliger Gestalt. An den Polen Exinenverdünnungen, am proximalen Pol in Form eines hellen Dreiecks, am distalen Pol in Form eines hellen Kreises. Parallel zum Äquator verlaufen zwei Ringfurchen (Brenner, 1986, p. 158).

Engl. Translation: Fossil pollen grains of spherical shape. Exine thinnings at the poles, at the proximal pole in the form of a hyaline triangle, at the distal pole in the form of a hyaline circle. Two ring furrows run parallel to the equator.

Botanical affinity: Gymnosperms – Cheirolepidiaceae (Mander et al. 2013).

Remarks: Morbey (1975) already depicts two specimens with additional ring furrows, but does not specifically discuss it and simply includes them in *Classopollis meyeriana*. Lund (1977) already recognises the crucial difference of two ring-furrows, but hesitates to designate a new genus as this potential new genus might be a junior synonym of *Corollina*. This is owed to the unclear situation as to the two genera *Corollina* and *Classopollis*, as discussed above. Similarly, Schuurman (1977) presents a form characterised primarily by the presence of two subequatorial circular furrows. He already notices, that this feature does not match the diagnosis of *Corollina/Classopollis*, but regards it "provisionally" as an extraordinary development of the sexine of pollen grains still to be compared to *Corollina*. Brenner (1986) than remedies that situation, designating *Corollina zwolinskae* as the holotype.

Distinction: Like *Granuloperculatipollis* and *Classopollis*, *Geopollis* possesses exine thinnings: distally in the shape of a circle, proximally in shape of a triangle. But the three genera can be distinguished by means of the sub-equatorial ring-furrow (rimula) which is often absent or not clearly developed in *Granuloperculatipollis*. *Classopollis* possesses one rimula distal of the equator, while *Geopollis* possesses two, one proximal and one distal rimula. In equatorial view this distinction is very apparent, in polar view Geopollis can be distinguished as the rimulae cross in two places, while the rimula of *Classopollis* simply shines through as a circle.

Geopollis zwolinskae (LUND 1977) BRENNER 1986

Pl. 15, Figs. 18–22

Holotype/Basionym: *Corollina zwolinskai* LUND 1977, Geological Survey of Denmark II 109: 70, Pl. 7, Fig. 5; Single Grain slide R 1930 SG 20

Other records:	1972	*Circulina* sp. nov. Fisher, p. 105, Pl. 8, Fig. 22.
	1975	*Gliscopollis meyeriana* (KLAUS 1960) VENKATACHALA & GOCZAN 1966 in Morbey, p. 38, Pl. 12, Fig. 10
	1977	*Corollina* sp. SCHUURMAN, p. 215, Pl. 22, Fig. 8.

Engl. Translation Diagnosis: A species with 2 subequatorial ring furrow (rimulae) one distal and one proximal from the equator (Lund, 1977, p. 70).

Description/Distinction: The specimens measure between 29–34 µm in diameter. Without close inspection, the specimens can be easily mistaken for *Classopollis meyeriana* because of their smooth exine (compare Pl. 18. Figs. 18–20). On closer inspection the two rimulae are visible. This is easiest perceivable in equatorial view (Pl. 18, Fig. 18) or when the specimen is slightly tilted (Pl. 18, Figs. 19–21). In this tilted view the two rimulae seem two cross each other (Pl. 18, Figs. 19–

20, arrow heads), which can only happen when there is more than one as in this taxon. When seen in polar view (Pl. 18, Fig. 22) they are the hardest to distinguish from *Classopollis meyeriana*, yet change of focal plane or fluorescence light helps to identify the two rimulae.

Granuloperculatipollis VENKATACHALA & GÓCZÁN 1964

Type: *Granuloperculatipollis rudis* VENKATACHALA & GÓCZÁN 1964, Acta Geologica 8:219, Pl. 3, Figs. 22–26

Diagnosis: Operculate, porate, granulose pollen grains; Y scar hardly perceptible. Outline circular; operculum and pore clearly delineated but its outline generally obscured by the ornamentation; exine granulose (Venkatachala and Góczán, 1964, p. 219).

Botanical affinity: Gymnosperms – Cheirolepidiaceae. Schulz (1967) and see *Classopollis*.

Remarks: *Granuloperculatipollis*, although often not depicting a rimula, still belongs to the former Circumpollis group, which is now included in the Zono-annulicolpates. Although Venkatachala and Góczán do not incorporate it in their diagnosis, they clarify in the distinction of other genera that the other circumpolles have a more distinct ring tenuitas, but that Granuloperculatipollis has a "weakly demarcated tenuitas". Orbell (1973) also stressed, that the rimula of *Granuloperculatipollis rudis* is very weakly developed in most specimens from the British Upper Triassic but can be entirely absent. The occurrences of tetrads, with some grains depicting a rimula, while others do not, renders the lack of a rimula not an excluding criterion for *Granuloperculatipollis* being part of the Circumpolles. Morbey (1975) consequently adjusted the species diagnosis accordingly to include this feature (see below).

Granuloperculatipollis rudis VENKATACHALA & GOCZAN 1964 emend. MORBEY 1975

Pl. 15, Figs. 16, 17 and Pl. 16, Fig. 1

Holotype: *Granuloperculatipollis rudis* VENKATACHALA & GÓCZÁN 1964, Acta Geologica 8:219, Pl. 3, Figs. 22–26

Diagnosis: Circular pollen grains, 35–40 µ. Y-mark or triangular scar hardly perceptible. Operculum and pore present but not clearly seen. Exine granulose, grana ± 2 µ, unevenly distributed (Venkatachala & Góczán 1964, p. 219 in Jansonius and Hills 1976).

Emended Diagnosis: Pollen monoporate. Exine two-layered. Intexine laevigate, exoexine laevigate, punctate, occasionally columellate, intexine closely appressed to exoexine. Characterised by an ornamentation of random, sparsely or densely distributed pila, gemmae, occasionally grana or coni, 1–2 µ. in height, upto ca. 1 µ in diameter. An annular distally sub-equatorial tenuitas is developed, often reflected in polar compressions by crescentic or annular polygonal folds. Occasionally, the exine is thickened equatorially to form a distinct girdle separated from the distal operculum by the tenuitas. Distal pore, where evident, ca. 4–9 µ in diameter. Proximally, a triangular area of exoexinal thinning is developed, ca. 4–8 µ across, through which an intexinal trilete mark may be visible. Suturae simple, short straight or sinuous. Specimens commonly in tetrads (Morbey, 1975, p. 35).

Description: Our specimens are ornamented with irregularly arranged small grana. The rimula is only faintly developed but variably distinct (compare Pl. 15, Figs. 16 and 17). Sometimes occurring in tetrads (Pl. 15, Fig. 1).

Rhaetipollis SCHULZ 1967

Type: *Rhaetipollis germanicus* SCHULZ 1967, Paläontologische Abhandlungen, Abteilung B, 2: 605–606, Pl. 12, Figs. 10 - 12, Möckern 1E, 10184/1 (!, refigured here in Pl. 18, Figs. 24 and 29)

Diagnosis: Inaperturater Pollen, equatorial von zonaler Ringfurche umgeben, die den Pollen in zwei bilateral symmetrische Hemisphären teilt. Die Polkappen werden jeweils durch eine zweite, weniger deutliche Ringfurche vom Zentralteil des Pollens getrennt. Innenwand der Exine mit Warzen besetzt (Schulz, 1967, pp. 605).

Engl. Translation: Inaperturate pollen, with an equatorial ring-furrow, which separates the pollen in two bilateral-symmetric hemispheres. The polar caps are separated from the central part of the pollen by a second, less distinct ring-furrow. Inner wall of the exine covered with warts.

Botanical affinity: unknown.

Remarks: Still a monotypic genus with strong stratigraphic significance.

Rhaetipollis germanicus SCHULZ 1967 ***emend***.

Pl. 18, Figs. 1–29

Holotype: *Rhaetipollis germanicus* SCHULZ 1967, Paläontologische Abhandlungen, Abteilung B, 2: 605–606, Pl. 12, Figs. 10 - 12, Möckern 1E, 10184/1 X11373 BGR-S (!, refigured here, visible from side A);

Preservation of the Holotype: The holotype (Pl. 18, Figs. 24, 29) is available, but only partially embedded, which obscures the outline partially. Only one side of the heteropolar specimen is visible. To depict the other side and epitype is designated here.

Epitype: *Rhaetipollis germanicus* SCHULZ 1967, Möckern 1E_S4, Q46/3 (side B), here designated, figured here in Pl. 14, Fig. 3 (here designated)

Diagnosis: Größe 35 - 40 µm (Holotypus 40 µm). Die Kontur ist oval bis rundlich, der Pollen wird equatorial von kräftiger, zonaler Ringfurche umgeben, die den Pollen deutlich in zwei bilateral symmetrische Hemisphären teilt. Die Ringfurche reißt oft auf. Die distale und proximale Polkalotte werden vom Zentralteil des Pollen durch je eine weitere Ringfurche abgegrenzt. Exine bis 4 µm dick, auf der Innenseite mit bis 6 µm breiten, unregelmäßigen Warzen mehr oder weniger dicht besetzt (Schulz, 1967, pp. 605–606).

Engl. Translation: Size 35 - 40 µm (Holotype 40 µm). The equatorial outline is oval to round. Equatorially, the pollen surrounded by a strong, zonal ring-furrow which separates the pollen in two bilateral-symmetric hemispheres. The ring-furrow breaks open. The distal and proximal polar caps are separated from the central part of the pollen by a second, less distinct ring-furrow. Exine up to 4 µm dick, on the inner side with up to 6 µm wide, irregular warts, more or less closely distributed warts.

Emended Diagnosis: Outline in presumed polar view elliptical. Nexine thin. Sexine distinctly two-layered. Inner sexine verrucate in presumed proximal and equatorial regions. Verrucae of varied basal diameter and height, often irregularly shaped and coalescent. Outer sexine thick, smooth and without distinct infrastructure. Outer sexine developed as two identical differentiations separated from one another by a central circular or semicircular meridional furrow of varying width. In the case of a semicircular furrow the connection between the differentiations is positioned in the presumed proximal face. Parallel to the central furrow each sexinal differentiation shows a relatively narrow semicircular furrow running from the presumed proximal face into the disto-equatorial region (Schuurman, 1977, p. 217).

Description: In general, it is very difficult to clearly identify proximal, distal and equatorial versus polar view, because it is neither clear what and where the aperture is (or whether it has one) nor what the specimen is. It could be a pollen, but the extremely strong fluorescence (more similar, but still less bright in comparison to specimens of *Tasmanites* than to other pollen like *Classopollis* show) could suggest an aquatic original as well. Superficially the specimens resemble a macaron, with two hemispheres often occurring isolated as well (Pl. 18, Fig. 10). Such a hemisphere consists of a thick oval ring and a central cap, that is merged with the ring on one side (Pl. 18, Fig. 10). The exine is rather thick (ca. 3.5 µm) and smooth. The two hemispheres enclose an aggregation of large verrucae that appear to be “inside” of the two hemispheres (Pl. 18, Fig.2). If one imagines a macaron laying on the table with its flat side, one has one side directed at the viewer (here called side “A”) and one directed away (side “B”) which are not identical. Using and transferring this analogy to the specimens in question we observe that the two hemispheres are gaping on one side (side “A”) (Text-Fig. 20). The two hemispheres are ca. 3.6–5.4 µm apart. On the other side (side “B”) the two hemispheres are (almost) merged. The way they merge appears to be variable

(Text-Fig. 20). The two rings from each hemisphere can be connected through a perpendicular bridge (Pl. 18, Fig. 3), they can merge in an X-shape (Pl. 18, Figs. 4a and 4b), or they can run closely parallel and touching each other (Pl. 14, Fig. 9) (schematic overview in Text-Fig. 20). Some specimens show that the two hemispheres open on the gaping side with this merged part functioning like the hinge in bivalves (e.g. Pl. 18, Figs. 7, 9, 12).

The entire specimens measure typically between 35–50 µm long. Some forms that are interpreted to be aberrant can be much smaller (25–35 µm) (Pl. 18, Figs. 25–28). These specimens have a less developed circular furrow between the two hemispheres and the verrucae are hardly visible/developed. Apart from this aberration in size and furrow development, we also observed specimens with three instead of two hemispheres (Pl. 18, Figs. 20, 21), and specimen with an aberrant furrow, which is not circular anymore, but windy and underdeveloped (Pl. 18, Figs. 22, 23). Its noteworthy that this was not only observed from specimen in Bonenburg but also in Kuhjoch (Pl. 24, Fig. 22).

Colour variation complies with that of many other taxa. Poorly preserved hyline forms or typically yellow specimen are found in the Contorta Beds and throughout the grey layer the colour is increasing in darkness (Text-Fig. 17). In the Triletes Beds specimen of varying colour can occur in one sample (Text-Fig. 17, D-18). The comparative Kuhjoch sample, has specimen of moderate yellow to light brown (Text-Fig. 17).

Remarks: It is very difficult to describe the specimen with official terminology, because many of the terms imply a certain biological origin. Additionally, it is hard to determine, proximal and distal face and aperture. Schuurman (1977), already provided an emended diagnosis, reinterpreting and adjusting some terms in respect to the orientation of the specimen (e.g. "meridional ring-furrow" instead of a "equatorial ring-furrow" (Schulz 1967)). Schuurman (1977) also pointed out the merging of the two hemispheres and illustrated the x-type and parallel merging, but not yet the perpendicular bridge.

Until further ultrastructural studies can provide a better insight into the anatomy and botanical affinity, we propose a more neutral description (see emendation below).

It is noteworthy, that Schulz captured only details visible from one side (side A) because of the position of the holotype, but omitted details from the other side, where the two hemispheres merge. We observed three types of merging: parallel, with a perpendicular bridge, and in an X-bridge (Text-Fig. 20). Depending on the reproductive mechanism, it is possible that they represent either ontogenetic developmental stages of successive merging, or in fact three different (sub?) species.

Clear description of the taxon is crucial not only to distinguish it from others, but also to define what should be included in normal as opposed to not normal. As teratology evolves as a potential proxy or marker for environmental disturbance (see Gravendyck et al., 2020b) such distinction might become just as important as taxonomic distinction for subsequent applications. To add information from all sides of the specimens and from the above made observations, we also determine an epitype (figured in Pl. 18., Fig. 3) from Schulz's original material, to cover aspects and perspectives that the holotype cannot. We propose the following emended diagnosis to integrate the previous diagnoses and our new observations.

Description *emend.*: Size 35–50 µm (Holotype 40 µm). The equatorial outline is oval. Sexine distinctly two-layered. Inner sexine verrucate; verrucae of varied diameter and height, often irregularly shaped and coalescent. Outer sexine thick, smooth and without distinct infrastructure. The taxon consists of two identical hemispheres that seem to enclose these verrucae. Each hemisphere consists of a ring and a central cap, that is merged with the ring on one side. On the side where the inner caps attach to the ring, the hemispheres are also merged with each other. Except for the area where the two hemispheres are merged, the hemispheres are gaping, creating a circular furrow of varying width through which the verrucae are visible. The two hemispheres can open like a bivalve and thus gape widely, facilitated through the hinge-like merging of the hemispheres.

Distinction: Although the ring-furrow can be reminiscent of the rimula in Circumpolles, it does not enclose the entire grain like in the Circumpolles, because of the hinge-like merging of the two hemispheres. A comparable triangle or pore on either side of the rimula as in *Classopollis* for example is also not present.

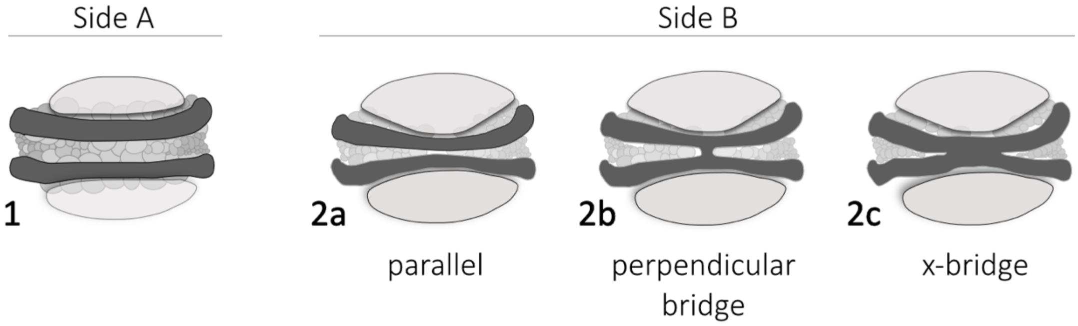


Fig. 7.20. Overview of "hinge" types in *Rhaetipollis germanicus.*

Turma MONOPORATES BURGER 1994

Perinopollenites Couper 1958

Type: *Perinopollenites elatoides* COUPER 1958, Palaeontographica, Abteilung B, 103: 152, Pl. 27, Fig. 9; slide C2/6, specimen K956, 34.5, 108.

Preservation of the Type: see description in *Perinopollenites elatoides*

Diagnosis: Monoporate, but pore not always clearly shown; grains originally more or less spherical, folding readily; exine consisting of two distinct layers: the outer loosely fitting (Couper, 1958, p. 152).

Emended Diagnosis: Miospores monoporate, pore not always clearly seen, spherical; body circular, enveloped by a loose fitting cover or perinosaccus. Body exine and perinosaccus surface structured or sculptured (Jain & Sah, 1969 in Jansonius and Hills, 1976, card 1954).

Botanical affinity: Gymnosperms – Cupressaceae. Pollen complying with this taxon were found *in situ* in a number of species of *Elatides*, *Masculostrobus*, *Stenomischus* (Jurassic to Createcous from around the world), all assigned to the Taxodiaceae, i.e. today the Cupressaceae that include that former family (Balme, 1995 and citations therein).

Perinopollenites elatoides COUPER 1958

Chapter 3, Fig. 8.16

Holotype: *Perinopollenites elatoides* COUPER 1958, Palaeontographica, Abteilung B, 103: 152, Pl. 27, Fig.9; slide C2/6, specimen K956, 34.5, 108.

Preservation of the Type: Although the slide that is supposed to hold the holotype is available, the holotype could not be relocated yet.

Synonymy:		
	? 1958	*Equisetosporites* NILSSON, pp. 66–67, Pl. 5 Fig. 20
	= 1964	*Ballosporites hians* MÄDLER, p. 179, Pl. 2 Figs. 6–10 (!)

Diagnosis: Monoporate, but pore not always clearly shown; grains originally spherical but fold readily; exine consisting of two distinct layers: the outer is scabrate and very thin (less than 0.5 µm) loosely fitting and wrinkles and tears easily, the inner is around 0.75 µm to 1 µm thick, smooth to finely scab rate (Couper, 1958, p. 152).

Description: Our specimen is a bit compressed and measures in that shape 50 x 33 µm including the outer coat and fits the size range (30–54 µm) given by Couper (1958). The distinctive characteristics, i.e. the two distinct exine layers and the pore are clearly visible.

Remarks: Mädler (1964) describes this genus newly as *Ballosporites*. In the comment to this description he remarks his surprise that no one else has described this pollen yet, but considers the resemblance to phytoplankton as a potential explanation. After examining his holo- and paratypes, this study however confirms, that his specimens depict the two distinct layers and some even the typical pore and thus comply with the genus diagnosis of Couper (1958) and are thus synonymous.

4. Discussion

Aside the palynotaxonomic work of assembling diagnoses, reevaluating type material, revising descriptions and comparing with new material, we made important observations on three main topics: (1) teratology, (2) colour alteration, (3) “lost” or “destroyed” type material. In the following we will discuss the implications of these qualitative findings and propose solutions to encountered problems and possibilities for future studies.

4.1. Teratology

Currently teratological studies are on the rise in palynological studies to get a deeper insight into potential environmental changes or mutagenic effects (Visscher et al. 2004; Foster & Afonin 2005; Prevec et al. 2010; Hochuli et al. 2017; Barth et al. 2018; Benca et al. 2018; Lindström et al. 2019; Marshall et al. 2020). Thus, to evaluate teratology, the understanding of taxonomy and intraspecific variation is key, because this is the baseline against which, non-normal, i.e. aberrant/malformed forms, can be compared to. However, taxonomy and intraspecific variation is often hard enough to evaluate on its own. A good understanding of the morphology of a taxon and up-to-date and well-circumscribed diagnoses are therefore important to support this evolving field of study in order to be able to evaluate where to draw the line between normal and non-normal, as this affects all subsequent analyses and interpretations that are not only used to evaluate past crises, but also to predict future processes of environmental change in the alleged sixth mass extinction.

Malformations are so far known from a variety of taxonomic palynomorph groups, terrestrial and aquatic alike, and from different time intervals. However, certain groups are reported to be affected more at some time intervals than others.

Aberrant spores for example come in several forms. (1) Increased occurrence in tetrads of lycophytic spores presumably caused by malfunction of the post-meiotic separation, is known from the Devonian–Carboniferous boundary (Marshall et al. 2020) and the latest Permian

(Visscher et al. 2004; Looy et al. 2005; Hochuli et al. 2017). In Bonenburg we did observe tetrads of *Uveasporites, Lycopodiacidites* and *Kraeuselisporites* as well (Gravendyck et al. 2020c), but it is difficult to say what drive such occurrences, because these forms were found already in the Contorta Beds and also at times where no malformations occur in other taxa. (2) Change of the outline from triangular to square or unequal triangles, as well as additional appendices and alterations of the trilete mark ,are known from laevigate deltoid spores from the Triassic-Jurassic transition (Barth et al. 2018; Lindström et al. 2019). Such forms could be observed in Bonenburg as well, but were very rare. Instead, we observed an additional variant of spore malformation, i.e. (3) the alteration of the outline as square or hybrid morphologies and ornamentation of different spore types (*Perinosporites* and *Cornutisporites*) was documented for the first time. Nevertheless, such spore malformation did not appear as such a prominent feature as malformations in pollen.

Aberrant bisaccates which show alterations in the number and arrangement of sacci have been reported from the latest Permian (Foster & Afonin 2005; Prevec et al. 2010; Hochuli et al. 2017; Mishra et al. 2018), from the Norian (Baranyi et al. 2018), from the Triassic-Jurassic boundary (van de Schootbrugge & Wignall 2016; Gravendyck et al. 2020c), the Jurassic (Vishnu-Mittre 1956), and the Pliocene (Leschik 1952). Such forms were extremely rare in Bonenburg compared to previous reports and diversity of such forms from the latest Permian and Norian (Gravendyck et al. 2020c).

The most prominent aberrations were observed in non-saccate pollen (*Classopollis* and *Ricciisporites*), i.e. in rimulate or sulcate pollen that show malformations expressed in the absence of typical features (pseudopore, triangle, rimula), reduced size, and thicker pollen walls found in isolation (Pl. 15, Figs. 24, 25). Due to the occurrence within tetrads, i.e. the direct result of meiosis, such forms can now be identified as malformed specimen of various *Classopollis*, and probably even *Geopollis* taxa (e.g. Pl. 16, Figs. 3, 5, 6, 9). Reports of *Classopollis* tetrads with one to four aberrant pollen grains (compare chapter 3, Fig. 13) have been reported from the post-extinction interval in the Hettangian (Kürschner et al. 2013). This thesis is also the first study to document tetrads with uneven sized grains as early as the latest Rhaetian, and in addition to occurrences in Bonenburg, we also documented aberrant *Classopollis* tetrads in the GSSP section Kuhjoch, St. Audrey's Bay, and at the sites in Camin, Seeberg bei Gotha, Möckern, and Marnitz from Schulz' original material, which suggests that malformations did not only occur within a local population, i.e. as the result of a mutation in one gene pool, but that the genus at large was affected by a supra-regional, probably environmental, process.

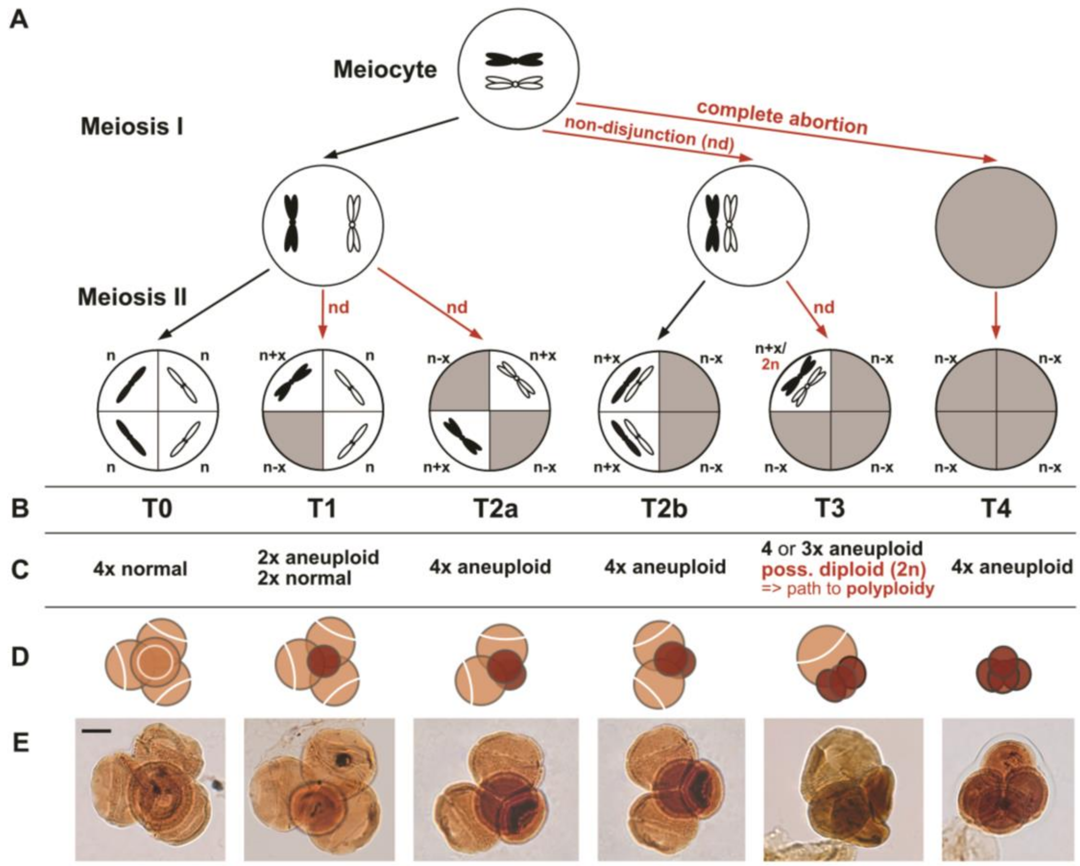


Fig. 21 Malfunction in microsporogenesis and resulting tetrad classes. A. Principles of microsporogenesis with simultaneous cytokinesis. Red arrows indicate malfunction in non-disjunction (nd) during meiosis or overall abortion. Assuming like Berdnikov et al. (2002) that nullisomy for a chromosome causes malformation and disomy is tolerable leads to different tetrad classes (B) with malformed grains indicated in grey. **B.** Resulting tetrad classes with one (T1), two (T2) three (T3) or four (T4) malformed grains. **C.** Genetic implication of resulting pollen from different tetrad classes. **D.** Schematic correspondents of tetrad classes found in *Classopollis* from Bonenburg (Germany). **E.** Photomicrographs of correspondents in *Classopollis* from chapter 3. A and B altered after Berdnikov et al. (2002). Scale bar = 10 µm.

In extant pollen different failures in meiosis produce tetrads with malformed grains (Berdnikov et al. 2002). Depending when what and how often things go wrong, results in different tetrads classes (T1-T4) with one to four malformed pollen grains as opposed to the normally produced tetrad (T0) (Text-Fig. 21. A, B). The tetrad classes then allow deduction on what the genetic set-up of the resulting pollen must be (Text-Fig. 21. A last row). Loss or gain of bivalents or whole chromosomes leads to aneuploid or even diploid pollen (Text-Fig. 21. C). Although not always leading to viable offspring, plants are known to be much more tolerant to ploidy variation than animals (Griffiths et al. 2015). This is particularly noteworthy as diploid pollen is the precondition for polyploidiisation events (Text-Fig. 21. C).

Kürschner and coworkers (2013) already suggested that unreduced pollen in *Classopollis* might provide evidence for potential polyploidy in the mother plant. They showed that grains from a pollen assemblage in North-America showed the same tetrad coordinations we observed in Bonenburg, and studied the assemblage for grains that are generally bigger and could represent diploid grains, if one assumes pollen size to correlate with ploidy level (Gould 1957; Pichot & El Maâtaoui 2000; De Storme et al. 2013; Marinho et al. 2014). In Bonenburg, we did observe the different tetrad coordinations by Kürschner and coworkers (2013), but not the abnormally large pollen grains with comparable sizes.

Given that our samples are predating the end-Triassic mass extinction and those post-extinction occurrences documented by Kürschner and coworkers (2013), we might be looking at the evolution of the potential polyploidisation event inferred in their study. If such mutation and potential polyploidiisation poses an advantage that might have helped the mother plant survive the end-Triassic biotic crisis, however, why one of the two lineages in which we observed these aberrant tetrads thrives after the TJ–transition (*Classopollis*) while the other one (*Ricciisporites*) goes extinct remains unknown.

Of course, mutations are random and could have thus produced a favourable result in one lineage and not in the other, or even have been detrimental in the second. One should also keep in mind that the cost of disadvantageous mutations is higher in slowly maturing, long-lived species, and more likely to cause their extinction than in small, rather herbaceous species, with short lifecycles and lesser offspring, because a single mutation in its haploid generation affects a larger percentage of its offspring (Bromham 2009). On top of that, wind pollinated species which produce larger quantities of pollen (as assumed for the Cheirolepidiaceae) than insect pollinated species, will likely tolerate higher mutation rates, as they are not necessarily result in offspring anyway. For *Ricciisporites*, very little is known about the parent plant, but the large, heavy tetrads with prominent projections are probably not following the same pollination strategy as the Cheirolepidiaceae. Depending on the longevity, age of maturity, and pollination mechanism, a mutation might have had a higher cost and likely deleterious outcome and fostered their extinction.

In this context it is also very interesting to consider the different tetrad coordinations. Tetrad class T3 is the most significant one, because this class potentially produces diploid pollen (Text-Fig. 10.1), which can, if fertilising an unreduced diploid female gametohypte, produce a tetraploid offspring. While all other tetrad classes need failure in meiosis in only one of the divisionary steps, this tetrad class needs two successive failures and is statistically rare (see also

Berdnikov et al., 2002). The occurrence of such tetrads shows that at least one of the preconditions for a polyploidiisation event is fulfilled. Since these occur prior to the TJ-transition and on top rather abundantly in one point in time where there is additional evidence for increased level of environmental stress, this could hypothetically be the time when potential polyploid Cheirolepidiaceae might have evolved. The fact that we did not find such tetrads in *Ricciisporites* might show that such an occurrence might not have occurred in its mother plant. With increasing environmental stress and mutation rates, the lineage might well have accumulated deleterious mutation that could have fostered its demise in the long-run after the TJ-transition.

The Cheirolepidiaceae on the other hand, would illustrate the opposite fate. If we assumed that environmental mutagenesis might have caused failures in meiosis, and also provided a selection process that permitted fixation of advantageuous mutations in the gene pool, then the end-Triassic biotic crisis might have fostered the necessary conditions for a polyploidiisation event in the Cheirolepidiaceae as speculated by Kürschner and coworkers (2013). Our results provide additional evidence “from the other side” of the boundary to support such interpretation, but further quantitative data on variation in abundance of malformed grains and tetrads leading up to the boundary is needed to further support these inferences. Due to continous occurrence of *Classopollis* and its frequent occurrence in tetrads, they represent an ideal study object to understand the paleogenetic history of this extinct plant lineage and its Mesozoic success story.

4.2. The Dark Zone

In many taxa discussed above, we highlighted the variation and change in colour and documented a successive darkening from the Contorta to the Triletes Beds (Text-Figs. 10, 11 and 15, 16). Since this is not an isolated phenomenon in this taxon, but observable throughout the assemblage, Van de Schootbrugge et al. (2009) called this the “dark zone”. Although this is supported by colour alteration in Bonenburg as well, it is not trivial to evaluate the intensity of “darkening” and abundance of “darkened” material. Interestingly, some taxa (especially *Polypodiisporites polymicroforatus*, *Ovalipollis pseudoalatus*, *Rhaetipollis germanicus*, *Ricciisporites tuberculatus*, *Classopollis* spp. and bisaccates) show strong variation in colour even within individual samples, whereas several others, especially the spore taxa with occurrence limited to the Triletes Beds do not. These spore taxa appear increasingly dark in our detailed sampling from the Contorta to the Triletes Beds. It is noteworthy that specimen from the black Contorta Beds are all still light brown or yellow in colour, in contrast to their very dark forms in the reddish Triletes Beds. Specimens from the grey layer in between them connect these two extremes and show increasing darkening from sample to sample, supporting the argument of gradational environmental change made in Gravendyck et al. (2020b)

Such dark occurrences are known from several localities in the Germanic Basin: Eitzendorf-8 core, Örrel-1, Braudel-1 (Lund 1977), and Hebelmeer-2 core (Blumenberg et al. 2016) from Germany, the Rødby-1 core in Denmark (Lund, 1977) and the Kamieñ Pomorski IG-1 borehole in Poland (Pieńkowski 2004; Pieńkowski & Waksmundzka 2009) and due to their basin wide distribution, have been suggested for stratigraphic purposes (Lund 2003; Lindström & Erlström 2006). It is noteworthy that most studies generalise the darkened occurrences as simply "redbrown", "darkbrown" or simply "dark" (Lund 1977, 2003; Lindström & Erlström 2006; van de Schootbrugge et al. 2009; Blumenberg et al. 2016). Pieńkowski et al. (2012) work with colour categories (dark yellow, yellow orange, orange, orange brown), but do not differentiate colours within one sample as they have documented in their previous study, where they showed coeval occurrence of differently coloured specimens of the same taxon (deltoid spores and the bisaccate *Vitreisporites* within a single sample from the the Kamieñ Pomorski IG-1 borehole (Pieńkowski 2004; Pieńkowski & Waksmundzka 2009).

Variation of colour in palynomorphs of the same age is normally interpreted as variation in thermal maturation, which can be classified using a variety of indices, e.g. the TAI (Thermal Alteration Index, Staplin, 1969) or the PDI (Palynomorph Darkness Index, Goodhue and Clayton, 2010) for the evaluation in source rocks. These indices already address the problem of how to objectively evaluate colour alteration. Given our above documented colour variation not only within one taxon but also in between taxa, it is especially important to look at colour alteration within a taxon and not only for the assemblage at large, because "darkness" may very from species to species depending on their specific morphological features. For example spores with relatively thin equatorial extensions (e.g. *Zebrasporites*, Pl. 5, Figs. 15–30) do not turn as "dark" as taxa with thick exines and dense ornamentation (e.g. *Lycopodiacidites*, Pl. 4, Figs. 11– 21).

Van de Schootbrugge et al. (2009) as well as Pieńkowski et al. (2012) argue that thermal alteration is not an adequate explanation for the colour variation observed the T–J boundary, because it is not an isolated phenomenon in one locality, but common across the basin for sections with very different burial histories. It should be noted, however, that specimens from correlatable layers from Kuhjoch, the original material from Schulz assumed to originate from the Triletes Beds (based on their assemblage composition), and from Bonenburg, show different degrees of darkness and are not uniformly "dark" as the term "dark zone" suggests.

Van de Schootbrugge et al. (2009) propose that the formation of the very dark palynomorphs could be a result of soil acidification from sulphuric acid rain deposition. They explain that this process is known from artificial acetolysis, which is used to enhance the contrast of bleached palynomorphs and could occur in nature as a result of sulphuric acid rains during CAMP eruptions. This hypothesis is supported by coeval occurrences of increased enrichment of polycyclic aromatic hydrocarbons (PAHs) and dark palynomorphs (van de Schootbrugge et al. 2009; Pienkowski et al. 2012), and the gradual darkening we observed in the grey layer could then be a result of an intensifying process. In addition, the colour and cooccurrence of zircons (Marzoli, personal communication 2020) could indeed support the interpretation of this layer as a bentonite and local volcanism, but unfortunately, the geochemistry of the grey layer in Bonenburg is not yet resolved to date. However, it would still not explain how specimens of different colour within one taxon and a single sample co-occur because soil acidification would suggest that all specimens are homeogeniously exposed to this process. Pieńkowski and coworkers attribute such occurrences to palynofacies inversion type 1, i.e. to an abnormal composition of palynomacerals (Pieńkowski 2004; Pieńkowski & Waksmundzka 2009; Pienkowski et al. 2012). They argue, that darker palynomorphs are reworked specimens that have undergone an early diagenetic cycle in which they were exposed, became darker and redeposited again, which is common in swampy environments as those assumed for the Triletes Beds.

It is very hard to integrate these hypotheses with the fact that the assemblage of the Triletes Beds is overall very dark, with only a few taxa showing coeval occurrence of lighter coloured specimens. The interpretation of Pieńkowski and coworkers would imply that almost the entire assemblage is reworked (including those species like *Semiretisporis* that appear to be limited to the Triletes Beds only).

Therefore, we here propose to turn the argument around. If we assume a continued release of volcanic pollutants, such as sulphuric acid, influencing the assemblage prior to and during deposition, the dark palynomorphs should be interpreted as the non-reworked specimens. Indeed, those that are lighter in colour are still slightly darker then those from the Contorta Beds, and could easily have been only shortly exposed to the unfavourable effect of these pollutants, and become darker than they were originally but not as dark as the non-reworked specimens.

The presence of reworking is indicated through several Palaeozoic and pre-Rhaetian Mesozoic taxa in Bonenburg Gravendyck et al. (2020b), and is further indicated by a recent study proposing severe reworking and soil loss for the Rhaetian (van de Schootbrugge et al. 2020). Since especially those taxa that already occurred abundantly in the Contorta Beds occur coevally in different colours in the Triletes Beds (i.e. *Rhaetipollis germanicus*, *Limbosporites lundbladiae*, deltoid spores, *Ovalipollis pseudoalatus*, *Classopollis* spp., *Ricciisporites* spp.), could support the argument that the lighter coloured forms are in fact specimen of only very recently deposited layers. The reworking itself could be fostered by those soil wasting processes that are also connected to the chemical colour alteration. The only taxon that does not fit this interpretation is *Polypodiisporites polymicroforatus* because it does occur in various degrees of colour within the Triletes Beds but not before (Text-Figs. 10, 11).

Interestingly, other taxa like *Lunatisporites* or *Ovalipollis* which almost disappear in the Triletes Beds occur there in various degrees of brown, but never as dark as they did before in the last samples of the grey layer before, which further supports the interpretation that the lighter coloured specimens in the Triletes Beds are the reworked ones. However, a conclusive explanation for coeval occurrence of different colours and integrating with existing hypothesis for the "dark zone" are thus still elusive. To resolve this question, further quantitative studies are needed to complement this preliminary qualitative assessment for variation in colour observed in Bonenburg.

For such quantitative studies, it will be important to compare colour alteration from taxon to taxon, because our results show that the maximum darkness is dependent on the morphology of the respective taxon. Additionally, clear categories to determine "darkness" will be needed, e.g. using indices like the PDI, which operates with standard camera equipment. Comparison of colour alteration from section to section within one taxon might then provide further insights to distinguish thermal maturation from chemical darkening effects. Potentially varying degrees of darkening as a result of environmental acetolysis due to acid rain might even help reconstruct varying degrees of volcanic influence on plants throughout the Germanic Basin. Tying this together with geochemical analyses and quantitative study of teratology could thus provide and unrivalled insight of past environmental stress.

4.3. A *Coded* paradox when neo-typifying names of fossil-taxa

We highlighted in how many cases type material is "lost" or "destroyed". Generally, one can then designate a lectotype or neotype to substitute the original one, but in the process of attempting neotypifications we did encounter a paradox in the *Code*, that currently prevents replacement of "lost" or "destroyed" types in several cases. We made the following proposal to rectify the problem:

(009) A proposal to solve a paradox when neotypifying names of fossil-taxa

Julia Gravendyck,[1] Julien B. Bachelier,[1] Wolfram M. Kürschner[2] & Patrick S. Herendeen[3]

1 *Freie Universität Berlin, Institut für Biologie, Altensteinstr. 6, 14195 Berlin, Germany*
2 *University of Oslo, Departments of Geosciences, P.O. Box 1047 Blindern, 0316 Oslo, Norway*
3 *Chicago Botanic Garden, 1000 Lake Cook Road, Glencoe, Illinois 60022, U.S.A.*
Address for correspondence: *Julia Gravendyck, julia.gravendyck@fu-berlin.de*

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History has given us too many examples where types of the names of taxa have been lost. For example, the destruction of the Berlin Herbarium (B) after a bombing raid in 1943 was a severe blow for the botanical world. A major part of one of the world's largest collections and most extensive neotropical type collection was damaged or destroyed, together with many type specimens from all over the world that were on loan in Berlin at the time. Even today, unfortunate events can cause the loss of scientifically valuable type specimens.

If a holotype is lost or destroyed, the *Code* (Turland & al. in Regnum Veg. 159. 2018) has provisions that govern its replacement. Typically, a lectotype must be selected from the surviving original material, but in the absence of the latter a neotype can be designated "to serve as nomenclatural type **if no original material exists**" (Art. 9.8, emphasis added). However, there is a problem for fossil-taxa because Art. 9.4 clauses (a) and (b) specify that original material includes illustrations, but Art. 8.5 requires that the type (epitypes excepted) "of the name of a fossil-taxon at the rank of species or below is always a specimen". It is therefore impossible under these rules to designate a neotype for the name of any fossil-species or infraspecific fossil-taxon when the protologue includes an illustration. Furthermore, this paradox also makes any such previously designated neotypes for fossil taxa ineffective.

This problem is substantial because new names of all fossil-taxa at the rank of species or below published on or after 1 January 1912 must be accompanied by an illustration or figure, or by a reference to one previously and effectively published, in order to be validly published (Art. 43.2). The problem also applies to any names published prior to this date that included an illustration in the protologue, which was common practice well before becoming a requirement in the rules of nomenclature. Numerous examples could be cited to illustrate the scope of this problem, but undoubtedly no field can surpass palaeopalynology for missing or destroyed holotypes. Traverse (in Taxon 59: 666. 2010) estimated that the types of about 25,000 palaeopalynological names are mostly not available, either through loss or degradation of specimens on microscope slides, or are impossible to relocate in a mixed sample with hundreds or thousands of other grains, even if the original slides, from which they were described, are still available. In palaeopalynology, it is also very common for new fossil-species (or infraspecific fossil-taxa) to be described based on just a single specimen of a fossil spore or pollen grain, plus an accompanying illustration.

For many palaeopalynological names described in the 1930s and 1940s in Germany, type specimens are missing. Our attempt to resolve the taxonomy of a disputed Rhaetian palynomorph illustrates the problems perfectly. We enquired for several type specimens for names of fossil-taxa designated by the proliferous group of R. Potonié and coworkers, who described more than 300 new species and later authored the *Synopsis der Gattungen der Sporae dispersae* I–V (in Beih. Geol. Jahrb. 23–87. 1956–1970). Except for a few samples from the Upper Carboniferous, Tertiary of the Geiseltal and A. Ibrahim's doctorate material from the Ruhr Basin, neither the institutes in Berlin and Krefeld, where Potonié worked, nor the Federal Institute for Geosciences and Natural Resources could account for the whereabouts of the requested types or any other of Potonié's material. As Traverse predicted, the majority of Potonié's types are most likely lost.

In the absence of the type and other specimens, the palaeobotanist or palynologist is left with only the illustration depicting the original type, but this does not solve the problem because the illustration cannot serve as the lectotype, although some authors may treat it as such even though it is not permitted. The illustration could be used to guide selection of an appropriate neotype, ideally from the same fossil locality or geological strata that was the source for the original specimens, either from existing museum collections or newly collected material. However, the inclusion of the illustration in original material as currently defined in the *Code* prevents the designation of a neotype. As a result, these names are left unresolved, and increasingly contribute to taxonomic and nomenclatural instability.

This absurd dilemma binds the hands of palaeobotanists and palynologists attempting neotypifications when no original material other than the illustrations are still available. We conclude that the current definition of "original material" has to be considered defective, at least with respect to its application to names of fossil-taxa. We therefore propose the following amendments to Art. 9.4. to clarify the definition of "original material" for names of fossil-taxa at specific or lower rank.

(009) Amend Art. 9.4(a) and (b) (new text in bold):

"***9.4.*** For the purposes of this *Code*, original material comprises the following elements: *(a)* those specimens and illustrations (both unpublished and published prior to publication of the protologue**; illustrations of fossils excepted: see Art. 8.5**) that the author associated with the taxon, and that were available to the author prior to, or at the time of, preparation of the description, diagnosis, or illustration with analysis (Art. 38.7 and 38.8) validating the name; *(b)* any illustrations published as part of the protologue **(fossils excepted: see Art. 8.5)**; …"

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5. Conclusion and perspectives

The overarching aim of this chapter was to document the taxonomic advances that were made during this thesis. It followed three main objectives. **(1)** To gather and translate (often for the first time) original diagnoses to compile a new reference work for important Rhaetian taxa. **(2)** Study and document intraspecific variation of palynomorphs in the Bonenburg section, and **(3)** reinvestigate relevant type material as well as the associated original material to document the preservation of holotypes, revise several key taxa, and identify potential lecto- and neotypes to ensure future taxonomic stability.

Palynotaxonomic literature is the basis for all classifications and subsequent applications. Unfortunately, the original diagnoses often dating back to the 1930s are increasingly hard to come by, and even when they are available, they are not always comprehensible or only ambiguously so, because a vast number of the diagnoses, especially for Rhaetian palynomorphs, is written in German. For more than 40 species we provided the first English translation and for more than 25 genera the first English translation by a native German speaker. Additionally, we reviewed and updated ambiguous terminology to the current standard of Punt et al. (2007). We met the first objective by assembling the most up to date palynotaxonomic catalogue for the Rhaetian of the Germanic Triassic, making original diagnoses available and comprehensible for an international audience.

Our second objective, studying intraspecific variation in several taxa from Bonenburg, was complemented by observation of available original material. We compared this variation with relevant type material and could expand typical characteristics and variations thereof for several taxa whose descriptions were based on only a few specimens. Our observations led to the emendation of nine species and two genera, one recombination and the description of two new species (*Ricciisporites cataphractes* sp. nov. and *Ricciisporites lundbladiae* sp. nov.). All these nomenclatural novelties are not yet effective but will be upon publication of this chapter as a separate paper. As a side observation, we not only documented the taxonomic variability, but also of the variation of preservation, especially the successive darkening towards the Triletes Beds. We discussed potential implications and made suggestion for future studies to enlarge on these preliminary results.

Studying important type material following the third objective, we documented the often poor state of holotypes and highlighted how many of them are lost and need replacement in form of neo- or neotypification. Unfortunately, the current phrasing of the *Code* contains an unintended paradox, which prevents designation of neotypes. This is a serious problem as most of the original material is also unavailable and leaving neotypification to be the only solution. Subsequently, we published a formal proposal how to face this dilemma (Gravendyck et al. 2020b). Pending acceptance of the proposal, we highlighted the extent to which neotypification is needed to ensure taxonomic stability, and reliable application of taxon names for Rhaetian palynomorphs presented in this extensive new and up to date catalogue.

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Plate 1. Verrucate, apiculate to baculate spores

Specimens indicated with ▢ and ◎ depict the original type of the genus and holotypes, respectively. Specimens retrieved from Bonenburg are indicated with BB-sample_slidenr. and England Finder references where available.

1. *Polypodiisporites polymicroforatus* (Orlowska-Zwolinska 1966) Lund 1977; BB-D-11_2; U55/4
2. *Polypodiisporites polymicroforatus* (Orlowska-Zwolinska 1966) Lund 1977; BB-D-09_2; H58/0
3. *Polypodiisporites polymicroforatus* (Orlowska-Zwolinska 1966) Lund 1977; BB-D-16_2; K35/2
4. *Polypodiisporites polymicroforatus* (Orlowska-Zwolinska 1966) Lund 1977; BB-D-09_2; M35/3
5. *Polypodiisporites polymicroforatus* (Orlowska-Zwolinska 1966) Lund 1977; BB-D-16_2; V61/4
6. *Polypodiisporites polymicroforatus* (Orlowska-Zwolinska 1966) Lund 1977; BB-D-13_2; G33/1
7. *Polypodiisporites polymicroforatus* (Orlowska-Zwolinska 1966) Lund 1977; BB-D-19; R59/1
8. *Polypodiisporites polymicroforatus* (Orlowska-Zwolinska 1966) Lund 1977; BB-D-11_2; X56/4
9. *Polypodiisporites polymicroforatus* (Orlowska-Zwolinska 1966) Lund 1977; BB-D-10_2; P53/4
10. *Polypodiisporites polymicroforatus* (Orlowska-Zwolinska 1966) Lund 1977; BB-D-01_2; E54/1
11. *Polypodiisporites polymicroforatus* (Orlowska-Zwolinska 1966) Lund 1977; BB-D-07_2; L57/0
12. *Polypodiisporites polymicroforatus* (Orlowska-Zwolinska 1966) Lund 1977; Kuhjoch_050926_5; R33/3
13. *Polypodiisporites polymicroforatus* (Orlowska-Zwolinska 1966) Lund 1977; Kuhjoch_050926_5; M32/4
14. *Polypodiisporites polymicroforatus* (Orlowska-Zwolinska 1966) Lund 1977; BB-D-16_2; Q29/0
15. *Polypodiisporites polymicroforatus* (Orlowska-Zwolinska 1966) Lund 1977; BB-D-13_2; G33/0
16. *Polypodiisporites polymicroforatus* (Orlowska-Zwolinska 1966) Lund 1977; BB-D-05; S62/0
17. *Polypodiisporites polymicroforatus* (Orlowska-Zwolinska 1966) Lund 1977; BB-D-02_2; Q35/3
18. *Polypodiisporites polymicroforatus* (Orlowska-Zwolinska 1966) Lund 1977; BB-D-08_1; Q22/3
19. *Polypodiisporites polymicroforatus* (Orlowska-Zwolinska 1966) Lund 1977; BB-D-13_2; P32/3
20. *Polypodiisporites polymicroforatus* (Orlowska-Zwolinska 1966) Lund 1977; BB-D-07; H58/1
21. *Polypodiisporites polymicroforatus* (Orlowska-Zwolinska 1966) Lund 1977; BB-D-07; K56/3
22. ? Holotype for *Convolutispora microrugulata*, Möckern 1 E-10184/1; R42/2;
    Original material from Schulz 1967,
23. *Polypodiisporites polymicroforatus* (Orlowska-Zwolinska 1966) Lund 1977; BB-D-07; O56/1
24. *Baculatisporites comaumensis* (Cookson 1953) Potonie 1956; BB-D-17_2; T28/3
25. *Baculatisporites comaumensis* (Cookson 1953) Potonié 1956; BB-D-16_2; X50/0
26. *Baculatisporites comaumensis* (Cookson 1953) Potonié 1956; BB-D-14_2; O38/3
27. *Baculatisporites comaumensis* (Cookson 1953) Potonié 1956; BB-D-13_2; N30/0
28. *Baculatisporites comaumensis* (Cookson 1953) Potonié 1956; BB-D-11_2; O31/2
29. *Baculatisporites comaumensis* (Cookson 1953) Potonié 1956; BB-D-10_1; W51/2
30. *Baculatisporites comaumensis* (Cookson 1953) Potonie 1956; BB-D-08_1; Q28/0
31. *Baculatisporites comaumensis* (Cookson 1953) Potonié 1956; BB-D-07_1; D36/0
32. *Baculatisporites comaumensis* (Cookson 1953) Potonié 1956; BB-D-01_2; X53/3
33. Aberrant? *Baculatisporites comaumensis* (Cookson 1953) Potonie 1956; BB-D-03_3; C36/0
34. Holotype (+Type of the genus) original photograph; *Conbaculatisporites mesozoicus* Klaus 1960;
35. Holotype (+Type of the genus) refigured; *Conbaculatisporites mesozoicus* Klaus 1960; sample Nr. 355
36. *Trachysporites asper* Nilsson 1958; BB3000_1
37. *Trachysporites* cf. *asper* Nilsson 1958; BB-D-05_1; R58/0
38. *Trachysporites* sp. A Nilsson 1958, BB-D-03_3; L40/2

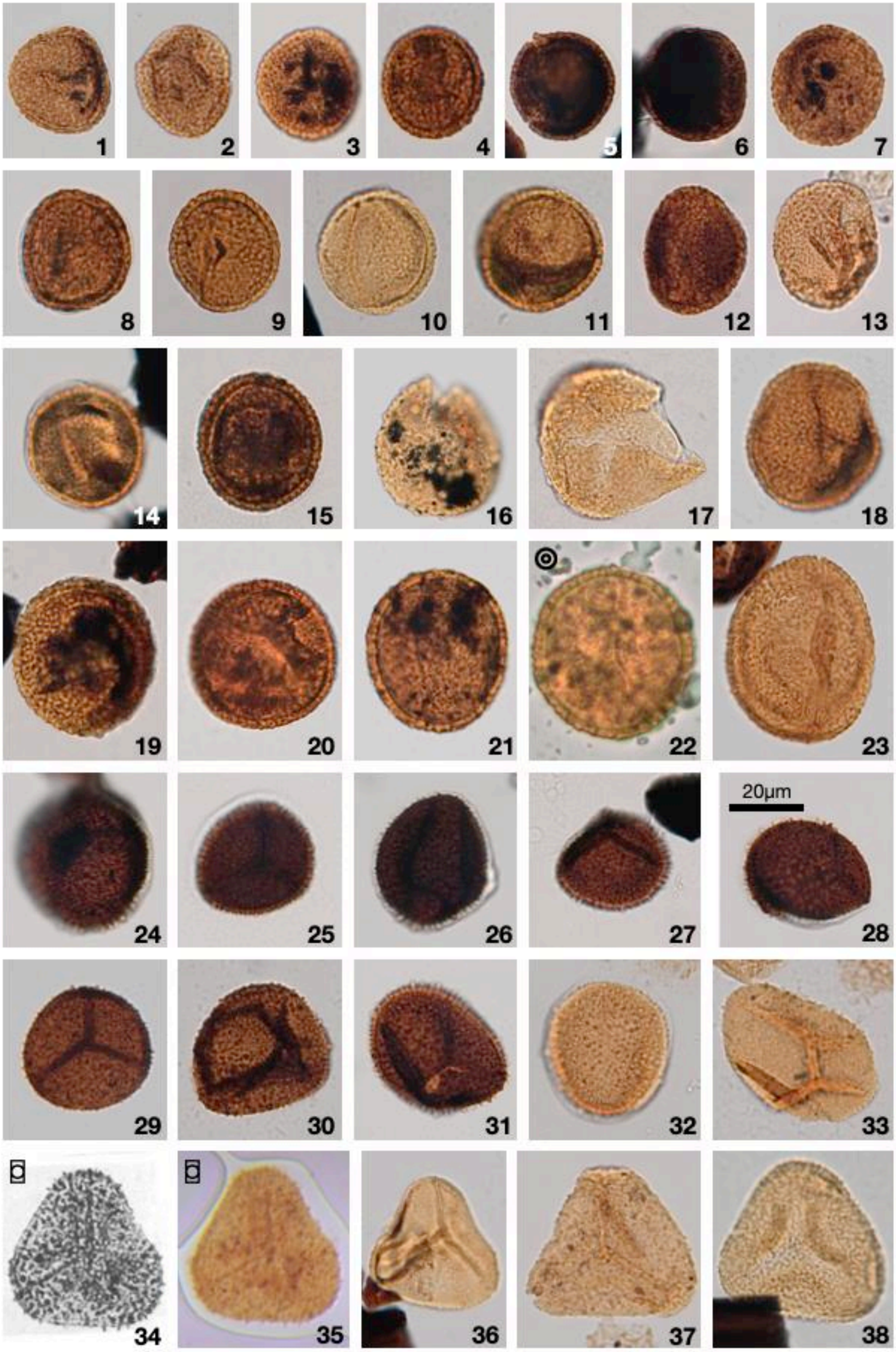
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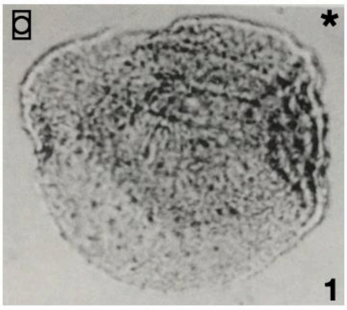
Plate 2. *Aratrisporites* spp.

Specimens indicated with ☒ and ☒ depict the original type of the genus and holotypes, respectively. Specimens indicated with an asterisk (*) not to scale (only approximate). Specimens retrieved from Bonenburg are indicated with BB-sample_slidenr. and England Finder references where available (otherwise microscope coordinates are given).

1. Holotype (+Type of the genus) original photograph; *Aratrisporites parvispinosus* Leschik 1955
2. Holotype refigured; *Aratrisporites paraspinosus* Klaus 1960
3. *Aratrisporites fimbriatus* Klaus 1960; BB-D-11_2, D50/0
4. *Aratrisporites fimbriatus* Klaus 1960*;* BB_1150_1, 158,162x8.5,10
5. *Aratrisporites fimbriatus* Klaus 1960*;* BB_1800_2, M65/4
6. Holotype original photograph; *Aratrisporites fischeri* Klaus 1960
7. Holotype original photograph; *Aratrisporites palettae* Klaus 1960
8. Holotype original photograph; *Aratrisporites scabratus* Klaus 1960
9. *Aratrisporites scabratus* Klaus 1960; BB_2085_1, 156,165x 5,13
10. *Aratrisporites scabratus* Klaus 1960; BB-D-07_2, C38/3
11. Holotype refigured; *Saturnisporites coryliseminis* Klaus 1960
12. Holotype original photograph; *Aratrisporites crassitectatus* Reinhard 1964
13. Holotype refigured; *Saturnisporites granulatus* Klaus 1960
14. Holotype refigured; *Saturnisporites fimbriatus* Klaus 1960
15. Holotype (lost) original photograph; *Pollenites Saturni* [sic] Thiergart 1949
16. Holotype original photograph; *Aratrisporites minimus* Schulz 1967
17. *Aratrisporites minimus* Schulz 1967; BB2950_2; P49/4



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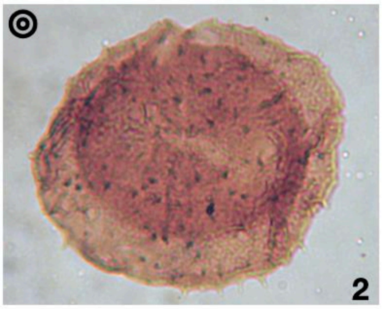

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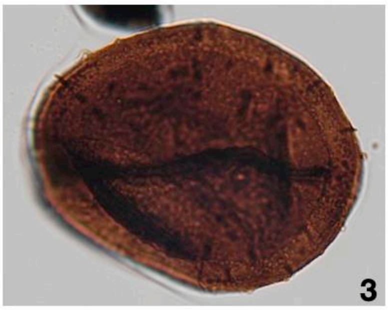

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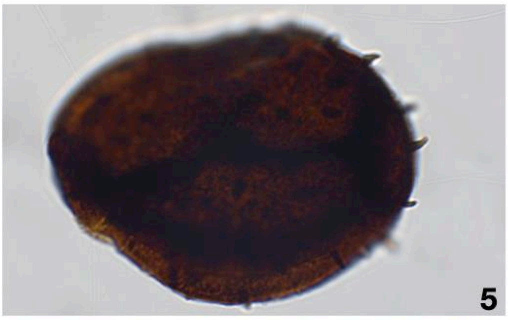

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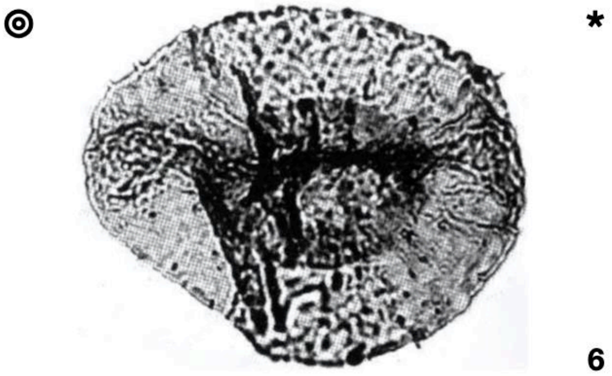

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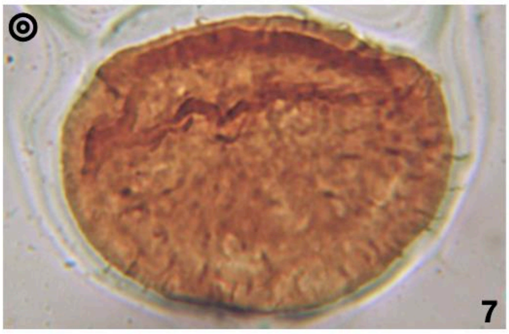

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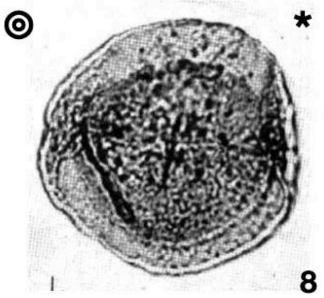

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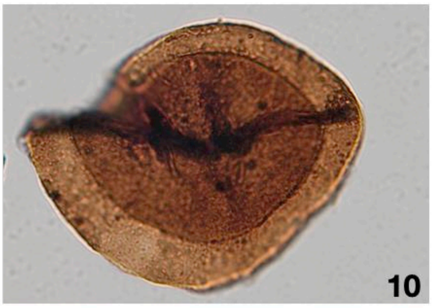

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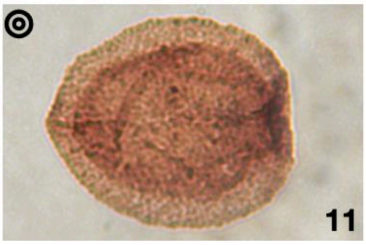

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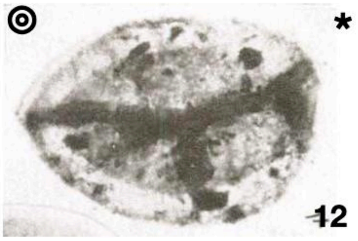

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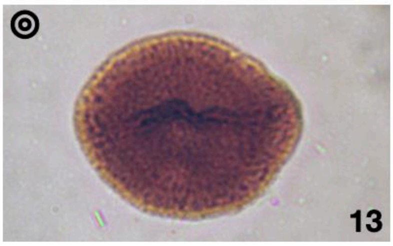

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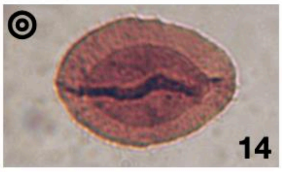

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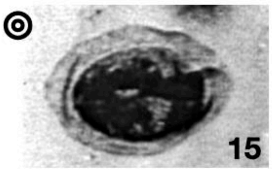

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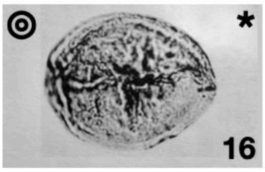

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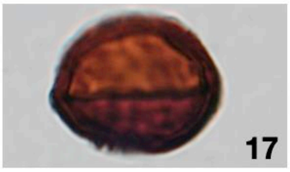

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Plate 3. Verrucate, apiculate to baculate spores

Specimens indicated with ▢ and ◎ depict the original type of the genus and holotypes, respectively. Specimens indicated with an asterisk (*) not to scale (only approximate). Original material from the original residue from Schulz is indicated with an ‘O’. Specimens retrieved from Bonenburg are indicated with BB-sample_slidenr. and England Finder references where available (otherwise microscope coordinates are given).

1. *Calamaspora nathorstii* in Klaus 1960, original photograph
2. *Calamaspora nathorstii* in Klaus 1960, refigured
3. *Calamaspora tener* (Leschik 1955) Mädler 1964; BB300_1; W53/3
4. *Calamaspora tener* (Leschik 1955) Mädler 1964; BB-D-16_2; M57/2
5. cf. *Punctatisporites* sp.; BB-D-18_2; R29/3
6. Holotype original photograph; *Retusotriletes mesozoicus* Klaus 1960
7. Holotype refigured; *Retusotriletes mesozoicus* Klaus 1960
8. *Retusotriletes mesozoicus* Klaus 1960; BB-D-08_1; K28/3
9. *Retusotriletes mesozoicus* Klaus 1960; BB1075_2; 54,161x9,14
10. *Retusotriletes mesozoicus* Klaus 1960; BB-D-10_2; T47/1
11. cf. *Cornutisporites seebergensis* Schulz 1962; BB-D-19_1; T39/4
12. cf. *Cornutisporites seebergensis* Schulz 1962; BB-D-09_1; S26/4
13. *Cornutisporites seebergensis* Schulz 1962; BB-D-14_2; V66/4
14. *Cornutisporites seebergensis* Schulz 1962; BB2550_1; 130,132x11,15
15. *Cornutisporites seebergensis* Schulz 1962; BB-D-05_1; H51/3
16. Holotype original photograph; *Cornutisporites rugulatus* Schulz 1967
17. *Cornutisporites rugulatus* Schulz 1967; BB-D-08_1; J27/2
18. *Cornutisporites rugulatus* Schulz 1967; BB-D-06_1; K24/4
19. *Cornutisporites rugulatus* Schulz 1967; BB-D-06_3; P39/4
20. Aberrant, *Cornutisporites/Perinosporites* hybrid; BB-D-15_1; M34/1
21. *Triancoraesporites ancorae* (Reinhard 1961) Schulz 1962; BB-D-08_1; C39/4
22. *Triancoraesporites ancorae* (Reinhard 1961) Schulz 1962; BB-D-12_1; G66/3
23. *Triancoraesporites ancorae* (Reinhard 1961) Schulz 1962; BB-D-09_1; N24/2
24. *Triancoraesporites ancorae* (Reinhard 1961) Schulz 1962; BB-D-08_1; U28/2
25. *Triancoraesporites ancorae* (Reinhard 1961) Schulz 1962; BB-D-11_2; E25/0
26. Cf. *Triancoraesporites* sp.; BB-D-12_1; G65/2
27. Cf. *Triancoraesporites* sp.; BB-D-11_2; B25/0
28. Holotype (+Type of the genus) original photograph; *Triancoraesporites reticulatus* Schulz 1962
29. Holotype (+Type of the genus) refigured; *Triancoraesporites reticulatus* Schulz 1962; Möckern 1E-10184/1; R46.3
30. *Triancoraesporites reticulatus* Schulz 1962; NeoMöckern 1 E-10184_2; N33/2
31. *Triancoraesporites reticulatus* Schulz 1962; NeoMöckern 1 E-10184_3; Q34/2
32. *Triancoraesporites reticulatus* Schulz 1962; NeoMöckern 1 E-10184_3; R41/3
33. *Triancoraesporites reticulatus* Schulz 1962; NeoMöckern 1 E-10184_2; M39/1
34. *Triancoraesporites reticulatus* Schulz 1962; BB2085_1; 167,172x6.5,14
35. *Triancoraesporites reticulatus* Schulz 1962; BB-D-09_2; G55/0
36. *Triancoraesporites reticulatus* Schulz 1962; BB-D-09_2; F29/0
37. *Triancoraesporites reticulatus* Schulz 1962; BB-D-07_2; C58/3
38. *Triancoraesporites reticulatus* Schulz 1962; BB2085_1; 126.5,130x14,19

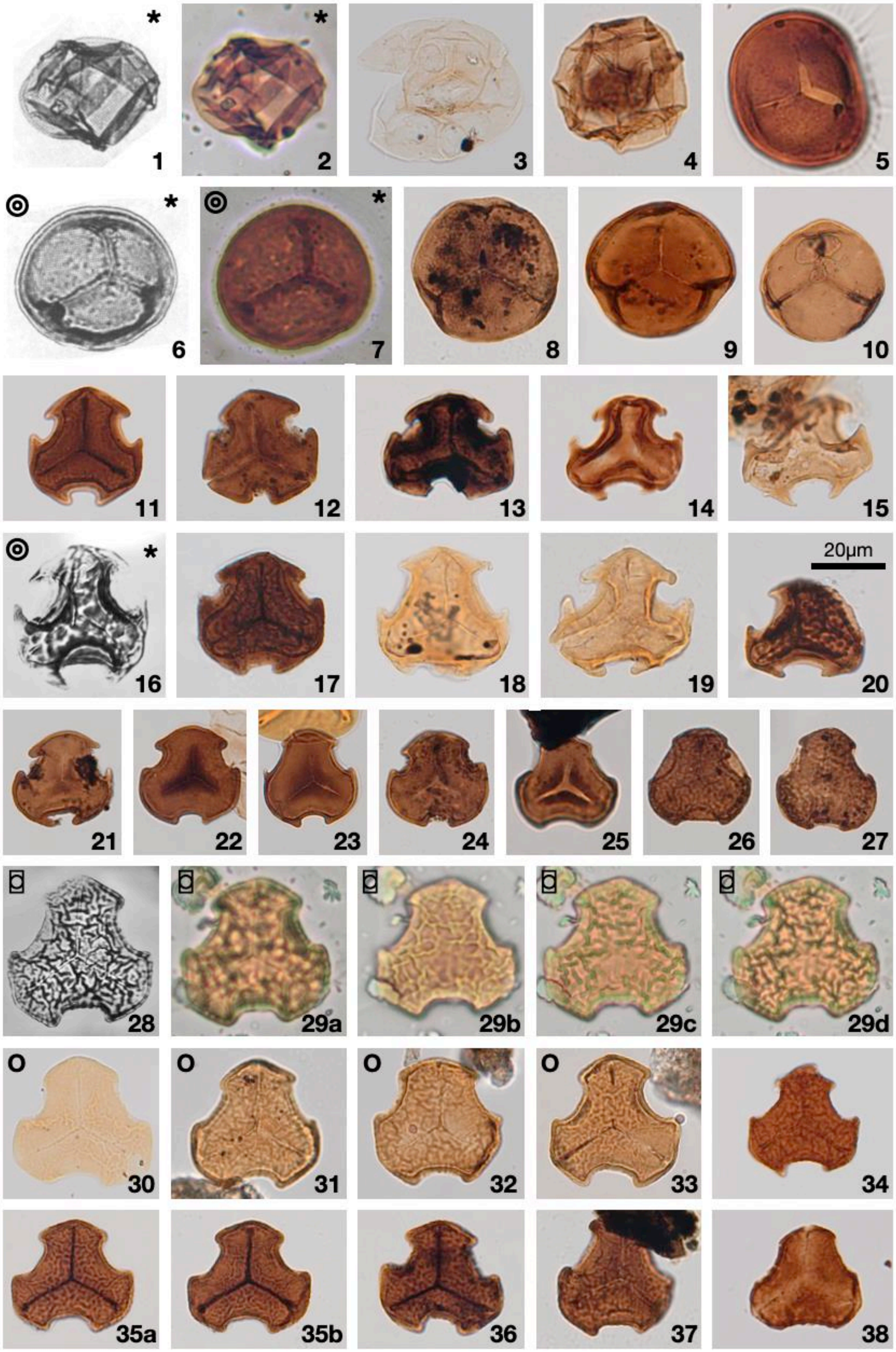
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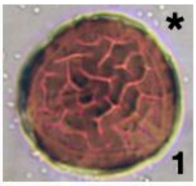
Plate 4. Cingulate and rugulate spores

Specimens indicated with an ◎ depict holotypes. Specimens indicated with an asterisk (*) not to scale (only approximate). Original material from the original residue from Schulz is indicated with an 'O'. Specimens retrieved from Bonenburg are indicated with BB-sample_slidenr. and England Finder references where available (otherwise microscope coordinates are given).

1. *Camarozonosporites rudis* LESCHIK 1955 in Klaus 1960, refigured
2. *Camarozonosporites rudis* LESCHIK 1955, BB-D-15; SEM image
3. *Camarozonosporites rudis* LESCHIK 1955, NeoMöckern 1 E-10184_2; P39/4
4. *Camarozonosporites rudis* LESCHIK 1955, BB-D-08_2; K36/4
5. HOLOTYPE refigured; *Camarozonosporites golzowensis* SCHULZ 1967; Golzow 3 -394/1; K41/4
6. *Camarozonosporites* cf. *rudis* LESCHIK 1955, BB-D-10_1; H29/0
7. *Camarozonosporites laevigatus* SCHULZ 1967, BB-D-13_2; G33/0
8. *Camarozonosporites laevigatus* SCHULZ 1967, BB-D-07_1; K42/3
9. *Camarozonosporites laevigatus* SCHULZ 1967, BB-D-06_3; N40/2
10. *Uvaesporites argentaeformis* (BOLCHOVITINA 1953) SCHULZ 1967; BB-980_1; 135.5,140x12,17
11. Cf. *Lycopodiacidites rugulatus* (COUPER 1958) SCHULZ 1967; BB-D-07_1; R40/2
12. HOLOTYPE refigured; *Lycopodiacidites kuepperi* KLAUS 1960,
13. *Lycopodiacidites rugulatus* (COUPER 1958) SCHULZ 1967; BB2950_1; J57/4
14. *? Camarozonosporites rudis/ Lycopodiacidites rugulatus;* BB2950_1; Q67/3
15. *Lycopodiacidites rugulatus* (COUPER 1958) SCHULZ 1967; Möckern 1E-10184/1; Q43/1
16. *Lycopodiacidites rugulatus* (COUPER 1958) SCHULZ 1967; NeoMöckern 1 E-10184_3; W41/3
17. *Lycopodiacidites rugulatus* (COUPER 1958) SCHULZ 1967; NeoMöckern 1 E-10184_3; Q46/3
18. HOLOTYPE refigured; *Lycopodiacidites rhaeticus* SCHULZ 1967, Möckern 1E-10184/21; G48/1
19. Fragment of *Lycopodiacidites rhaeticus* SCHULZ 1967; NeoMöckern 1E-10184_2; T29/1
20. Fragment of *Lycopodiacidites rugulatus* (COUPER 1958) SCHULZ 1967; NeoMöckern 1E-10184_2; U32/1
21. *Lycopodiacidites rhaeticus* SCHULZ 1967; BB-D-13_1; D22/0
22. *Lycopodiacidites rhaeticus* SCHULZ 1967; BB-D-06_3; N37/4
23. HOLOTYPE refigured; *Tigrisporites halleinis* KLAUS 1960
24. *Tigrisporites halleinis* KLAUS 1960; BB-D-06_3; N37/4



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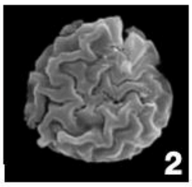
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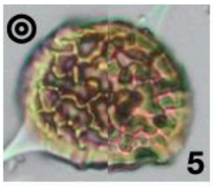

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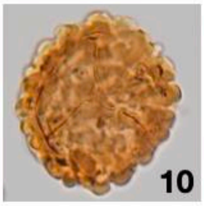
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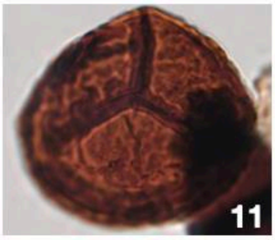
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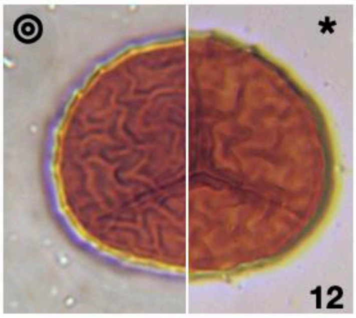

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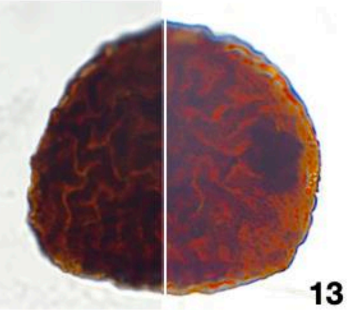
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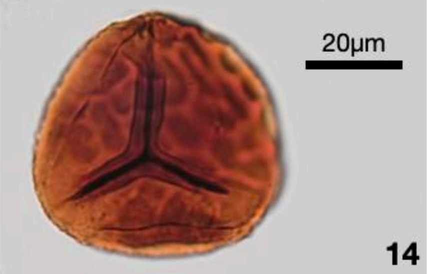

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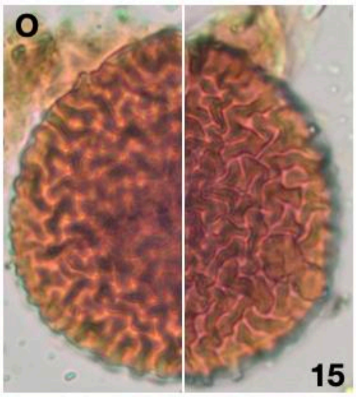

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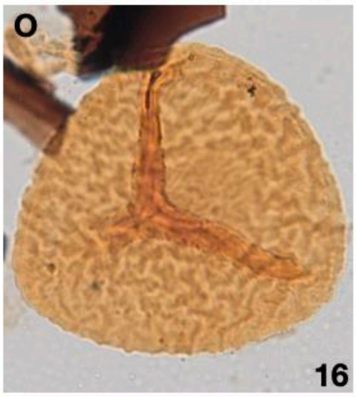

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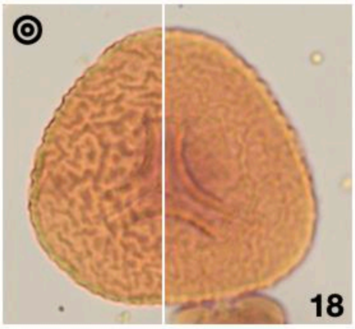

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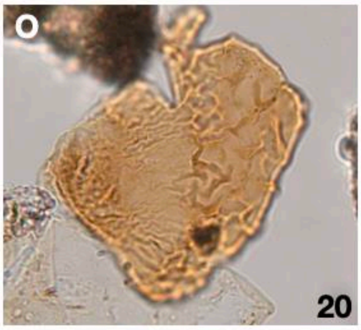

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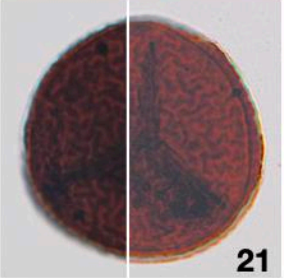
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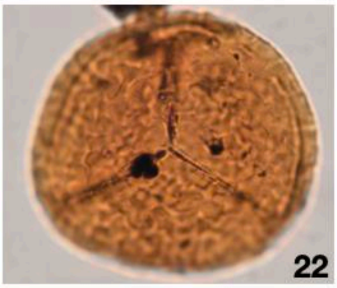
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Plate 5. Rugulate and zonate spores

Specimens indicated with ▢ and ◎ depict the original type of the genus and holotypes, respectively. Original material from the original residue from Schulz is indicated with an 'O'. Specimens retrieved from Bonenburg are below indicated with BB-sample_slidenr. and England Finder references.

1. Holotype (+Type of the genus) refigured; *Striatella seebergensis* Mädler 1964b, M318, EK 7, TK-Nr. 3150
2. *Striatella seebergensis* Mädler 1964b; BB-D-10_2; T46/0
3. *Striatella seebergensis* Mädler 1964b; BB-D-07_1; M56/3
4. Holotype (+Type of the genus) refigured; *Striatella jurassica* Mädler 1964b, TK-Nr. 3150; N19/4
5. *Striatella seebergensis* Mädler 1964b; BB2450_2; T49/0
6. *Striatella seebergensis* Mädler 1964b; BB2550_1; N48/4
7. *Striatella seebergensis* Mädler 1964b; BB2550_1; P47/1
8. *Striatella seebergensis* Mädler 1964b; BB-D-03_3; Q38/0
9. *Striatella seebergensis* Mädler 1964b; BB-D-07_1; M36/3
10. Holotype original photograph*, Thuringiasporites laevigatus* Schulz 1962
11. Holotype original photograph overlain with refigured specimen*, Thuringiasporites laevigatus* Schulz 1962
12. Holotype refigured; *Thuringiasporites laevigatus* Schulz 1962; Möckern 1E-10184/1; G47/3
13. *Zebrasporites laevigatus* (Schulz 1962) Schulz 1967; Möckern 1E-10184/1; C42/4
14. Indet.; BB-D-12_1; G65/2
15. *Zebrasporites laevigatus* (Schulz 1962) Schulz 1967; NeoMöckern 1E_2-10184_3; N19/4
16. *Zebrasporites laevigatus* (Schulz 1962) Schulz 1967; NeoMöckern 1E_2-10184_1; T35/1
17. *Zebrasporites laevigatus* (Schulz 1962) Schulz 1967; NeoMöckern 1E-10184_3; M31/3
18. *Zebrasporites laevigatus* (Schulz 1962) Schulz 1967; NeoMöckern 1E_2-10184_3; T36/4
19. *Zebrasporites laevigatus* (Schulz 1962) Schulz 1967; NeoMöckern 1E_2-10184_1; F52/1
20. *Zebrasporites laevigatus* (Schulz 1962) Schulz 1967; NeoMöckern 1E-10184_2; M29/1
21. *Zebrasporites laevigatus* (Schulz 1962) Schulz 1967; NeoMöckern 1E-10184_2; P42/0
22. *Zebrasporites laevigatus* (Schulz 1962) Schulz 1967; NeoMöckern 1E_2-10184_3; L45/1
23. *Zebrasporites laevigatus* (Schulz 1962) Schulz 1967; BB-D-07_1; C57/2
24. *Zebrasporites laevigatus* (Schulz 1962) Schulz 1967; BB-D-09_2; Q35/2
25. *Zebrasporites laevigatus* (Schulz 1962) Schulz 1967; BB-D-18_1; Q27/4
26. *Zebrasporites laevigatus* (Schulz 1962) Schulz 1967; BB-D-08_1; W29/1
27. *Zebrasporites laevigatus* (Schulz 1962) Schulz 1967; BB-D-10_2; T54/1
28. Intermediate *Zebrasporites laevigatus* (Schulz 1962) Schulz 1967; BB-D-11_2; T51/1
29. Intermediate *Zebrasporites laevigatus* (Schulz 1962) Schulz 1967; BB-D-12_1; D26/4
30. Intermediate *Zebrasporites laevigatus* (Schulz 1962) Schulz 1967; BB-D-18_2; O37/4
31. Intermediate *Zebrasporites laevigatus* (Schulz 1962) Schulz 1967; NeoMöckern 1E-10184_2; R31/0
32. Intermediate *Zebrasporites laevigatus* (Schulz 1962) Schulz 1967; NeoMöckern 1E_2-10184_3; P35/1
33. Intermediate *Zebrasporites laevigatus* (Schulz 1962) Schulz 1967; NeoMöckern 1E_2-10184_1; N40/3
34. *Zebrasporites interscriptus* remain (Schulz 1962) Schulz 1967; NeoMöckern 1E-10184_2; N50/1
35. Holotype refigured; *Zebrasporites corneolus* Leschik 1955 in Klaus 1960
36. *Zebrasporites kahleri* Klaus 1960; NeoMöckern 1E_2-10184_2; M 31/3
37. Holotype (+Type of the genus) refigured; *Zebrasporites kahleri* Klaus 1960

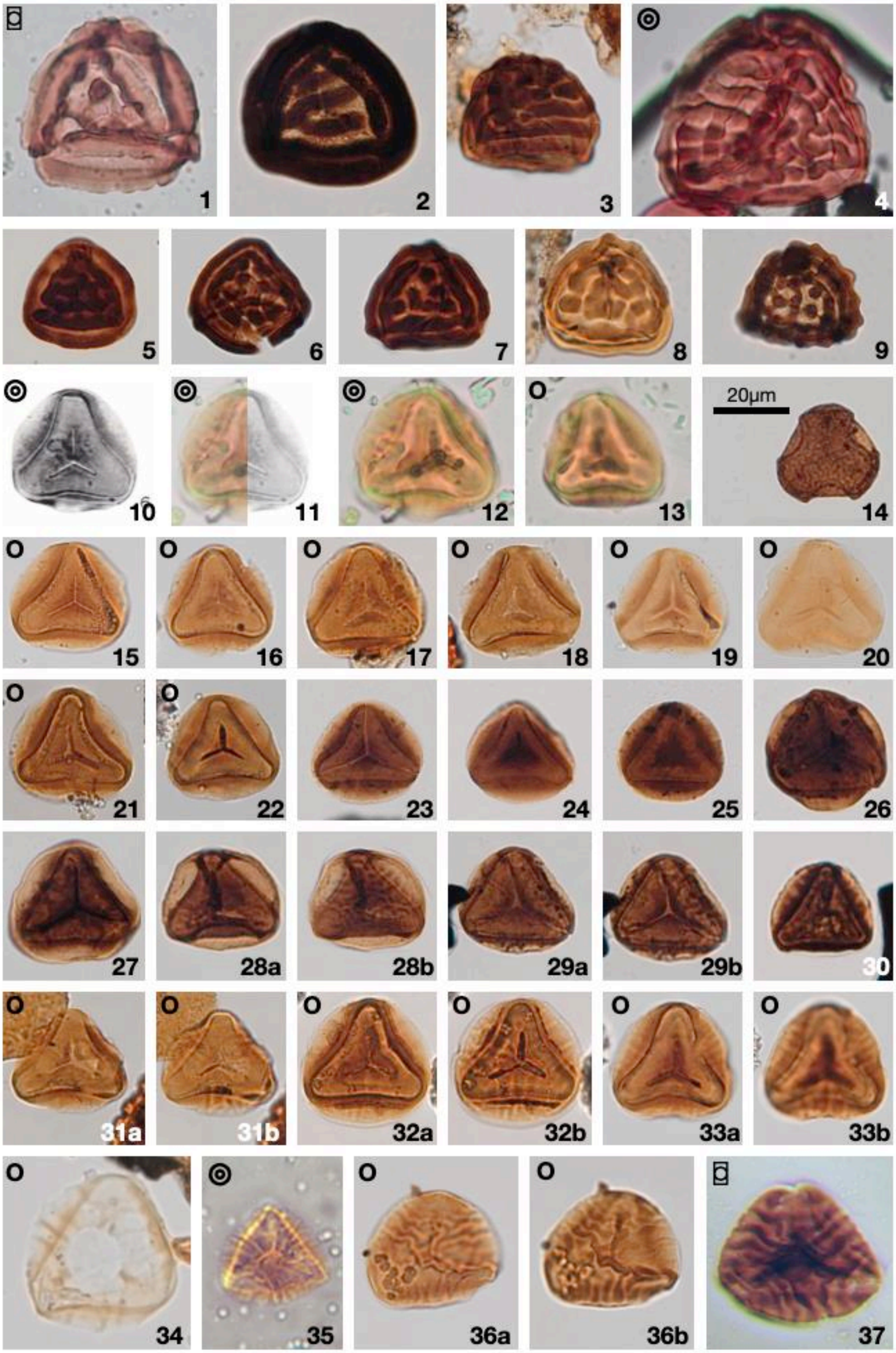
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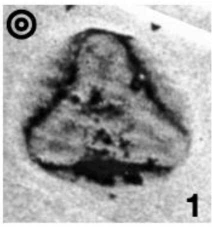
Plate 6. Murornate and reticulate spores with a zona

Specimens indicated with ⧇ and ◎ depict the original type of the genus and holotypes, respectively. Specimens indicated with an asterisk (*) not to scale (only approximate). Original material from the original slides from Thiergart (1949) is indicated with an ‘O’. Specimens retrieved from Bonenburg are below indicated with BB-sample_slidenr. and England Finder references where available (otherwise microscope coordinates are given).

1. Holotype original photograph, *Sporites interscriptus* Thiergart 1949
2. Holotype refigured; *Sporites interscriptus* Thiergart 1949; Helmstedt_1; S45/1
3. Original material for *Sporites interscriptus* Thiergart 1949; Helmstedt_1; S51/4
4. Holotype (+Type of the genus) refigured; *Zebrasporites kahleri* Klaus 1960
5. *Zebrasporites interscriptus* (Thiergart 1949) Klaus 1960; BB-D-09_2; K58/0
6. *Zebrasporites interscriptus* (Thiergart 1949) Klaus 1960; BB-D-12_1; E23/4
7. *Zebrasporites interscriptus* (Thiergart 1949) Klaus 1960; BB1450_1; E38/1
8. *Zebrasporites interscriptus* (Thiergart 1949) Klaus 1960; BB-D-16_2; J57/4
9. *Zebrasporites interscriptus* (Thiergart 1949) Klaus 1960; BB-D-14_2; G59/4
10. *Zebrasporites interscriptus* (Thiergart 1949) Klaus 1960; BB-D-07_1; K57/1
11. *Zebrasporites interscriptus* (Thiergart 1949) Klaus 1960; BB1800_1; 126,127x21,23
12. Two focal planes of cf. *Zebrasporites interscriptus* (Thiergart 1949) Klaus 1960; BB2550_4; Y31/4
13. *Zebrasporites interscriptus* (Thiergart 1949) Klaus 1960; BB-D-08_1; L33/3
14. *Zebrasporites interscriptus* (Thiergart 1949) Klaus 1960; BB-D-17_2; S27/0
15. *Zebrasporites interscriptus* (Thiergart 1949) Klaus 1960; BB-D-07_1; R49/4
16. *Zebrasporites interscriptus* (Thiergart 1949) Klaus 1960; BB-D-18_2; O37/4
17. Holotype refigured; *Zebrasporites fimbriatus* Klaus 1960
18. *Semiretisporites gothae* Reinhardt 1961; BB-D-12_1; D29/3
19. *Semiretisporites gothae* Reinhardt 1961; BB2550_1; T38/2
20. Holotype original photograph; *Semiretisporites gothae* Reinhardt 1961
21. *Semiretisporites gothae* Reinhardt 1961; BB1450_1; 167,177x14.5,18
22. *Semiretisporites gothae* Reinhardt 1961; BB2085_1; 171,175x12.5,16
23. *Semiretisporites gothae* Reinhardt 1961; BB-D-15_1; D38/4
24. Holotype refigured; *Semiretisporites achimensis* Mädler 1964b; M116; TK.-Nr. 3140
25. refigured; *Semiretisporites gothae* Reinhardt 1961 in Mädler 1964b; M116; Netz 1 B1; TK.-Nr. 3138
26. *Semiretisporites ornatus* Orłowska-Zwolińska 1966, BB-2550_4; K32/4
27. *Semiretisporites ornatus* Orłowska-Zwolińska 1966; BB1450_1; K39/0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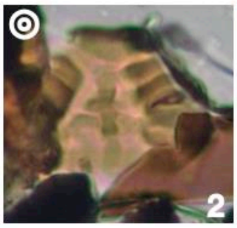
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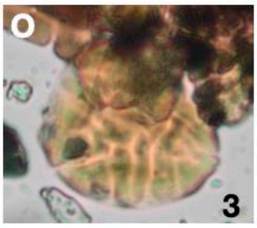
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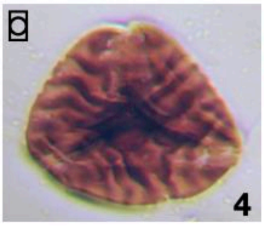
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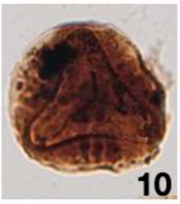
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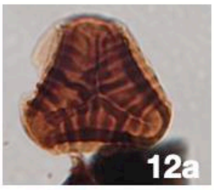
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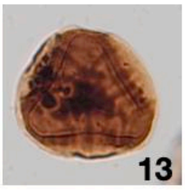
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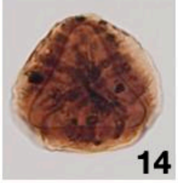
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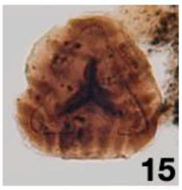
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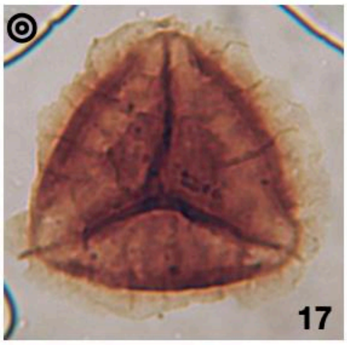
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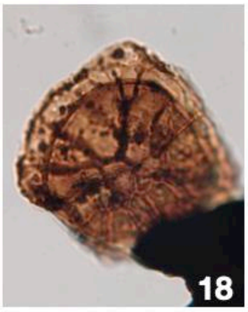
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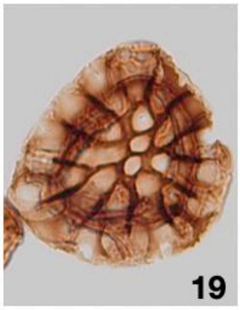
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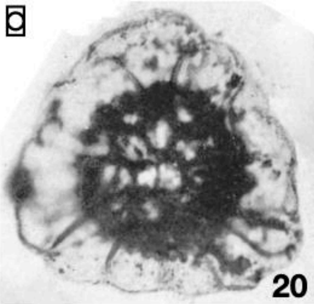
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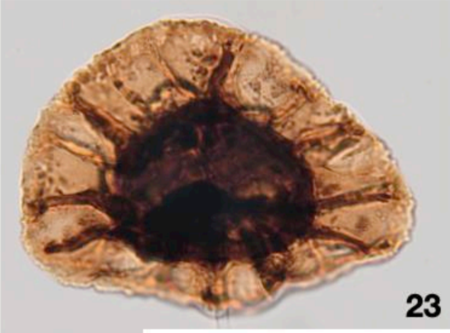
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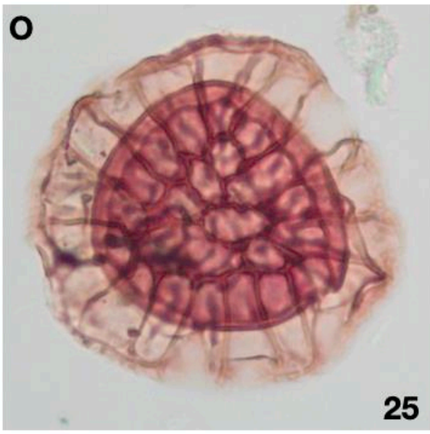
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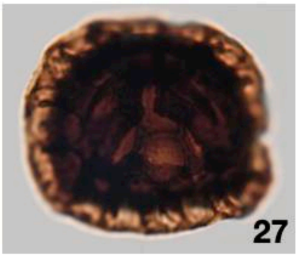
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Plate 7. Reticulate spores with a zona

Specimens indicated with ▢ and ◎ depict the original type of the genus and holotypes, respectively. Specimens indicated with an asterisk (*) not to scale (only approximate). Original material from the original slides from Mädler (1964b) or original residues from Schulz (1967) is indicated with an 'O'. Specimens retrieved from Bonenburg are below indicated with BB-sample_slidenr. and England Finder references where available (otherwise microscope coordinates are given).

1. *Semiretisporites wielichovinsis* Orłowska-Zwolińska 1966; BB-2550_1; X40/0
2. *Semiretisporites wielichovinsis* Orłowska-Zwolińska 1966; NeoMöckern 1E-10184_3; M30/0
3. Cf. *Semiretisporites wielichovinsis* Orłowska-Zwolińska 1966; Achim 2 (Mädler 1964b); M116, Netz 1 G1
4. Cf. *Semiretisporites wielichovinsis* Orłowska-Zwolińska 1966; BB-D-12_1; H52.1
5. Holotype refigured; *Semiretisporites reticulatus* Mädler 1964b; M703/III; TK.-Nr. 3129; C17/3
6. Holotype refigured; *Semiretisporites maljavkinae* Schulz 1967; Möckern 1E-10184_21; L39/1
7. *Semiretisporites wielichovinsis* Orłowska-Zwolińska 1966; NeoMöckern 1E-10184_1; E50/3
8. *Semiretisporites wielichovinsis* Orłowska-Zwolińska 1966; NeoMöckern 1E-10184_1; H52/3


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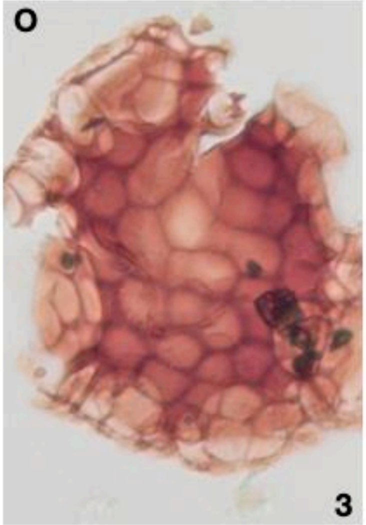
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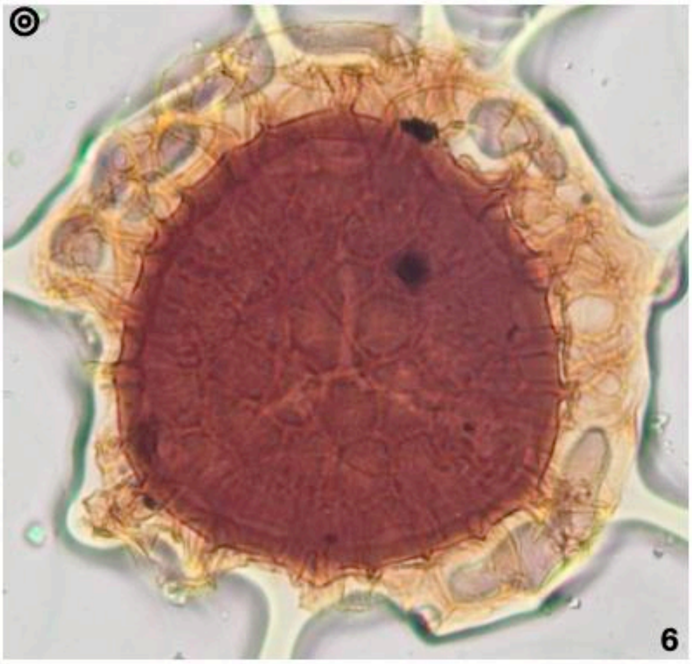
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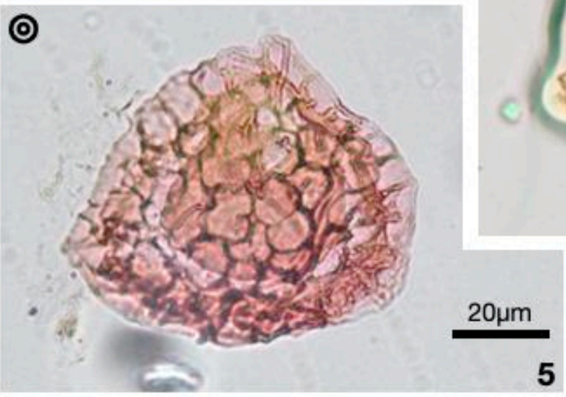
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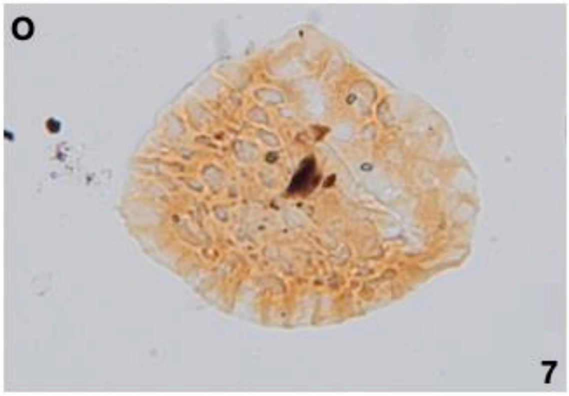
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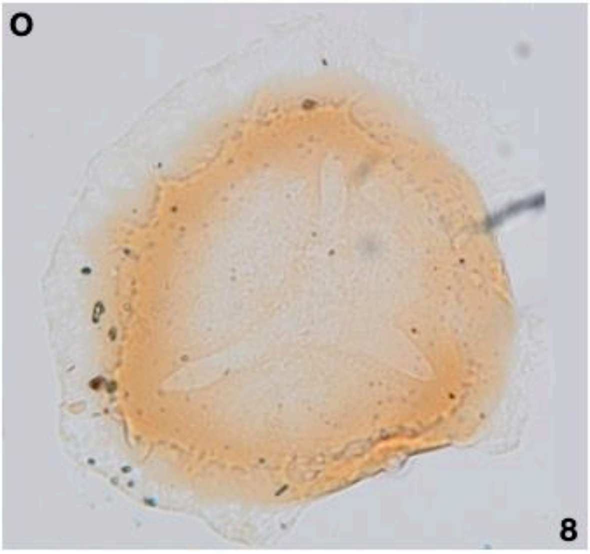
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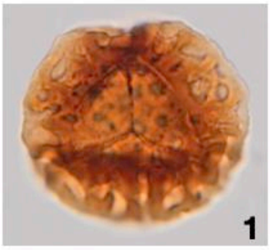
Plate 8. Zonate and cingulate spores

Specimens indicated with an ◎ depict holotypes. Specimens indicated with an asterisk (*) not to scale (only approximate). Original material from the original residue from Schulz is indicated with an 'O'. Specimens retrieved from Bonenburg are indicated with BB-sample_slidenr. and England Finder references where available (otherwise microscope coordinates are given).

1. *Limbosporites lundbladiae* NILSSON 1958; BB750_1; 163,165x17,20
2. *Limbosporites lundbladiae* NILSSON 1958; BB0_1; 138,141x6,10
3. *Limbosporites lundbladiae* NILSSON 1958; BB-D-02_2; B31/3
4. *Semiretisporis/(Limbosporites*?); NeoMöckern 1E-10184_4; M41/2
5. *Limbosporites lundbladiae* NILSSON 1958; BB-D-01_2; K53/0
6. *Limbosporites* cf. *microfoveatus* (ZHANG 1979) BAI et al. 1983; BB-D-11_2; J28/2
7. *Limbosporites* cf. *microfoveatus* (ZHANG 1979) BAI et al. 1983; BB2085_1; 126,132x17.5,25
8. *Limbosporites lundbladiae* NILSSON 1958; BB-D-10_2; O32/2
9. Aberrant; *Limbosporites lundbladiae* NILSSON 1958; BB-D-10_2; L31/3
10. Cf. *Limbosporites* sp.; BB-D-18_2; V32/3
11. Cf. *Limbosporites* sp. A; BB2450_2; Q40.1
12. *Limbosporites* cf. *denmeadii* (DE JERSEY 1962) DE JERSEY & RAINE 1990; BB2450_4; L38/0
13. *Limbosporites lundbladiae* NILSSON 1958; BB2550_4; J31/0
14. HOLOTYPE original photograph; *Densoisporites fissus* REINHARDT 1964 (Jan/Feb)
15. Cf. *Limbosporites* sp. A; BB-D-17_2; R28/0
16. *Limbosporites* cf. *foveocingulatus* SCHULZ 1967; BB-D-12_1; H66/4
17. *Limbosporites* cf. *denmeadii* (DE JERSEY 1962) DE JERSEY & RAINE 1990; BB2550_2; 134,138x14,19
18. *Limbosporites* cf. *denmeadii* (DE JERSEY 1962) DE JERSEY & RAINE 1990; BB-D-04_2; D44/4
19. HOLOTYPE refigured; *Cingulatizonites rhaeticus* MÄDLER 1964 (Dec.); M116, TK.Nr. 3142; O23/0; stained
20. PARATYPE refigured; *Cingulatizonites rhaeticus* MÄDLER 1964 (Dec.); M116, net 1 K1; TK.Nr. 3143; stained
21. *Densosporites fissus* (REINHARDT 1964) SCHULZ 1967; BB1800_1; 125,129x21,30
22. *Densosporites fissus* (REINHARDT 1964) SCHULZ 1967; BB-D-11_2; R48/0
23. *Densosporites* sp.; BB1800_1; 162,170x6,15
24. HOLOTYPE original photograph; *Aequitriradites rhaeticus* REINHARDT 1961
25. HOLOTYPE refigured; *Anulatizonites drawehni* MÄDLER 1964; M703, net 1 J8; TK.Nr. 3125; stained
26. *Cingulizonates rhaeticus* (REINHARDT 1961) SCHULZ 1967; BB-D-07_1; J55/1
27. PARATYPE refigured; *Anulatizonites drawehni* MÄDLER 1964; M703, net 2 C3; TK.Nr. 3126; stained
28. HOLOTYPE refigured; *Anulatizonites rotundus* MÄDLER 1964; M703, net 2 A1; TK.Nr. 3127; stained
29. *Anulatizonites sp.* in Mädler 1964; M703, net 2 C5; TK.Nr. 3128; refigured
30. *Cingulizonates rhaeticus* (REINHARDT 1961) SCHULZ 1967; BB-D-12_1; W52/0; contrast enhanced in right half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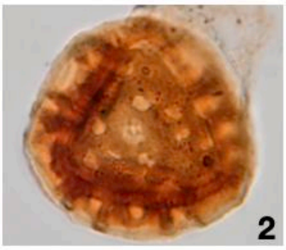
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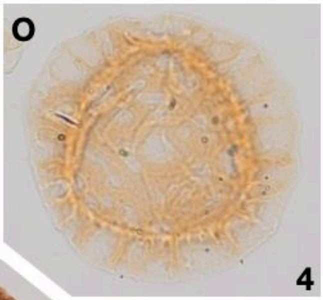

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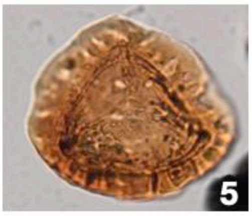
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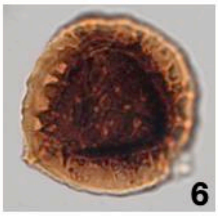
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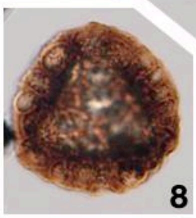
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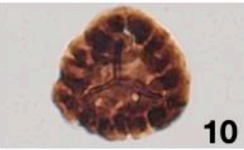
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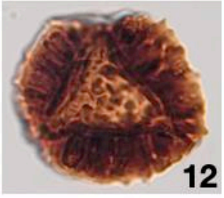
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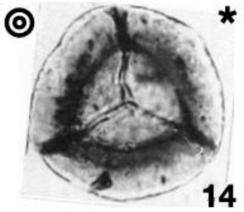

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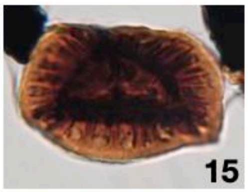
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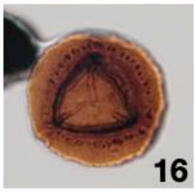
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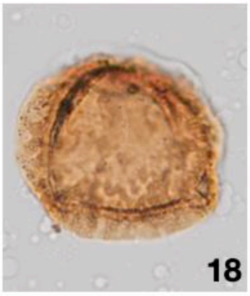
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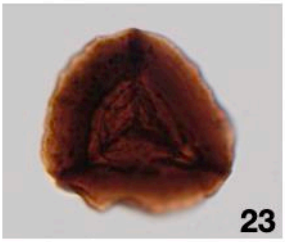
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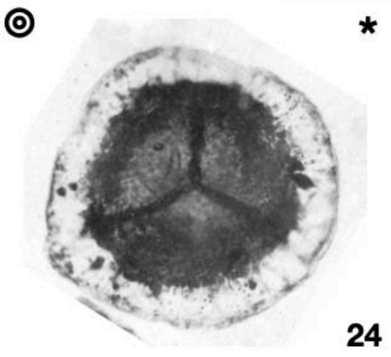

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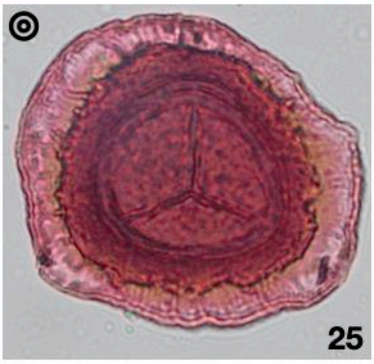

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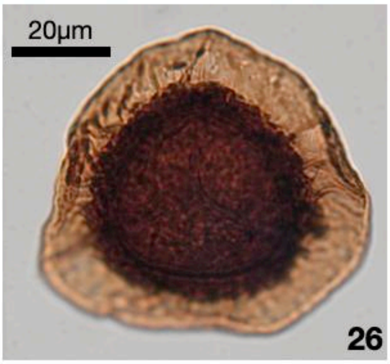

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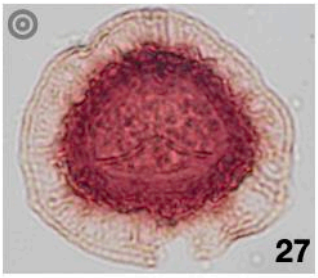

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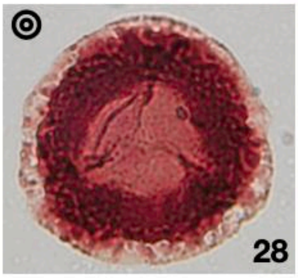

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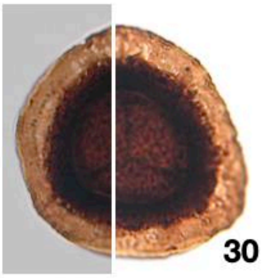
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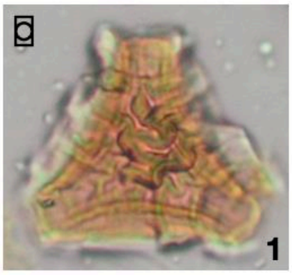
Plate 9. *Perinosporites* spp.

Specimens indicated with ▢ and ◎ depict the original type of the genus and holotypes, respectively. Original material from the original residue from Schulz is indicated with an ‘O’. Specimens retrieved from Bonenburg are indicated with BB-sample_slidenr. and England Finder references where available (otherwise microscope coordinates are given).

1. HOLOTYPE refigured*; Perinosporites thuringiacus* SCHULZ 1962 *emend*.;
2. Potential LECTOTYPE; *Perinosporites thuringiacus* SCHULZ 1962 *emend.*; NeoMöckern 1E_2-10184_2; E40/3
3. *Perinosporites thuringiacus* SCHULZ 1962 *emend.;* Kuhjoch_050926.5; J28/4
4. *Perinosporites thuringiacus* SCHULZ 1962 *emend.;* BB2450_2; 139,142x17,26
5. HOLOTYPE refigured*; Perinosporites thuringiacus* SCHULZ 1962
6. a. and b. Two focal planes of *Perinosporites thuringiacus* SCHULZ 1962 *emend*; BB-D-06_1; L30/3
7. *Perinosporites thuringiacus* SCHULZ 1962 *emend.*; BB-D-06_1; M28/2
8. HOLOTYPE refigured*; Trizonites rugulatus* MÄDLER 1964b; K26/1
9. *Perinosporites rugulatus* (MÄDLER 1964b) nov. comb.; BB-D-02_2; T53/1
10. *Perinosporites rugulatus* (MÄDLER 1964b) nov. comb.; BB-D-11_2; M52/0
11. Aberrant*; Perinosporites rugulatus* (MÄDLER 1964b) nov. comb.; BB-D-07_1; L22/4
12. *Perinosporites thuringiacus* SCHULZ 1962 *emend.;* NeoMöckern 1E_2-10184_2; K46/2
13. *Perinosporites rugulatus* (MÄDLER 1964b) nov. comb.; Kuhjoch_050926.5; S37/2
14. *Perinosporites thuringiacus* SCHULZ 1962 *emend.;* NeoMöckern 1E_1-10184_2; Y50/3
15. *Perinosporites* sp.; NeoMöckern 1E_2-10184_2; Q47/0
16. *Perinosporites thuringiacus* SCHULZ 1962 *emend.;* Kuhjoch_050926.5; T38/3
17. *Perinosporites rugulatus* (MÄDLER 1964b) nov. comb.; BB-D-19_1; Q46/1
18. *Perinosporites* sp.; BB-D-09_2; C32/4
19. Distal side of *Perinosporites thuringiacus* SCHULZ 1962 *emend;* Kuhjoch_050926.5; J28/1
20. cf. *Perinosporites* sp.; BB-D-19_1; Q50/1
21. cf. *Perinosporites* sp.; BB-D-09_2; J33/4
22. *Perinosporites* sp.; NeoMöckern 1E_2-10184_2; K37/4
23. cf. *Perinosporites* sp.; BB-D-18_2; V32/4
24. cf. *Perinosporites* sp.; BB-D-09_2; J33/4
25. cf. *Perinosporites* sp.; BB-D-08_1; E26/1
26. Aberrant*, Cornutisporites/Perinosporites* hybrid; BB-D-15_1; M34/1
27. *Perinosporites rugulatus* (MÄDLER 1964b) nov. comb.; NeoMöckern 1E_1-10184_2; L50/3
28. Remain of *Perinosporites thuringiacus* SCHULZ 1962 *emend*.; NeoMöckern 1E_1-10184_2; S54/3
29. Remain of cf. *Perinosporites* sp.; BB-D-04_2; K44/4
30. Remain of cf. *Perinosporites* sp.; NeoMöckern 1E_-10184_2; Y49/0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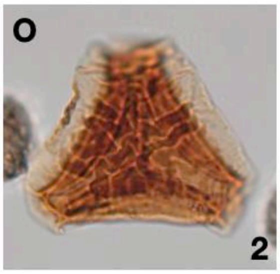

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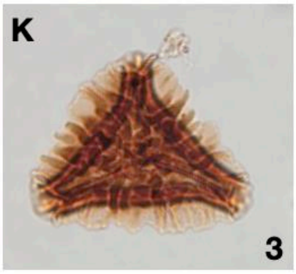

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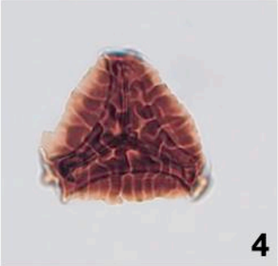
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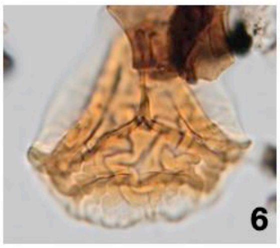
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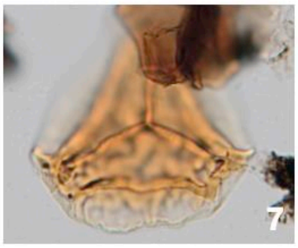
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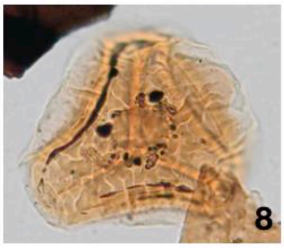
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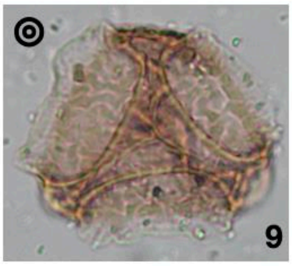
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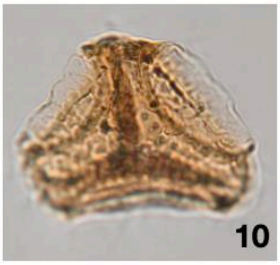
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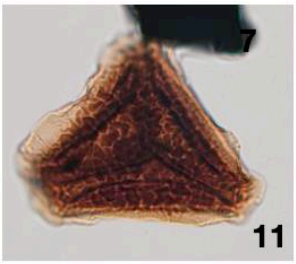

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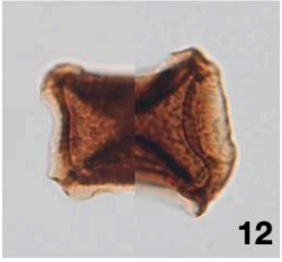
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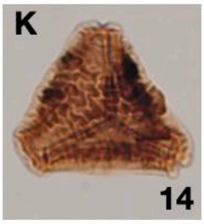

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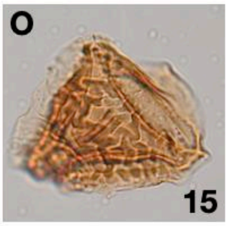

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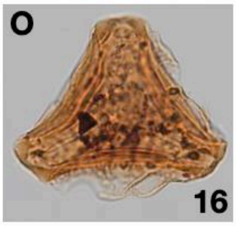

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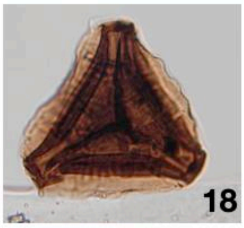
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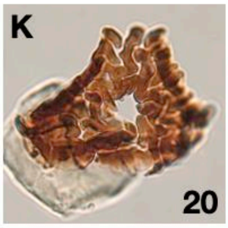

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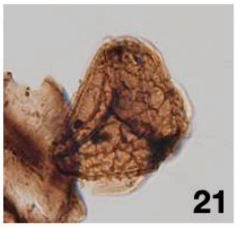
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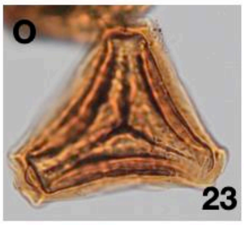

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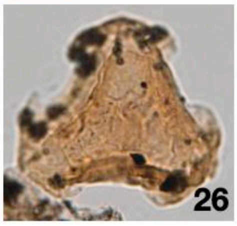
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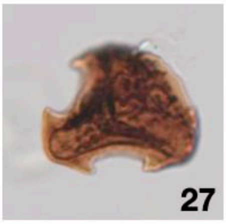
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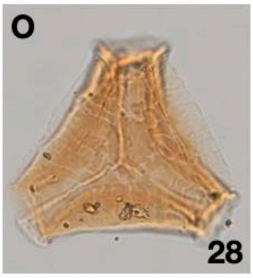

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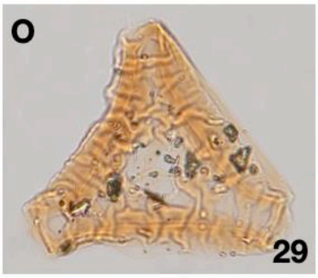

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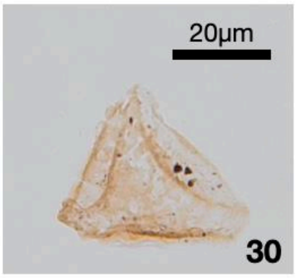

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Plate 10. Taeniate pollen

Specimens indicated with an ◎ depict holotypes. Original material from the original residue from Schulz is indicated with an 'O'. Specimens from Kuhjoch are indicated with a 'K' in the Plate. Specimens retrieved from Bonenburg are indicated with BB-sample_slidenr. and England Finder references where available (otherwise microscope coordinates are given).

1. HOLOTYPE refigured*;* *Taeniaeporites rhaeticus* SCHULZ 1967, Möckern 1E – 10184.1; M42/2
2. Potential LECTOTYPE; *Lunatisporites rhaeticus* (SCHULZ 1967) WARRINGTON 1974, Möckern 1E – 10184_S2, P29/4
3. Potential LECTOTYPE; *Lunatisporites rhaeticus* (SCHULZ 1967) WARRINGTON 1974, Möckern 1E – 10184_S2, N44/1
4. *Lunatisporites rhaeticus* (SCHULZ 1967) WARRINGTON 1974, BB-D-02_2L; U57.1
5. *Lunatisporites rhaeticus* (SCHULZ 1967) WARRINGTON 1974*,* BB-2552_S4; R41.2
6. *Lunatisporites rhaeticus* (SCHULZ 1967) WARRINGTON 1974*,* BB-D-15_1; H36.3
7. *Lunatisporites rhaeticus* (SCHULZ 1967) WARRINGTON 1974*,* BB-D-15_1; E58.0
8. *Lunatisporites rhaeticus* (SCHULZ 1967) WARRINGTON 1974*,* BB-2085; no EF references
9. *Lunatisporites rhaeticus* (SCHULZ 1967) WARRINGTON 1974*,* BB-D-12_1; X27.4
10. *Lunatisporites rhaeticus* (SCHULZ 1967) WARRINGTON 1974*,* BB-D-01_2; E57.2
11. *Lunatisporites* cf. *acutus* LESCHIK 1955 emend. SCHEURING 1970, BB-D-04_2; W51.3
12. *Lunatisporites rhaeticus* (SCHULZ 1967) WARRINGTON 1974, BB-1150_1; no EF references
13. *Lunatisporites rhaeticus* (SCHULZ 1967) WARRINGTON 1974*,* BB-D-03_3; R38.0
14. *Lunatisporites rhaeticus* (SCHULZ 1967) WARRINGTON 1974*,* BB-D-05_1; F50.2
15. *Lunatisporites rhaeticus* (SCHULZ 1967) WARRINGTON 1974*,* BB-D-10_2; W53.1
16. *Protohaploxypinus* sp., similar to Scheuring (1970), Pl. 12, Fig. 73, BB-D-02_2; F31.4
17. *Striatoabieites aytugii* VISSCHER 1966 emend. SCHEURING 1970*,* BB-2550_1; Z39.3
18. *Striatoabieites* sp., BB-1800_1; no EF references
19. *Striatoabieites* sp., Kuhjoch_050926_5; J29.3

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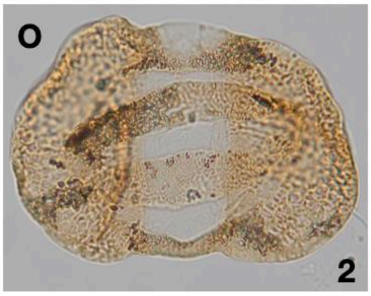

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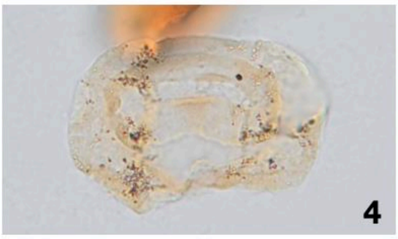
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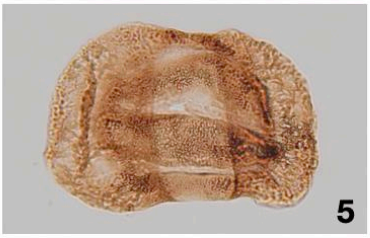
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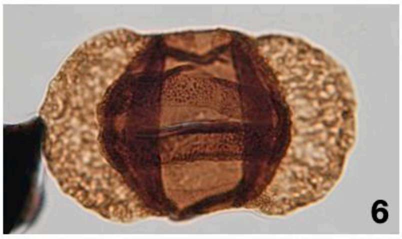
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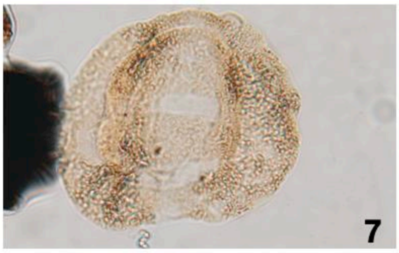
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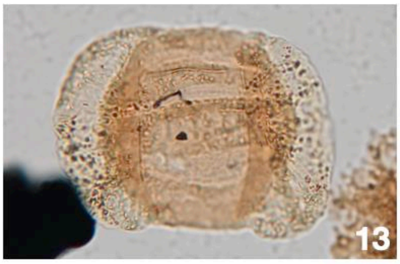
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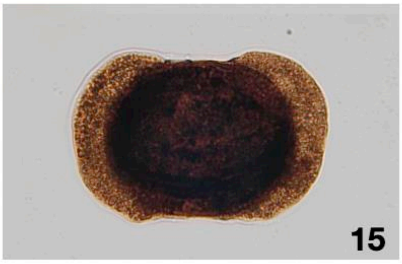
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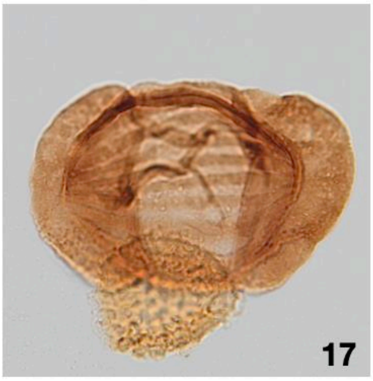
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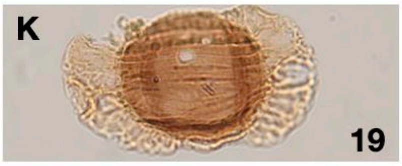

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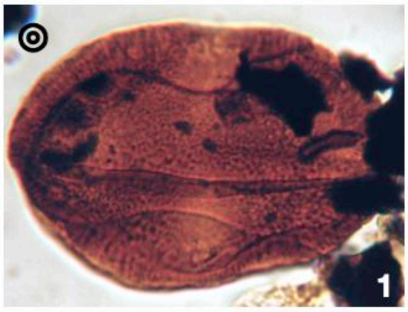
Plate 11. *Ovalipollis* spp. pollen

Specimens indicated with an ◎ depict holotypes. Specimens retrieved from Bonenburg are indicated with BB-sample_slidenr. and England Finder references where available (otherwise microscope coordinates are given).

1. Holotype refigured; *Ovalipollis rarus* Klaus 1960
2. Holotype refigured; *Ovalipollis lunzensis* Klaus 1960
3. Holotype refigured; *Ovalipollis grebe* Klaus 1960
4. Holotype (‘lost’) original photograph; *Pollenites pseudoalatus* Thiergart 1949, Pl. 1, Fig. 15
5. *Ovalipollis pseudoalatus* (Thiergart 1949) Schuurman 1976, BB-D-13_2; N59/3
6. *Ovalipollis pseudoalatus* (Thiergart 1949) Schuurman 1976, BB-D-14_2; N38/0
7. *Ovalipollis pseudoalatus* (Thiergart 1949) Schuurman 1976, BB-D-16_2; P58/1
8. *Ovalipollis pseudoalatus* (Thiergart 1949) Schuurman 1976, BB-D-17_2; O29/1
9. *Ovalipollis pseudoalatus* (Thiergart 1949) Schuurman 1976, BB-D-07_1; N55/2
10. *Ovalipollis pseudoalatus* (Thiergart 1949) Schuurman 1976, BB-D-12_1; E26/1
11. *Ovalipollis pseudoalatus* (Thiergart 1949) Schuurman 1976, BB-D-05_1; K62/1
12. *Ovalipollis pseudoalatus* (Thiergart 1949) Schuurman 1976, BB-D-08_1; Q33/1
13. *Ovalipollis pseudoalatus* (Thiergart 1949) Schuurman 1976, BB-D-17_2; R26/0
14. *Ovalipollis pseudoalatus* (Thiergart 1949) Schuurman 1976, BB750_1; 158, 160 x 17,21
15. *Ovalipollis pseudoalatus* (Thiergart 1949) Schuurman 1976, BB-D-11_2; J53/0
16. *Ovalipollis pseudoalatus* (Thiergart 1949) Schuurman 1976, BB-D-07_1; N56/4
17. *Ovalipollis pseudoalatus* (Thiergart 1949) Schuurman 1976, BB-D-04_2; J35/1
18. *Ovalipollis pseudoalatus* (Thiergart 1949) Schuurman 1976, BB-D-07_1; M57/1
19. *Ovalipollis pseudoalatus* (Thiergart 1949) Schuurman 1976, BB-D-06_1; N23/4
20. *Ovalipollis pseudoalatus* (Thiergart 1949) Schuurman 1976, BB750_1; 158,165 x 14,16
21. *Ovalipollis pseudoalatus* (Thiergart 1949) Schuurman 1976, BB-D-02_2; X58/1
22. *Ovalipollis pseudoalatus* (Thiergart 1949) Schuurman 1976, BB-D-08_1; R32/4
23. *Ovalipollis pseudoalatus* (Thiergart 1949) Schuurman 1976, BB-D-10_2; W51/0
24. *Ovalipollis pseudoalatus* (Thiergart 1949) Schuurman 1976, BB_2550_4; J33/0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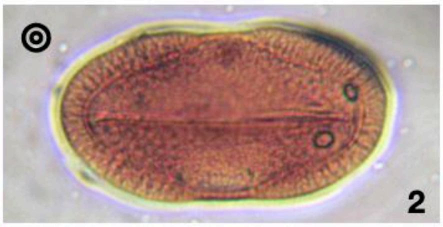
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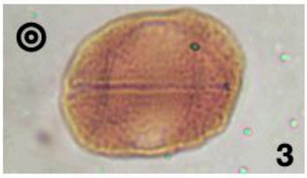
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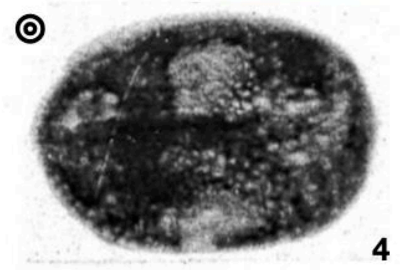
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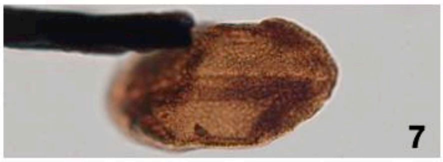
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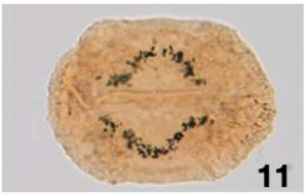
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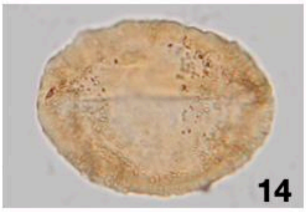
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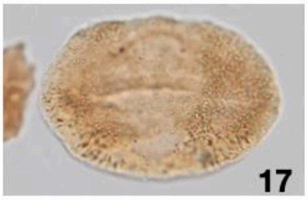
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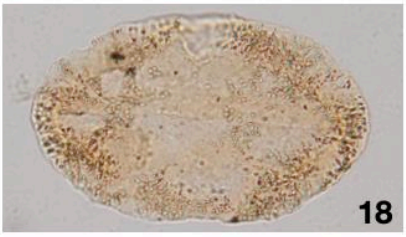
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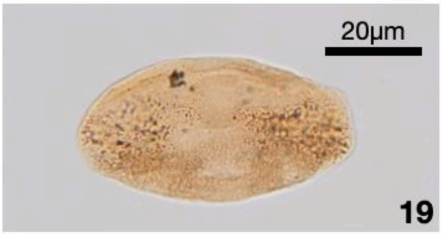
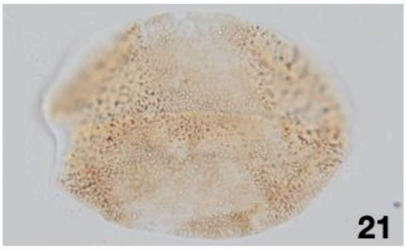

20µm
19


20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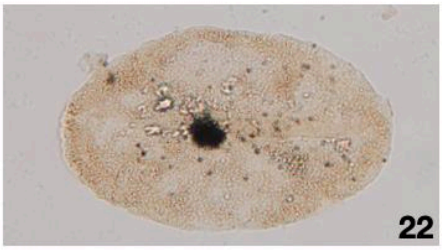

22


23


24

Plate 12. Monosulcate pollen

Specimens retrieved from Bonenburg are indicated with BB-sample_slidenr. and England Finder references where available (otherwise microscope coordinates are given).

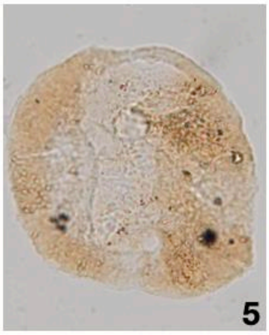
1. *Quadraeculina annelaeformis* MALYAVKINA 1949, BB-D-12_1; M29/0
2. *Quadraeculina annelaeformis* MALYAVKINA 1949, BB-D-07_1; F36/2
3. *Quadraeculina annelaeformis* MALYAVKINA 1949, BB-D-02_2; X57/4
4. *Quadraeculina annelaeformis* MALYAVKINA 1949, BB-D-08_2; H29/3
5. *Quadraeculina annelaeformis* MALYAVKINA 1949, BB-D-08_1; E23/3
6. *Quadraeculina annelaeformis* MALYAVKINA 1949, BB-D-09_2; R30/2
7. *Quadraeculina annelaeformis* MALYAVKINA 1949, BB-D-15_1; S57/0
8. *Quadraeculina annelaeformis* MALYAVKINA 1949, BB-D-05_1; S57/4
9. *Quadraeculina annelaeformis* MALYAVKINA 1949, BB-D-12_1; N28/0
10. *Quadraeculina annelaeformis* MALYAVKINA 1949, BB-D-13_2; H57/3
11. cf. *Quadraeculina annelaeformis* MALYAVKINA 1949, BB-D-19_2; N60/3
12. *Chasmatosporites apertus* (MALYAVKINA 1949) NILSSON 1958, BB-D-07_1; J55/1
13. *Chasmatosporites apertus* (MALYAVKINA 1949) NILSSON 1958, BB_300_2; 155,163 x 12.5,17
14. *Chasmatosporites apertus* (MALYAVKINA 1949) NILSSON 1958, BB-D-04_2; S31/2
15. *Chasmatosporites apertus* (MALYAVKINA 1949) NILSSON 1958, BB-D-01_2; T64/1
16. *Chasmatosporites hians* NILSSON 1958, BB_1650_1, 129,135 x 15,20
17. *Chasmatosporites hians* NILSSON 1958, BB-D-05_1; U63/3
18. *Chasmatosporites hians* NILSSON 1958, BB_+600_1; T62/2
19. *Chasmatosporites hians* NILSSON 1958, BB-D-01_2; E56/0
20. *Chasmatosporites* cf. *hians* NILSSON 1958, BB-D-01_2; T64/3
21. *Chasmatosporites major* NILSSON 1958 emend. POCOCK & JANSONIUS 1969*,* BB-D-02_2; W58/2
22. cf. *Chasmatosporites major* NILSSON 1958 emend. POCOCK & JANSONIUS 1969, BB_1075_2; 155,156x5,12
23. *Chasmatosporites hians* NILSSON 1958, BB-D-02_2; C47/4
24. cf. *Chasmatosporites*, BB-D-05_1; S62/2
25. *Chasmatosporites elegans* NILSSON 1958, BB-D-01_2; 135,142 x 3,7
26. *Chasmatosporites elegans* NILSSON 1958, BB-D-04_2; E31/0


1


2


3


4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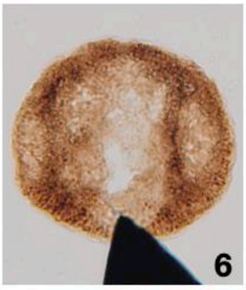
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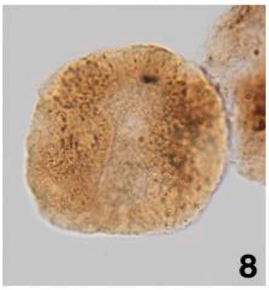
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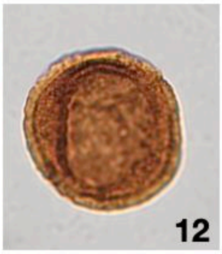
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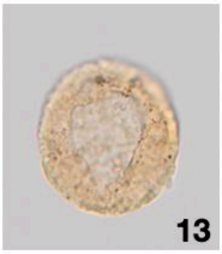
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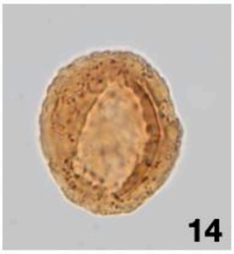
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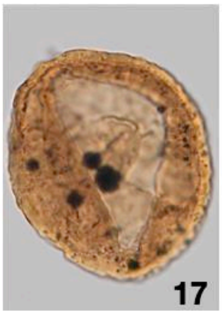
16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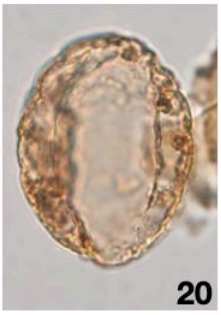
18


19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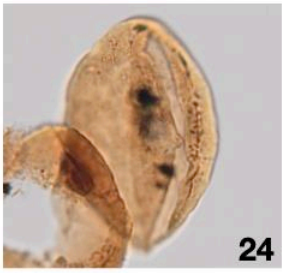
22


23


24


25


26

Plate 13. *Ricciisporites* spp. I

Specimens indicated with an ◎ depict holotypes. Original material from the original residue from Schulz is indicated with an ‘O’. Specimens from Kuhjoch are indicated with a ‘K’ in the Plate. Specimens retrieved from Bonenburg are indicated with BB-sample_slidenr. and England Finder references where available (otherwise microscope coordinates are given)

1. a. *Ricciisporites tuberculatus* LUNDBLAD 1954 LUNDBLAD 1969 *emend.*, BB-952_2; no references, partial overlay of fluorescence and Aptom image
   b. same specimen seen with fluorescence light and ApoTome
2. *Ricciisporites tuberculatus* LUNDBLAD 1954 LUNDBLAD 1969 *emend.*, BB-D-01_2; K63/1
3. *Ricciisporites tuberculatus* LUNDBLAD 1954 LUNDBLAD 1969 *emend.*, Drawehn2; J18/1
4. *Ricciisporites tuberculatus* LUNDBLAD 1954 LUNDBLAD 1969 *emend.*, BB_900_1; P60/3
5. *Ricciisporites tuberculatus* LUNDBLAD 1954 LUNDBLAD 1969 *emend.*, BB-D-07_1; K36/4
6. *Ricciisporites tuberculatus* LUNDBLAD 1954 LUNDBLAD 1969 *emend.*, BB_1000_1; no references, seen with fluorescence and ApoTome
7. *Ricciisporites tuberculatus* LUNDBLAD 1954 LUNDBLAD 1969 *emend.*, BB-D-05; R54/3
8. *Ricciisporites tuberculatus* LUNDBLAD 1954 LUNDBLAD 1969 *emend.*, BB_1000_1; no references, seen with fluorescence and ApoTome
9. *Ricciisporites tuberculatus* LUNDBLAD 1954 LUNDBLAD 1969 *emend.*, BB-D-03_3; S39/0
10. a. *Ricciisporites tuberculatus* LUNDBLAD 1954 LUNDBLAD 1969 *emend.*, BB_952_2; no references, partial overlay of fluorescence and ApoTome image
    b. same specimen seen with fluorescence and ApoTome
    c. *Ricciisporites tuberculatus* LUNDBLAD 1954 LUNDBLAD 1969 *emend.*, BB_952, SEM image
11. *Ricciisporites tuberculatus* LUNDBLAD 1954 LUNDBLAD 1969 *emend.*, BB_1042_3; F27/1
12. *Ricciisporites tuberculatus* LUNDBLAD 1954 LUNDBLAD 1969 *emend.*, BB-D-13_2; G32/2
13. *Ricciisporites tuberculatus* LUNDBLAD 1954 LUNDBLAD 1969 *emend.*, Marnitz 59.2, P46/4

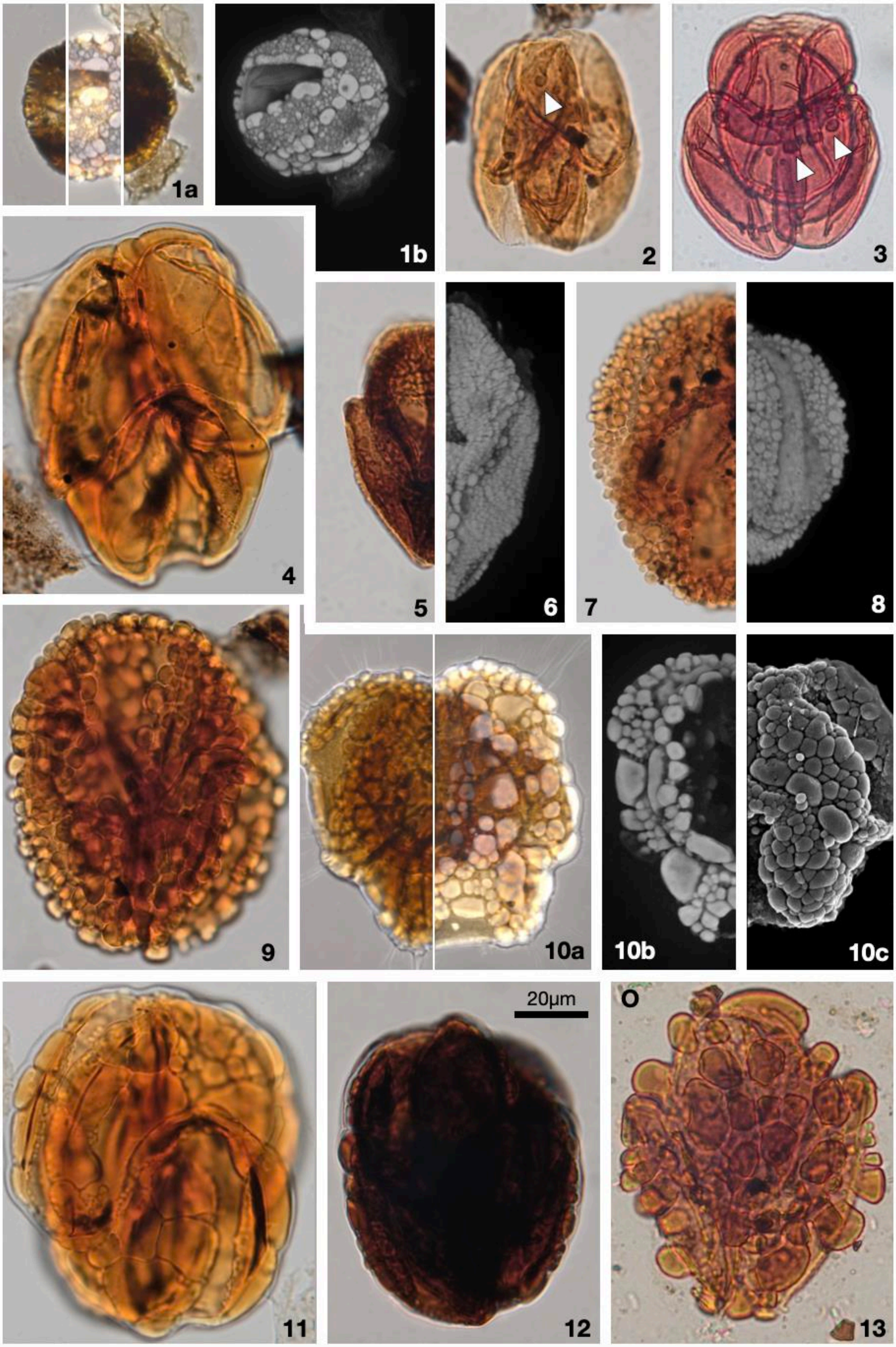

1a
1b
2
3
4
5
6
7
8
9
10a
10b
10c
20µm
O
11
12
13

Plate 14. *Ricciisporites* spp. II

Specimens indicated with an ◎ depict holotypes. Original material from the original residue from Schulz is indicated with an ‘O’. Specimens from Kuhjoch are indicated with a ‘K’ in the Plate. Specimens retrieved from Bonenburg are indicated with BB-sample_slidenr. and England Finder references where available (otherwise microscope coordinates are given).

1. Aberrant; *Ricciisporites tuberculatus* LUNDBLAD 1954 LUNDBLAD 1969 *emend.*, Neo-Möckern 1E_2; V40/1
2. a. Aberrant; *Ricciisporites tuberculatus* LUNDBLAD 1954 LUNDBLAD 1969 *emend*., BB_1000_1; no references
   b. same specimen seen with fluorescence and ApoTome
3. a. Aberrant; *Ricciisporites tuberculatus* LUNDBLAD 1954 LUNDBLAD 1969 *emend*., BB_1000_1; no references
   b. same specimen seen with fluorescence and ApoTome
4. Aberrant; *Ricciisporites tuberculatus* LUNDBLAD 1954 LUNDBLAD 1969 *emend*., BB-D-05_1; P50/0
5. *Ricciisporites tuberculatus* LUNDBLAD 1954 LUNDBLAD 1969 *emend*., BB_900_1; 153,163x 11,20
6. *Ricciisporites tuberculatus* LUNDBLAD 1954 LUNDBLAD 1969 *emend*., BB-D-19; K60/3
7. Aberrant; *Ricciisporites tuberculatus* LUNDBLAD 1954 LUNDBLAD 1969 *emend.*, Neo-Möckern 1E_4; Q47/0
8. ? Aberrant; *Ricciisporites tuberculatus* LUNDBLAD 1954 LUNDBLAD 1969 *emend*., BB-D-01_2; G58/4
9. *Ricciisporites tuberculatus* LUNDBLAD 1954 LUNDBLAD 1969 *emend*., BB-D-01_2; G58/2
10. Fragment of ornamentation from *Ricciisporites tuberculatus* LUNDBLAD 1954 LUNDBLAD 1969 *emend*., BB-D-01_2; O55/2
11. Single grain of tetrad of *Ricciisporites tuberculatus* LUNDBLAD 1954 LUNDBLAD 1969 *emend*., BB-D-02_2; N34/2
12. Single grain of tetrad of *Ricciisporites tuberculatus* LUNDBLAD 1954 LUNDBLAD 1969 *emend*., BB_2550_1; M46/3
13. Single grain of tetrad of *Ricciisporites tuberculatus* LUNDBLAD 1954 LUNDBLAD 1969 *emend*., BB-D-06_3; W34/3

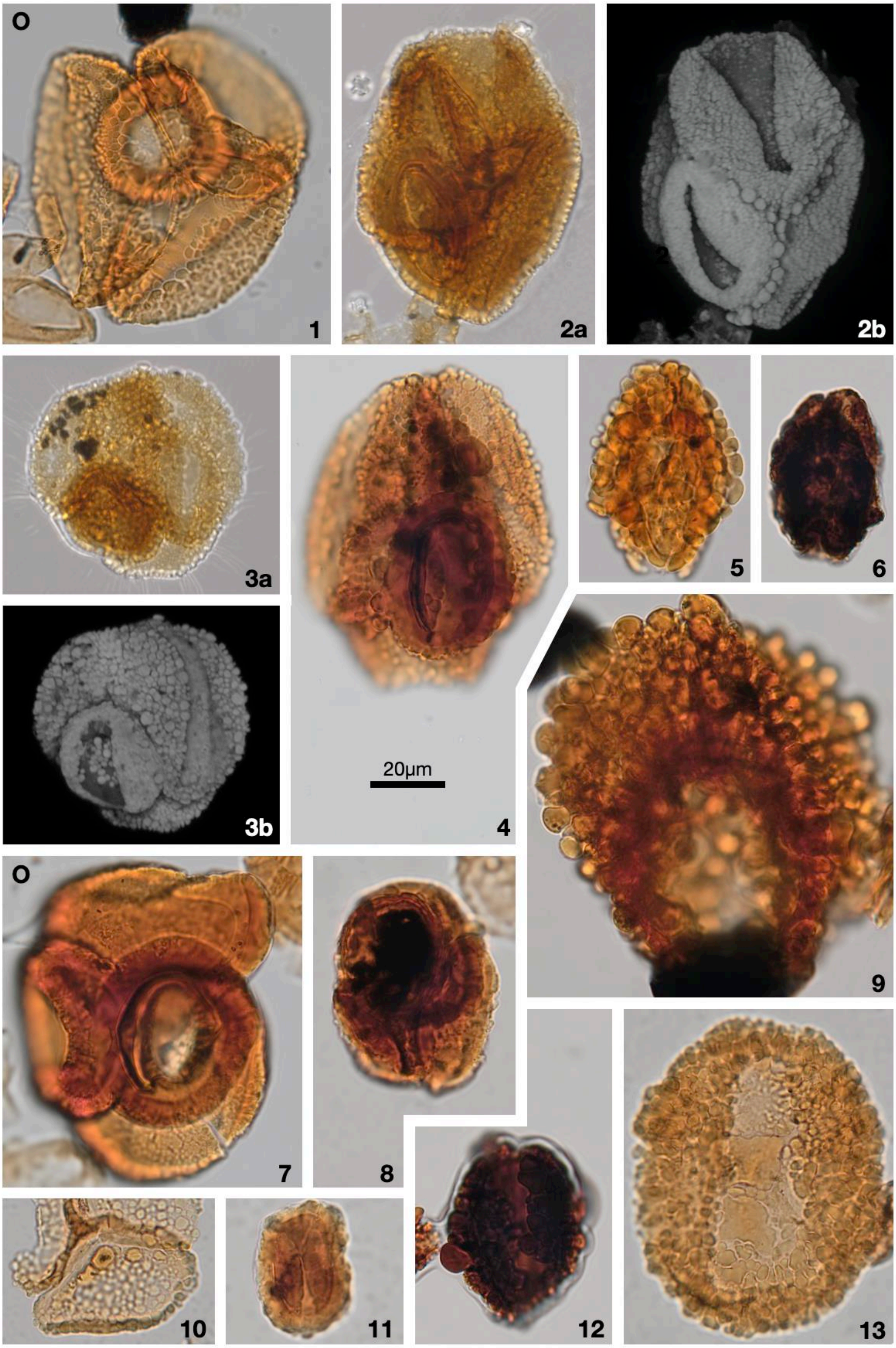

O
1
2a
2b
3a
3b
4
20µm
5
6
9
O
7
8
10
11
12
13

Plate 15. Circumpolles pollen I

Specimens indicated with an ◎ depict type material. Original material from the original residue from Schulz is indicated with an ‘O’. Specimens from St. Audrey’s Bay are indicated with a ‘S’ in the plate. Specimens retrieved from Bonenburg are indicated with BB-sample_slidenr. and England Finder references where available (otherwise microscope coordinates are given). Specimen according to scale in Fig. 30 unless vertical scale (=10 µm micron) is given.

1. a. *Classopollis meyeriana* (Klaus 1960) Venkatachala & Goczan 1964; BB_900_1; no references
   b. same specimen seen with DIC, seen from distal side, proximal shining through
   c. same specimen seen with fluorescence and ApoTome, distal view
2. *Classopollis meyeriana* (Klaus 1960) Venkatachala & Goczan 1964, proximal side seen with standard fluorescene without ApoTome; BB_1012(7)_1; 101,110x 9,18
3. Holotype refigured*; Circulina meyeriana* Klaus 1960
4. *Classopollis classoides* Pflug 1953 tetrad; BB_300_1; C57/1
5. *Classopollis classoides* Pflug 1953 tetrad remain; BB-D-18_2; M39/4
6. *Classopollis meyeriana* (Klaus 1960) Venkatachala & Goczan 1964 tetrad; BB_300_1, P63/4
7. Paratype refigured*; Circulina meyeriana* Klaus 1960
8. *Classopollis classoides* Pflug 1953; BB-D-08_1; E27/0
9. *Classopollis classoides* Pflug 1953; BB-D-12_1; O32/2
10. *Classopollis classoides* Pflug 1953; BB-D-09_1; S27/3
11. *Classopollis classoides* Pflug 1953; BB-D-05_1; V61/1
12. Lectotype refigured; *Pollenites reclusus* Thiergart 1949
13. *Classopollis classoides* Pflug 1953; BB-D-16_2; O58/3
14. *Classopollis classoides* Pflug 1953; BB_1000_2; no references
15. *Classopollis classoides* Pflug 1953; BB-D-09_2; N30/3
16. *Granuloperculatipollis rudis* Venkatachala & Goczan 1964, BB_1042_S3; 131,133 x 6,15
17. *Granuloperculatipollis rudis* Venkatachala & Goczan 1964, BB_1042_S3; 142,145 x 9,14
18. *Geopollis zwolinskai* (Lund 1977) Brenner 1986; BB-D-06_1; S28/3
19. *Geopollis zwolinskai* (Lund 1977) Brenner 1986; BB-D-05_1; P62/0, visual crossing of the rimulae is indicated by arrow heads
20. *Geopollis zwolinskai* (Lund 1977) Brenner 1986; BB-D-05_1; P62/1, visual crossing of the rimulae is indicated by arrow heads
21. *Geopollis zwolinskai* (Lund 1977) Brenner 1986; BB-D-10_2; Q53/2
22. *Cf. Geopollis zwolinskai* (Lund 1977) Brenner 1986; BB-D-08_1; M30/0
23. cf. *Classopollis* sp. tetrad, unusually small and hyaline, SAB_118_2; V38/0
24. Aberrant *Classopollis* sp.; SAB_118_2; P39/2
25. Aberrant *Classopollis* sp.; NeoCamin_148_1; R61/3
26. *Classopollis classoides* Pflug 1953; NeoCamin_148_1; U45/4
27. *Classopollis classoides* Pflug 1953; BB_-150_1; 154.2,157 x 17,27
28. *Classopollis meyeriana* (Klaus 1960) Venkatachala & Goczan 1964, arrow heads indicate the distal pore and the proximal triangle, BB-D-02_2; O54/3
29. *Classopollis classoides* Pflug 1953; BB-D-04_2; G31/0 arrow heads indicate the sub-rimulate striae and proximal hairs
30. *Classopollis classoides* Pflug 1953 remain, detailing the proximal side and ornamentation, Kuhjoch_050926_5; R35/0
31. *Classopollis classoides* Pflug 1953, proximal side, detail on hairs, BB-D-08_1; BB-D-08; L28/3

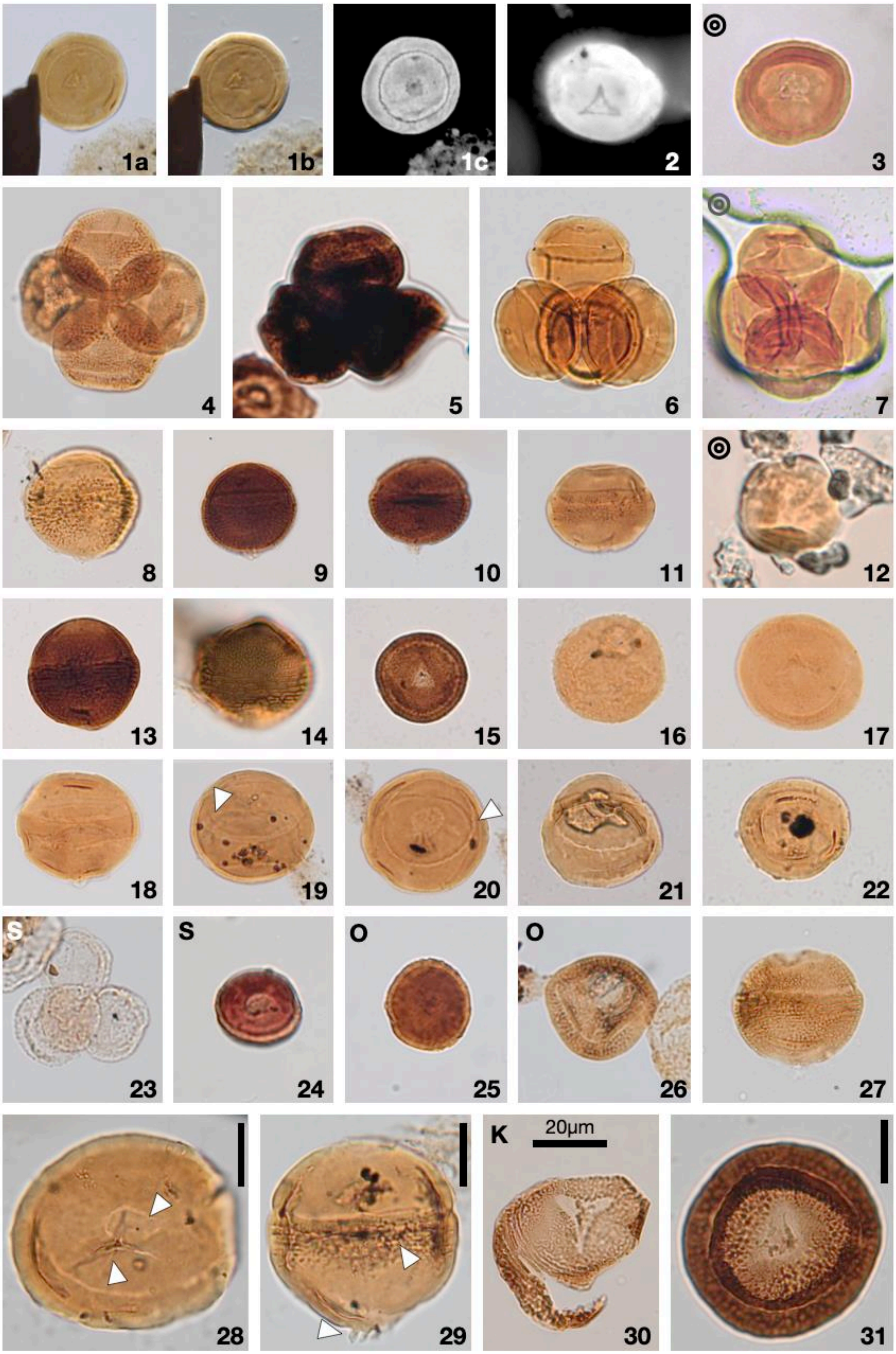

1a
1b
1c
2
◎
3
4
5
6
◎
7
8
9
10
11
◎
12
13
14
15
16
17
18
19
20
21
22
S
23
S
24
O
25
O
26
27
28
29
K
20µm
30
31

Plate 16. Circumpolles pollen II

Original material from the original residues from Schulz (Camin, Marnitz, Seeberg) is indicated with an ‘O’. Specimens from St. Audrey’s Bay are indicated with a ‘S’ in the plate. Specimens retrieved from Bonenburg are indicated with BB-sample_slidenr. and England Finder references where available (otherwise microscope coordinates are given).

1. *Granuloperculatipollis rudis* Venkatachala & Goczan 1964, BB-D-03_1;
2. Aberrant tetrad, *Classopollis meyeriana* (Klaus 1960) Venkatachala & Goczan 1964, SAB_118_2; Q36/4
3. Aberrant tetrad, *Classopollis meyeriana* (Klaus 1960) Venkatachala & Goczan 1964, SAB_118_2; C33/4
4. Aberrant tetrad, *Classopollis meyeriana* (Klaus 1960) Venkatachala & Goczan 1964, Seeberg 1.1; N34/2
5. Aberrant tetrad, *Classopollis classoides* Pflug 1953, BB_150_1; X30/0
6. Aberrant tetrad, *Classopollis meyeriana* (Klaus 1960) Venkatachala & Goczan 1964, SAB_118_2; E45/4
7. Aberrant tetrad, *Classopollis meyeriana* (Klaus 1960) Venkatachala & Goczan 1964, SAB_118_2; D41/4
8. Aberrant *Classopollis* sp.; SAB_118_2; P39/2
9. Aberrant tetrad, *Classopollis classoides* Pflug 1953, BB-D-05_1; Q51/1
10. Aberrant tetrad, *Classopollis classoides* Pflug 1953, BB_150_1; L22/3
11. Aberrant tetrad, *Classopollis* sp.; BB3040_1; no references
12. Aberrant tetrad, *Classopollis* sp.; Kuhjoch_050926_5; D26/1
13. Aberrant tetrad remain *Classopollis* sp.; SAB_118_2; V38/4
14. Aberrant tetrad remain *Classopollis* sp.; SAB_118_2; S48/2
15. Aberrant tetrad remain *Classopollis* sp.; SAB_118_2; N40/2
16. Aberrant tetrad remain *Classopollis* sp.; Marnitz, no references, Camin_148.1
17. Aberrant tetrad remain, *Classopollis* sp. BB_450_3; O41/1
18. Aberrant tetrad remain, *Classopollis classoides* Pflug 1953, BB_150_1; 126,127x 8,11
19. Aberrant tetrad remain, *Classopollis classoides* Pflug 1953, Camin_148.1; N62/4
20. Aberrant tetrad, *Classopollis* sp. BB_300_2; 122,129x16,20
21. Aberrant tetrad remain *Classopollis* sp.; BB-D-01_2; G61/4
22. Aberrant tetrad, *Classopollis* sp.; SAB_118_2; Q37/0
23. Aberrant tetrad, *Classopollis* sp.; BB_150_1; H22/3
24. Aberrant tetrad, *Classopollis* sp.; SAB_118_2; S33/4
25. Aberrant tetrad, *Classopollis* sp.; SAB_118_2; V38/2
26. Aberrant tetrad remains of *Classopollis* sp. (left); lying apart from, but close to a normal *Classopollis meyeriana* (right), SAB_118_2; Q35/2
27. Aberrant tetrad, *Classopollis* sp.; SAB_118_2; T40/3
28. Aberrant tetrad, *Classopollis* sp.; SAB_118_2; P26/2
29. Aberrant tetrad, *Classopollis* sp.; BB_150_1; V37/3
30. *Classopollis meyeriana* (Klaus 1960) Venkatachala & Goczan 1964, cluster of 6, SAB_118_2; J35/47es.

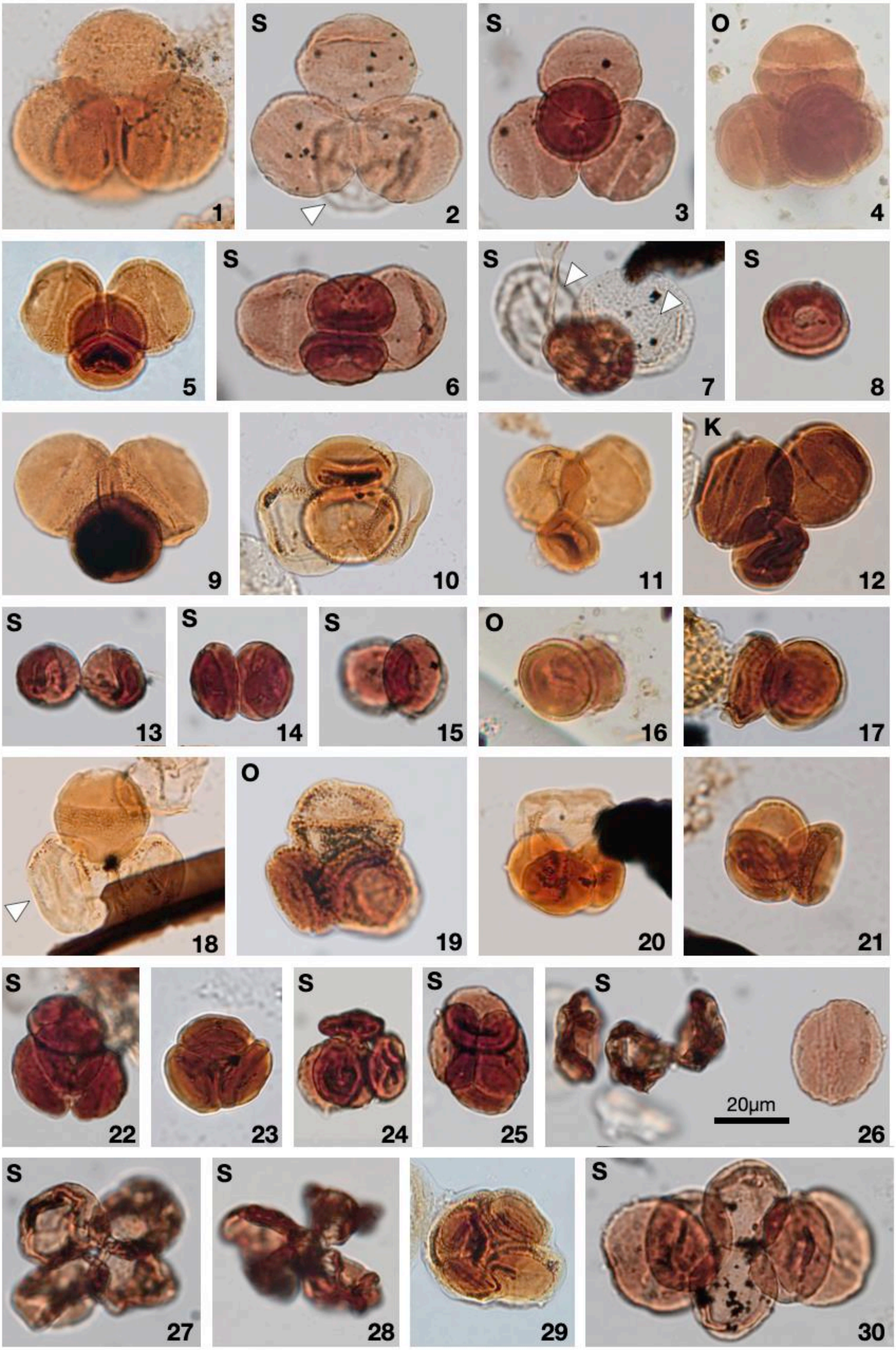
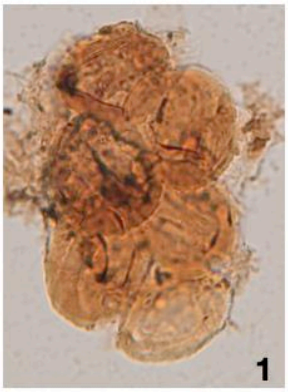

1
S
2
S
3
O
4
5
S
6
S
7
S
8
9
10
11
K
12
S
13
S
14
S
15
O
16
17
18
O
19
20
21
S
22
23
S
24
S
25
S
20µm
26
S
27
S
28
29
S
30

Plate 17. Circumpolles pollen II

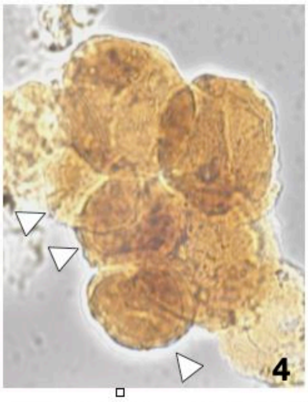
Specimens retrieved from Bonenburg are indicated with BB-sample_slidenr. and England Finder references where available (otherwise microscope coordinates are given).

1. *Classopollis* sp., cluster of 6; BB-D-03_1; P55/1
2. *Classopollis* sp., cluster of 6; BB_300_1; S75/3
3. *Classopollis meyeriana* (Klaus 1960) Venkatachala & Goczan 1964, cluster of 9, BB1000_1, no references
4. *Classopollis* sp. cluster of 8 uneven sized grains; BB_3040_1; no references, arrow heads indicate smaller grains
5. a. *Geopollis zwolinskai* (Lund 1977) Brenner 1986, cluster of 11; BB_1000_1; J32/4
   b. same specimens seen as an overlay of the DIC and ApoTome images
   c. same specimens seen with fluorescence and ApoTome
6. cf. *Classopollis classoides* Pflug 1953, cluster of 7, BB_300_2; 172,173 x 6.5,11
7. a. *Classopollis meyeriana* (Klaus 1960) Venkatachala & Goczan 1964, tetrad, BB952_2
   b. same specimens seen with fluorescence and ApoTome
8. *Classopollis classoides* Pflug 1953, tetrad with one aberrant grain;
9. *Classopollis meyeriana* (Klaus 1960) Venkatachala & Goczan 1964, tetrad with grains of different preservation, BB300_1; P58/4
10. *Classopollis meyeriana* (Klaus 1960) Venkatachala & Goczan 1964, tetrad, BB_300_1, U25/4
11. *Classopollis classoides* Pflug 1953, BB_150_1, V68/2
12. *Classopollis* sp. cluster of aberrant or underdeveloped grains, BB-D-06_3; W24/3
13. a. *Classopollis meyeriana* (Klaus 1960) Venkatachala & Goczan 1964, tetrad remain of 2; BB_1000_1; no references
    b. same specimens seen as an overlay of the DIC and ApoTome images,
    c. same specimens seen with fluorescence and ApoTome


1


2


3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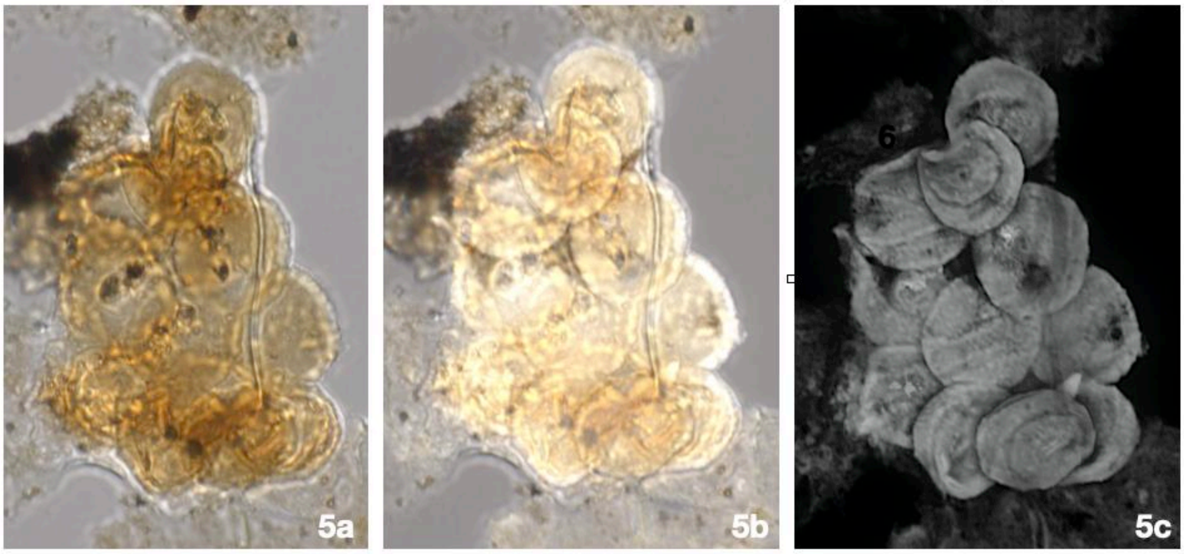
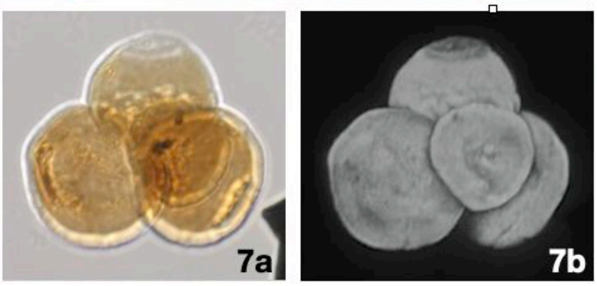

5a
5b
6
5c


20µm
6

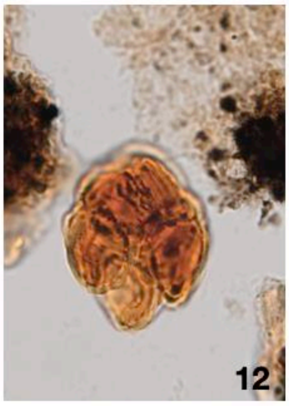

7a
7b


8


9


10


11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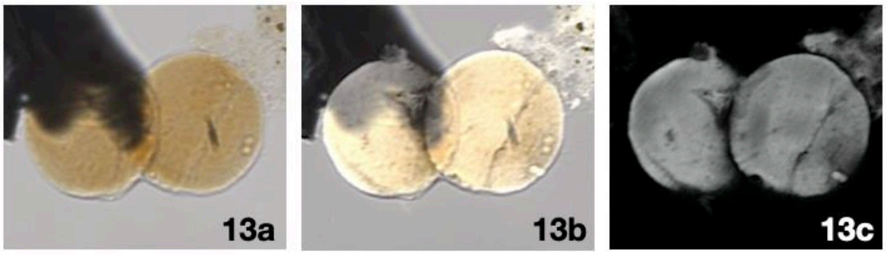
13a
13b
13c

Plate 18. *Rhaetipollis germanicus*

Specimens indicated with an ◎ depict holotypes. Original material from the original residue from Schulz is indicated with an 'O'. Specimens from Kuhjoch are indicated with a 'K' in the Plate. Specimens retrieved from Bonenburg are indicated with BB-sample_slidenr. and England Finder references where available (otherwise microscope coordinates are given) below.

1. *Rhaetipollis germanicus* SCHULZ 1967, side A, BB_952_1; V59.1
2. *Rhaetipollis germanicus* SCHULZ 1967, BB_-75_1, no references available, standard fluorescence
3. *Rhaetipollis germanicus* SCHULZ 1967, side B, Möckern 1E_4; Q46/3
4. a – *Rhaetipollis germanicus* SCHULZ 1967, BB_900_1, 65515x58996, with DIC
   b – same specimen, documented with fluorescence and ApoTome
5. *Rhaetipollis germanicus* SCHULZ 1967, BB_900_1; 169,174x9,14
6. *Rhaetipollis germanicus* SCHULZ 1967, BB_952_1; S22/3
7. *Rhaetipollis germanicus* SCHULZ 1967, Möckern 2-1E_2; Q28/0
8. *Rhaetipollis germanicus* SCHULZ 1967, BB-D-01_2; P53/2
9. *Rhaetipollis germanicus* SCHULZ 1967, BB-D-18_2; T52/2
10. *Rhaetipollis germanicus* SCHULZ 1967, fragment, Kuhjoch_050926_5; G35/2
11. *Rhaetipollis germanicus* SCHULZ 1967, poorly preserved, BB-D-01_2; S54/3
12. *Rhaetipollis germanicus* SCHULZ 1967, poorly preserved, BB-D-03_2; E54/1
13. *Rhaetipollis germanicus* SCHULZ 1967, BB_900_1; 160,169x8.5,13
14. *Rhaetipollis germanicus* SCHULZ 1967, BB_3550_1; no references available
15. *Rhaetipollis germanicus* SCHULZ 1967, BB-D-05_1; H62/0
16. *Rhaetipollis germanicus* SCHULZ 1967, BB-D-05_1; P61/4
17. *Rhaetipollis germanicus* SCHULZ 1967, BB-D-11_2; H52/1
18. ?Aberrant; *Rhaetipollis germanicus* SCHULZ 1967, BB-D-10_2; S54/1
19. *Rhaetipollis germanicus* SCHULZ 1967, BB-D-18_2; O28/3
20. Aberrant; *Rhaetipollis germanicus* SCHULZ 1967, BB_300_1; O36/5
21. Aberrant; *Rhaetipollis germanicus* SCHULZ 1967, BB-D-07_1; B36/4
22. *Rhaetipollis germanicus* SCHULZ 1967, aberrant, Kuhjoch_050926_5; T33/4
23. a- *Rhaetipollis germanicus* SCHULZ 1967, BB_952_2, no references available, with DIC
    b- same specimen, documented with fluorescence and ApoTome
24. HOLOTYPE (+TYPE of the genus)*; Rhaetipollis germanicus* SCHULZ 1967, Möckern 1E – 10184.1/50; X28/0
25. Aberrant; *Rhaetipollis germanicus* SCHULZ 1967, BB-D-05_1; R61/2
26. Aberrant; *Rhaetipollis germanicus* SCHULZ 1967, BB_952_1; G29/4
27. Aberrant; *Rhaetipollis germanicus* SCHULZ 1967, BB-D-08_1; O22/3
28. Aberrant; *Rhaetipollis germanicus* SCHULZ 1967, BB_952_1; O40/0
29. HOLOTYPE (+TYPE of the genus)*; Rhaetipollis germanicus* SCHULZ 1967, Möckern 1E – 10184.1/50; X28/0


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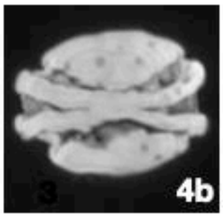
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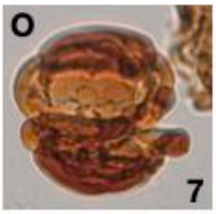

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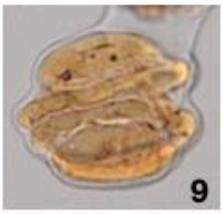
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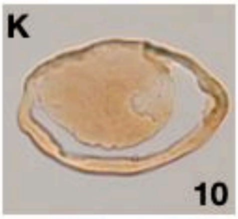

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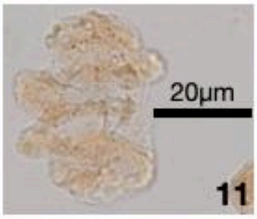

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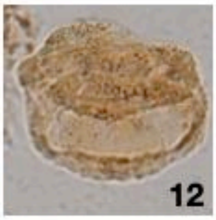
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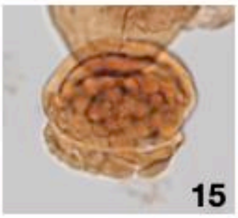
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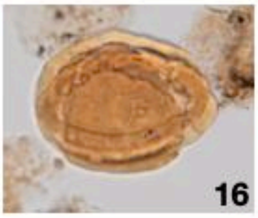
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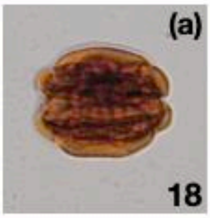

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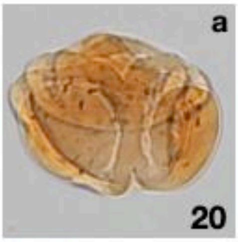

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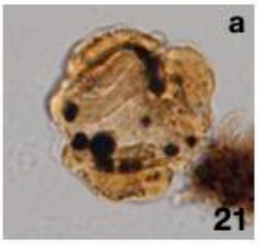

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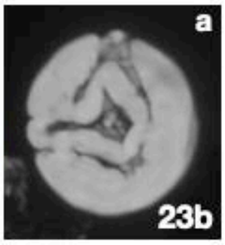

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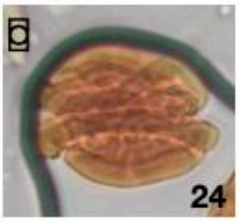
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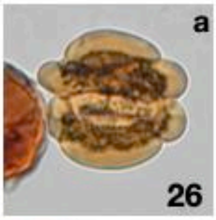

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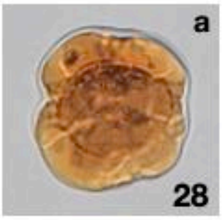

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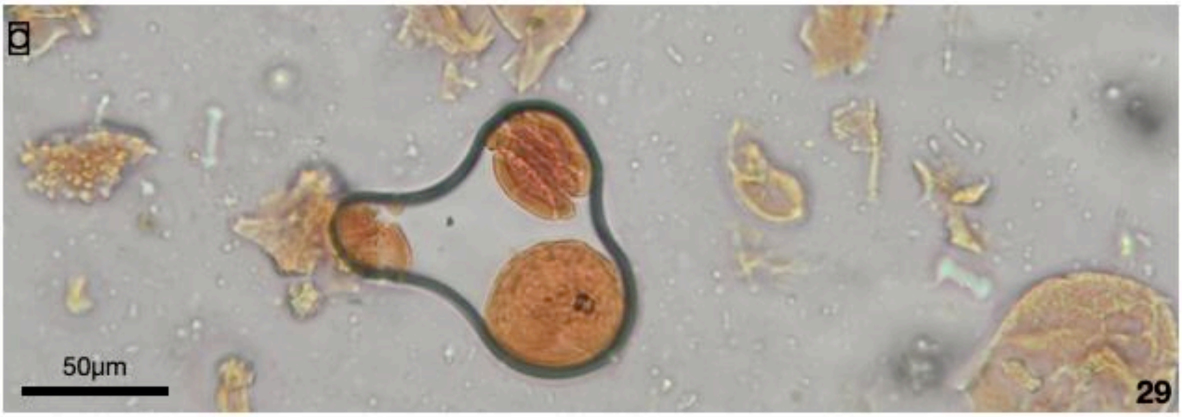

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Chapter 8

Re-evaluation of *Cerebropollenites thiergartii* Schulz 1967 and related taxa: priority of *Sciadopityspollenites* and other nomenclatural novelties

Abstract

The important marker species for the base of the Jurassic, *Cerebropollenites thiergartii*, is occurring contemporaneously with at least nine related taxa. However, their distinction is difficult and potentially, they could potentially be and have been confused in the past. History of numerous recombinations with different genus names (e.g., *Tsugaepollenites* and *Sciadopityspollenites*), and inconsistent classifications or synonymisations, further complicate the taxonomic framework of *Cerebropollenites thiergartii*. Unfortunately, an actual comprehensive study of these ten taxa relevant to the Triassic–Jurassic transition summarising their crucial distinctive characteristics and potential synonymy is currently missing, and limits the stratigraphic value of *Cerebropollenites thiergartii* and associated taxa. Here, we thus revisited the relevant holotype material in related taxa and investigated new material for inter- and intraspecific morphological potential variation. Based on an empirical analysis of name usage and an extensive literature review, we identified previous sources of confusion, re-evaluated the distinctive characteristics and stratigraphic value of these taxa, and their relevance for the Triassic–Jurassic transition. We subsequently propose a series of nomenclatural novelties: *Sciadopityspollenites* **emend.**, *S. thiergartii* **comb. nov. emend.**, *S. thiergartii* **ssp. nov.** *schulzii*, *S. thiergartii* **ssp. nov.** *multiverrucosus*, *S. megaorbicularius* **sp. nov.**, *S. carlylensis* **emend.**, *S. macroverrucosus* **emend.**, *Sciadopityspollenites mesozoicus* **emend.**, *Pseudomassulites* **gen. nov.**, *P. pseudomassulae* **comb. nov. emend.** We also argue that the recombination as *Sciadopityspollenites thiergartii* is taxonomically and nomenclaturally imperative, not only due to priority, but also because it unifies previous disjunct use of *Cerebropollenites* for Mesozoic and *Sciadopityspollenites* for Cenozoic taxa, or Mesozoic species in many Russian studies.

1. Introduction

In Mesozoic flora, *Cerebropollenites thiergartii* and other related taxa like *Sciadopityspollenites multiverrucosus* (Sachanova et Ilyina 1968) Ilyina 1985, *Cerebropollenites macroverrucosus* (Thiergart 1949) Schulz 1967 and *Cerebropollenites mesozoicus* (Couper 1958) Nilsson 1958 are some of the few elements to join the Jurassic palynofloral assemblages after the end-Triassic biotic crisis (Kürschner et al. 2007; Bonis et al. 2009; von Hillebrandt et al. 2013; Lindström et al. 2017b; Gravendyck et al. 2020c). After diversification, their relatively low abundances in the Jurassic increase to relatively significant abundances in the Cretaceous, even constituting the *Cerebropollenites* palynofloral province in the Northern Hemisphere (Zauer & Mchedlishvili 1966; Krutzsch 1971; Herngreen et al. 1996).

Unfortunately, a vast taxonomical confusion exists for the more than 10 pollen taxa related to *Cerebropollenites thiergartii*, especially *Tsugaepollenites pseudomassulae* (Mädler 1964b) Morbey 1975. Additionally, the potentially synonymous *Cerebropollenites mesozoicus* (Couper 1958) Nilsson 1958 and *Cerebropollenites macroverrucosus* (Thiergart 1949) Schulz 1967 (Nilsson 1958; Mädler 1963; Pocock 1964) have caused some authors to inconsistently use either name (Lund & Pedersen 1984) and others to use consistently only one (*Cerebropollenites mesozoicus*: Nilsson 1958; Guy-Ohlson 1978, 1986; De Renéville and Raynaud 1981; Shang and Zavada 2003) or the other (Bóna 1969; Morbey & Neves 1974; Guy-Ohlson & Malmquist 1985; Srivastava 1987; Dybkjær 1991). This has subsequently lead to a great deal of confusion, to the extent that even the authorities are used inconsistently (compare *Cerebropollenites macroverrucosus* Nilsson 1958 in Boulter and Windle 1993). Last but not least, the recombination of some *Cerebropollenites* species with the genus *Sciadopityspollenites* in many Eastern European and Russian publications, e.g. *Sciadopityspollenites macroverrucosus* (Thiergart 1919) Ilyina 1985, complements the taxonomic and nomenclatural patchwork (Waksmundzka 1981; Ilyina 1985).

Inconsistent identification and naming of *Cerebropollenites thiergartii* and related taxa is particularly problematic because of its stratigraphic significance for the base of the Jurassic (e.g. Kürschner et al. 2007; Bonis et al. 2009; von Hillebrandt et al. 2013), and of *Cerebropollenites macroverrucosus* for the Lower Jurassic (Dybkjær 1991). Although some authors partially revised and/or commented on the subject (e.g., Mädler 1963; Schulz 1967; Pocock 1970; Morbey 1975; Waksmundzka 1981), a comprehensive study summarizing the crucial distinctive characteristics and potential synonymy is currently still missing.

The present study thus aims to clarify the taxonomic and nomenclatural confusion (**1**) at a genus level between ***Cerebropollenites*** Nilsson 1958, ***Tsugaepollenites*** (Potonié & Venitz 1934)

Potonié 1958 and ***Sciadopityspollenites*** Raatz 1937 ex Potonié 1958 and (**2**) at the species level for 10 Mesozoic taxa relevant for the Triassic–Jurassic transition, such as *Cerebropollenites* ***thiergartii****,* *Cerebropollenites* ***macroverrucosus/mesozoicus*** and *Tsugaepollenites* ***pseudomassulae****.* To achieve this, we re-evaluated the type material for *Cerebropollenites* ***thiergartii*** Schulz 1967 and type material for 6 other taxa associated over the years such as the prominent *Pollenites* ***macroverrucosus*** Thiergart 1949, *Camerosporites* ***pseudomassulae*** Mädler 1964b, and *Tsugaepollenites* ***mesozoicus*** Couper 1958 but also *Sciadopityspollenites* ***multiverrucosus*** (Sachanova et Ilyina 1968) Ilyina 1985 and the dubious *Pollenites* ***serratus fa. helmstedtensis*** Thiergart 1949, *Pollenites* ***macroserratus keuperianus*** Thiergart 1949, and *Pollenites* ***macroserratus doggerensis*** Thiergart 1949, that have been associated with the taxon in question in the past. Additionally, we compared the holo-/paratypes to original and new material, and reviewed inter- and intraspecific morphological variation. Together with an empirical analysis of name usage and an extensive literature review, we also identified previous sources of confusion, re-evaluated their taxonomic relation to other previously described taxa for whom type material is presumably lost (*Cerebropollenites* ***carlylensis*** Pocock 1970 and *Cerebropollenites* ***findlaterensis*** Pocock 1970) and clarified distinctive characteristics.

2. Materials and methods

2.1. Material

To clarify distinctions at both the genus and species level between *Cerebropollenites thiergartii* and related species, we tried to gather the type material for generic names (Fig. 1.1.) and holotype material for species names (Fig. 1.2) from the relevant publications (Potonié 1931; Potonié & Venitz 1934; Thiergart 1949; Couper 1958; Mädler 1964a; Schulz 1967; Ilyina 1968; Pocock 1970). Unfortunately, type specimens were often no longer stored at the location indicated in the original publication or were lost completely. Some type material (for Potonié (1931), Potonié and Venitz (1934) and Pocock (1970) has to be assumed to be lost (Geological Survey of Krefeld and Geological Survey of Canada personal communication), or unavailable for study (Ilyina 1968). In the following we explain the provenance and details of the material that could be retrieved and is presented in chronological order of their description, beginning first with the three types for genus names and followed with the seven available holotypes/paratypes for species names. Herbarium codes are according to the Index Herbariorum and given to refer to collections where the material is currently stored. Abbreviations for collections without international herbarium codes are indicated with an asterisk (*).

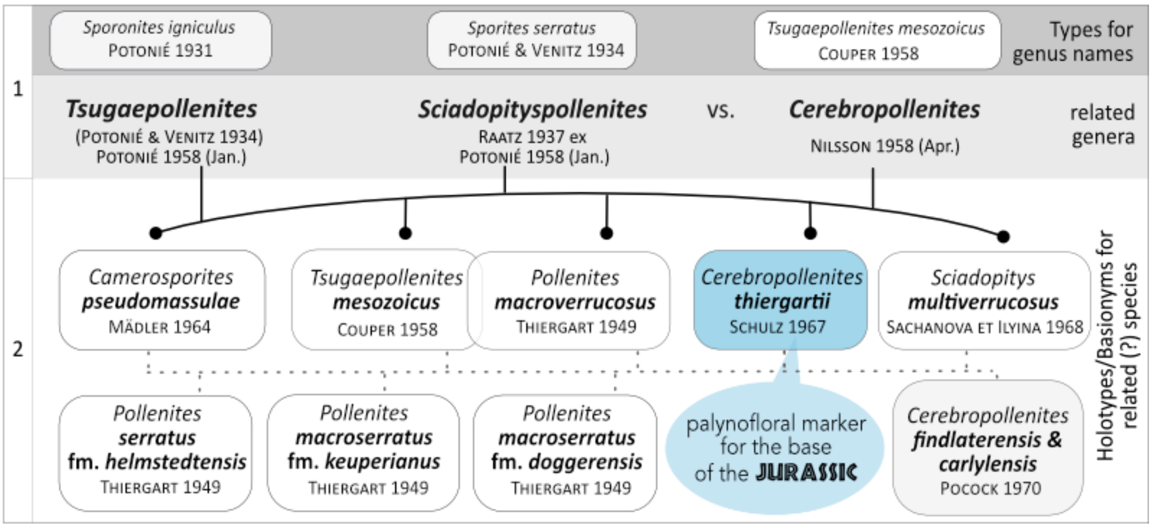


Fig. 1. Problem and material overview. 1. Relevant names and types for distinction on genus level. **2.** *Cerebropollenites thiergartii* and associated taxa relevant for distinction on species level. Holotypes unavailable for study are shown in grey rectangle. The distinction and relationship between several species is problematic as well as their genus assignation (black lines ending in points).

2.1.1. Type material, provenance and details

2.1.1.1. Type for the genus *Tsugaepollenites* (Potonié & Venitz 1934) Potonié 1958 (Jan.)

Potonié (1931) showed a first drawing of *Sporonites* (≡ *Tsugaepollenites*) *igniculus* based on a specimen from the Beisselgrube (Miocene) and with the first diagnosis, designated it 1958 as type for the genus. Unfortunately, the original type material from the Beisselgrube (Miocene) could not be recovered. In fact, most of Potonié's material has to be assumed to be lost and was probably destroyed in WWII (see Gravendyck et al. 2020b). The closest we might get to the holotype is with slides made by Thiergart (1938) from the Grube Marga, and that might be interpreted as original material in the sense of the *International Code of Nomenclature for algae, fungi, and plants* (hereafter *Code*) Art. 9.4. Thiergart was Potonié's doctoral student (Stach 1975) and Potonié had suggested the project to Thiergart which resulted in a publication (Thiergart 1938). Later, accompanying Potonié's genus diagnosis for *Tsugaepollenites* (Potonié 1958), he cites from one of his own publications that he wrote together with Thiergart (Potonié et al. 1951), another specimen (aside the lost specimen) for the species *Tsugaepollenites igniculus* (Potonié 1931) Potonié & Venitz 1934 It is a specimen that was figured first by Thiergart and appeared in several publications (Thiergart 1938, 1940; Potonié 1951; Potonié et al. 1951). This specimen is designated as a lectotype to replace the lost type and is particularly valuable, since Potonié himself confirmed classification as *Tsugaepollenites igniculus.*

The Thiergart collection could be rediscovered only after intensive search. After Thiergart's death in 1977 (Pegler 2017), the curator for paleobotany at the time from the Natural History Museum in Berlin (Barbara Mohr) retrieved the remaining material and transferred it to the museum's collection, where they are currently stored at the external storage in the Reuchlinstraße (Berlin, BHUPM). Going through the uninventoried part of the collection we could relocate and help inventory the relevant Thiergart samples. The slide with a red-circled label saying "*igniculus*" has an ink ring marking the frequently reproduced specimen (Fig. 2.1) that dates back to Thiergart (1938) where it was first classified as *Tsuga-pollenites igniculus.* The slide holding the specimen is now listed under the inventory number MB.Pb.2019/0228) and was borrowed in summer 2019.

2.1.1.2. Type for the genus *Sciadopityspollenites* Raatz 1937 ex Potonié 1958 (Jan.)

Potonié (1958) designated the specimen from the Beisselgrube (*Sporites serratus* (≡ *Sciadopityspollenites serratus*)) that served as model for the drawing in Potonié and Venitz (1934) as the type for the genus name. The specimen originates from the same location from which *Sporonites iginiculus* was described and is also considered as being lost. Potonié (1958), alongside his genus validating generic diagnosis again cites one additional specimen for *Sciadopityspollenites serratus* (aside the lost one) from Thiergart from the Grube Marga, which was figured in several publication (Thiergart 1938, 1940; Potonié 1951; Potonié et al. 1951). The slide (inventory number MB.Pb.2019/0230) has a red-circled label indicated with "*serratus*" (Fig. 2.4) and holds several specimens that were published as *Sciadopitys-pollenites serratus* in Thiergart (1938). The slide was borrowed in summer 2019 from the BHUPM and one specimen is designated as lectotype in this study.

2.1.1.3. Type for the genus *Cerebropollenites* Nilsson 1958 (Apr.)

Nilsson (1958) designated the holotype of *Tsugaepollenites mesozoicus* (≡ *Cerebropollenites mesozoicus*) of Couper (1958) as the type for his newly erected genus *Cerebropollenites*. Couper's holotype is still stored at the Sedgewick Museum in Cambridge (CGE) as originally indicated (Couper 1958). The slide (Fig.3.5) was loaned and studied by the first author in winter 2020/21. Note that the type for the genus is the same specimen as the holotype for the basionym *Tsugaepollenites mesozoicus* Couper (1958).

2.1.1.4. Holo- or Paratypes for names designated in Thiergart (1949)

The material for Thiergart (1949) is located located like the slides for Thiergart (1938) at the external storage in the Reuchlinstraße (Berlin, BHUPM). However, in contrast to the 1938 publication, none of the slides was specially labelled in red. Thanks to the standard location, depth, and slide number, we could still identify the slides that should contain three syntypes for *Pollenites serratus fa. helmstedtensis* and two syntypes for *Pollenites macroserratus Keuperianus* (both inventory number 'MB.Pb.2021/0101, Fig. 2.8), the holotype for *Pollenites macroverrucosus* (inventory number 'MB.Pb.2019/0231') (Fig. 3.1) and the last remaining syntype of *Pollenites macroserratus doggerensis* on the same slide (Fig. 4.9). The slides were borrowed and studied in summer 2019.

2.1.1.5. Holotype for *Camerosporites pseudomassulae* Mädler 1964

The holotype (Fig. 3.9) is still stored at its original institution, since its designation in 1964, and can be found at the Landesamt für Bergbau, Energie und Geologie in Hannover in Germany (LBEG*) under the inventory number of the 'Typenkatalog' 'TK-Nr.3141'. It was borrowed in summer 2018 for further investigation.

2.1.1.6. Holotype for *Cerebropollenites thiergartii* Schulz 1967

The holotype is stored at the Bundesanstalt für Geowissenschaften und Rohstoffe at the side-branch in Berlin-Spandau (BGR-S*) in the 'Mikroflora Originale' collection. The slide Marnitz 5/30; 59/2 holds the holotype specimen for *Cerebropollenites thiergartii* Schulz 1967 and is indicated with the inventory number X 11369. Unfortunately, the storage conditions in the facility are not optimal. The type material is stored in metal cupboards in an old, brick building with very cold temperatures and winter, and very hot conditions in summer. The slide in question together with other reference material from Schulz that was borrowed from this facility was altogether in relatively poor condition with the glycerine jelly being desiccated visible with the naked eye. The slide with the holotype (Fig. 4.4) was borrowed in 2018 for study and documented yearly from then onwards, to document the ongoing decay of some remaining glycerine gelatine pockets.

2.1.1.7. Holotype for *Sciadopitys multiverrucosus* Sachanova et Ilyina 1968

The holotype is stored at the Trofimuk Institute of Petroleum Geology and Geophysics – Siberian Branch of the Russian Academy of Sciences (IPGG SB RAS). Since the holotype was not available for loan, Ekaterina Peshchevitskaya from the IPGG SB RAS documented the holotype for us in February 2021 as shown in the following.

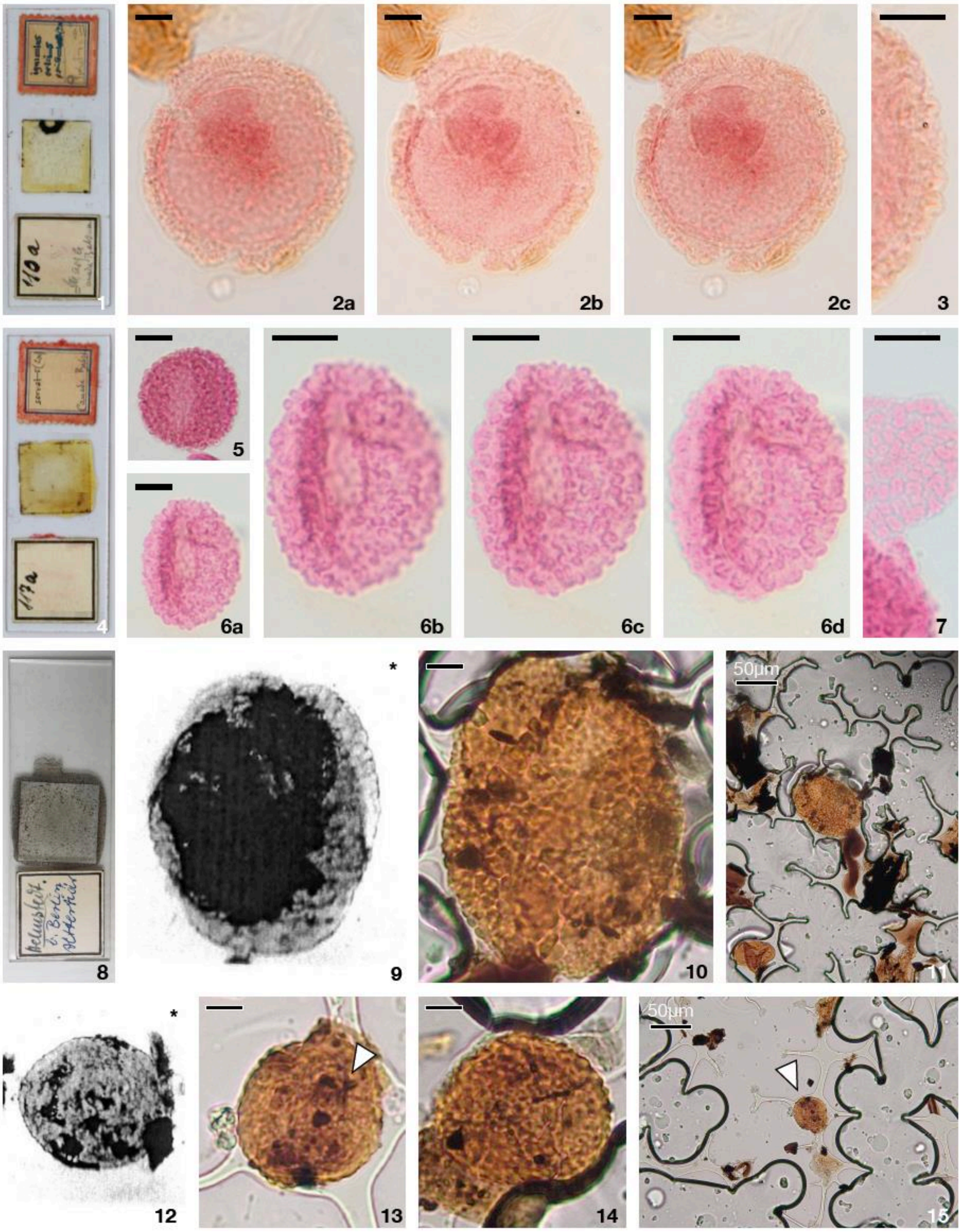
2.1.2. Intra and interspecific variation in original and new material

An author's perception of a new species might be primed by the taxon's intra and interspecific variation that one observes prior to or during the process of description. Slides holding holotypes were mostly strew mounts (except for Mädler's slide with *Camerosporites pseudomassulae*), and were also studied for their microfloral assemblage (e.g. stratigraphically important taxa and preservation) and especially for their inter- and intra-specific variation of the newly described and associated taxa.

Additionally, new material from the Bonenburg section (Schobben et al. 2019; Gravendyck et al. 2020c) and two samples from the Swedish Höllviken-2 core (HV1308.95m and 1316.5m, Toarcian–Aalenian) (sedimentary log in Lindström et al. 2017a) were studied for inter- and infraspecific variation. The Höllviken-2 material was also chosen because abundant *Cerebropollenites thiergartii* and *Cerebropollenites macroverrucosus* were documented from those samples (Sofie Lindström, personal communication, unpublished results). Courtesy of Sofie Lindström and the Geological Survey of Sweden.

In the figures summarising the results of this analysis, the respective locality of the material is indicated in the top left corner using the following abbreviations: **B** = Bonenburg, **C** = original material from Couper (1958); **HV** = Höllviken; **S** = original material from Schulz (1957); **T** = original material from Thiergart (1938, 1949). Types for genus names are indicated with a circle in a square (⧇), holotypes with a double circle (◎).

Fig. 2. (Original) Material for Thiergart (1938) and Thiergart (1949). 1–3. *Tsuga-pollenites igniculus* from Thiergart (1938)**; 1.** strew slide, specimen indicated with ink ring; **2.** *Tsuga-pollenites igniculus* in three focal planes; **3**. Detail of the fringe, i.e., the monosaccus. **4–7.** *Sciadopitys-pollenites serratus* from Thiergart (1939) cited in the protologue of Potonié (1958); **4.** strew slide, **5.** and **6.** *Sciadopitys-pollenites serratus;* **6.** *Sciadopitys-pollenites serratus* in different focal planes.; **7.** Detail of ornamentation on a fragment of a *Sciadopitys-pollenites serratus* specimen; **8–11.** *Pollenites serratus fa. helmstedtensis* Thiergart (1949)*;* **8.** strew slide, cover slip not sealed; **9.** Original photograph of Thiergart (1949) for *Pollenites serratus fa. helmstedtensis,* original photograph from Thiergart (1949) (Pl. II, Fig. 19) reprinted with permission from Schweizerbart Science Publishers www.schweizerbart.de/journals/palb; **10**. the exact specimen could not be relocated, but a conspecific specimen is shown; **11.** Preservation of the slide, glycerine gelatine desiccated; **12–15**. *Pollenites macroserratus Keuperianus;* the specimen from the original photograph (**12,** reprinted with permission from Schweizerbart Science Publishers www.schweizerbart.de/journals/palb); could not be relocated, but conspecific specimen (**13** and **14)** are shown, in **13**. The trilete mark is visible (arrowhead);15. Preservation of the slide, original glycerine gelatine could be partially re-embedded, hence the double desiccation lines. Scale = 10 µm (unless indicated otherwise).



2.2. Microscopy

Light microscopy was conducted using an Olympus CX31 mounted with an Olympus SC50 camera. Most specimens were studied with an x100 oil immersion objective. Only those of Schulz and

Couper were mostly documented with a 40x objective because the sealing of the slide and the location of the type at the very edge of the cover slip did not permit oil immersion without risking further damage. All SEM images are reproductions from existing literature, and indicated and cited accordingly.

2.3. Empirical analysis of name usage

Data on the usage of names was retrieved from Palynodata, the John Williams Index of Paleopalynology and Google Scholar (chapter 5), to study the stratigraphic range and geographical association of the name usage, which was grouped and colour-coded in nine regions (see Fig. 12–14): North America (dark green), South America (turquoise), Greenland and the Arctic Sea (moss-green), Africa and middle East (dark red), Europe (dark blue) but excluding Eastern Europe (light blue), Russia (yellow), Asia (light red), Australia and New Zealand (orange). Rather than strict geographical regions, this grouping is meant to roughly reflect the different schools of palynologists, usually operating in particular regions and languages of the world. Citation rates (CR) were calculated for all studied taxa (Fig. 12) and the establishment index (EI) was calculated for competing names (Fig. 13 and see chapter 6 for further information on these metrics).

3. Results

3.1. Taxonomy: Revisiting the type material

Palynomorphs are studied in chronological order, first those of types for genus names and then the holotypes for species names (compare Fig. 1 for an overview of studied material). The state of preservation is described as condition. Many of the original description are published in fairly old and often hard to obtain publications. Therefore, the original descriptions are here restated together with several first English translations, and complemented with a re-description of the holotype or descriptions of the newly chosen lectotype. Our reevaluation of the material allowed us to now give standardised England finder (EF) references instead of variable microscope coordinates.

3.1.1. Type for the genus *Tsugaepollenites* (Potonié & Venitz 1934) Potonié 1958 (Jan.) (Fig. 2.2)

Type. – *Sporonites igniculus* Potonié 1931, p. 556, specimen from sample V80a drawn in Fig. 2

Condition. – The original holotype is presumed to be lost.

Lectotype. – *Tsuga-pollenites igniculus* in Thiergart (1938), Marga 110a, specimen indicated with an ink ring, EF: M43/2; Pl. 23, Fig. 16; refigured here (Fig. 2.2) – *designated here*

Condition. – The specimen cited by Potonié is easily recognizable because of a smaller pollen lying behind the specimen in question, which also permits reidentification of the very same specimen through a series of publications (Thiergart 1938, 1940; Potonié 1951; Potonié et al. 1951). Thiergart stated that the strew mount is embedded in Kayser's glycerine gelatine and stained with fuchsin (Thiergart 1938). The slide itself, however, says 'Canada balsam'. The polymorphs found in this embedding from Thiergart (1938) were the best-preserved specimens of the entire study, despite being the oldest. Some minor yellowing of the embedding medium and some bleaching of the palynomorphs was compensated by the staining and is thus not problematic for use as a lectotype.

Original Description. – Polygonal bis kreisförmig. Umriß unregelmäßig gewellt bis gekerbt. Dicke der Exoexine 4–6 µ. Oberfläche „netzig“; „Netzleisten" heller als die wahrscheinlich vorgewölbten Zwischenräume (Potonié and Venitz 1934, p. 17).

Translation of the Original Description. – Polygonal to circular. Outline irregularly wavy to notched. Thickness of exoexine 4–6 µm. Surface like a network [reticulate]; "lines of the net" lighter in colour than protruding interspaces.

Description. – Thiergart's specimen (Fig. 2.2) is almost circular. The specimen is ca. 61 µm long and 59 µm wide. The corpus of the pollen is ca. 49 µm in diameter and has a distinct equatorial fringe of ca. 6 µm thickness (i.e., 10% of the overall pollen diameter). The fringe has a very different structure than the corpus (Fig. 2.3). The corpus possesses rounded to elongate sculptural elements that are 2-4 µm in size, varied in shape and up to 1 µm high. (Note, that the darker element in figures (Fig. 2.2) in the top left corner is not a feature of the described pollen, but another palynomorph that is lying behind the pollen in question.)

3.1.2. Type for the genus *Sciadopityspollenites* Raatz 1937 ex Potonié 1958 (Jan.) (Fig. 2.4 – 2.7)

Type. – *Sporites serratus* Potonié & Venitz 1934, p. 15, Pl. 1, Fig. 6, specimen in sample VII 17

Condition. – The original holotype is presumed to be lost.

Lectotype. – *Sciadopityspollenites serratus,* Marga 117a (material from Thiergart (1938)), EF: U38/3, Fig. 2.6, this study – *designated here*

Condition. – The exact specimen depicted by Thiergart cannot be relocated with certainty (probably specimen depicted in figure 2.5, which does not allow a very clear view on the ornamentation), but the slide provides plenty of other more representative specimens from which the holotype was chosen.

Original Description. – Gestalt meist spindelförmig bis oval, aber mitunter auch rundlich. Umrißlinie unregelmäßig gewellt; die vorspringenden Höcker manchmal 1–1,5 µ groß. Skulptur runzelig-schlierig. Dehiszenz nicht erkennbar (Potonié and Venitz 1934, p.15).

Translation of the Original Description. – Shape mostly spindle-shaped to oval, but sometimes also rounded. Outline irregularly wavy/sinuate; the protruding sculptural elements (‘humps’) sometimes 1–1.5 µm in size. Sculpture wrinkled-‘streaky’. Dehiscence not visible.

Description. – Shape oval to rounded, 25–45 µm long and 27–32 µm wide (see Fig. 2.5-2.6). Outline finely serrated/corrugated because of the rounded sculptural elements which are between 1–2.5 µm wide and long. The elements are not homogeneous in size or shape, some are more rounded, others more elongate (see Fig. 2.6). Sulcus sometimes indistinct, but usually visible, oval and ca. 15–35 µm long (Figs. 2.5, 2.6). Exine between 0.7 and 1 µm thick.

3.1.3. Type for the genus *Cerebropollenites* Nilsson 1958 (Apr.) (Figs. 3.7 and 3.8)

Note that holotype for the species name *Tsugaepollenites mesozoicus* Couper (1958) also serves as the type for the genus *Cerebropollenites* and will therefore be described only once.

Type/Holotype. – Tsugaepollenites mesozoicus Couper 1958, p. 155, Pl. 30, Fig. 8; refigured here (Fig. 3.8)

Condition. – The slide is in excellent condition, but unfortunately, the holotype lies right at the edge of the corner of the cover slip, and is partially covered by the sealing of the cover slip. (Fig. 3.6).

Original Description. – Grains saccate; equatorial contour circular to broadly elliptical; exine of distal surface very thin and almost smooth over a circular area (corresponding to the distal sulcus of disaccate grains); surrounding this circular area is a well developed equatorial fringe of twisted saccate protrusions, about 5 to 6 µ high; exine at the proximal pole is also saccate , but individual sacs are not so well developed as around the equatorial area, sculpture pattern of the polar area gradually merges into the pattern of the equatorial fringe (Couper 1958, p. 155).

Re-description. – The holotype is 67 µm long and 49.5 µm wide, i.e., overall oval in shape. The pollen lies partially on the side with the sulcus on the left. The sulcus area appears smooth, but this is hard to describe, because the underlying ornamentation obscures a clear view. The most characteristic feature is the very big protrusions, that are far bigger than in the previously described material. They are 3–6 µm high and winding creating a maze-like pattern, similar to what was described for *Pollenites macroverrucosus*, but in the present specimen, the spaces in between these winding elements are bigger, and the elements themselves are bigger as well, i.e. overall less compact and generally bigger than in *Pollenites macroverrucosus.* It is important to note that due to the size of the protrusions, they can create the impression of an equatorial fringe. However, this is merely an optical effect of the ornamentation protruding at the equator, which is perceived differently for the ornamentation on the corpus. Except for the sulcus area the ornamentation is uniform on either side of the grain, consisting of heterogeneously long and short protrusions. While the protrusions are varying a bit in height and length (due to their meandering), their width is relatively uniform of about 1.5–2 µm (Fig. 3.8).

3.1.4. Holotype for *Pollenites serratus* fa. *helmstedtensis* Thiergart 1949

Syntypes (no holotype designated). – *Pollenites serratus* fa. *helmstedtensis* Thiergart 1949, p.13, Pl. 2, Figs. 2, 6, 8

Condition. – All syntypes are lost. Thiergart shows three specimens for this new taxon. Two of them (Pl. 2 Figs. 6 and 8, Thiergart (1949)) are spores, probably *Polypodiisporites,* and are therefore not described in detail here. The pollen tetrad shown in plate 2 figure 2 depicts a pollen with serrated outline and could not be relocated either, but a taxonomically identical specimen is studied here.

Original Description. – Größe 42 µ. Der Pollen ist in der Aufsicht gleichmäßig oval, die Umrißlinien wellig, entsprechend der welligen Oberflächenstruktur, ohne Andeutung einer Keimstelle. Zur Keimung scheint er, wie Tafel II, Abb. 8 zeigt, ähnlich den Taxodieen (*Pollenites hiatus* Roe. Potonié) aufzuplatzen. Vom *Sciadopityspollen*, mit dem man ihn vergleichen kann, unterscheidet ihn die regelmäßige ovale Gestalt und die gröbere Oberflächenstruktur. Im Präparat tritt er mehrfach zu vier Stück verklebt auf (Taf. II, Abb. 2). Er gehört wahrscheinlich zu einer Konifere (Thiergart 1949, p. 13)

Translation of the Original Description. – Size 42 µm. The pollen is evenly oval, the outline is wavy, as a result of the wavy/sinuate surface sculpture, without any indication of a germination area. As plate II, figure 8 shows, the pollen seems to burst open, similar as described for the taxodiae (*Pollenites hiatus* Roe. Potonié). It differs from *Sciadopitys* pollen, with which it can be compared, by its regular oval shape and the coarser ornamentation. In the slide it occurs several times that four pollen are glued together (Plate II, Fig. 2). It probably belongs to a conifer.

Re-description. – The tetrahedral pollen tetrad consists of monosulcate grains. The sulcus is only visible as a thinner area when focusing through the different focal planes of the tetrad. The sulcus is directed outward. The tetrad measures 83 x 63 µm and consist of big and irregularly shaped and sized verrucae of 3–7 µm in diameter. All in all, the pollen as described is conspecific with *Ricciisporites tuberculatus*.

3.1.5. Holotype for *Pollenites macroverrucosus* Thiergart 1949 (Figs. 3.3 and 3.4)

Holotype. – *Pollenites macroverrucosus* Thiergart 1949, p. 17, Pl. 2, Fig. 19

Condition. – The slide Degow 253–255m a (Fig. 3.1) is in very poor condition (Fig. 3.2), the glycerine gelatine has desiccated to a great degree, leaving mostly some dendritic remains of the medium partially embedding the organic material on the slide (Fig. 3.2). Despite the poor embedding, a pollen identified as the holotype is relocated. However, this relocation is a bit ambiguous, due to the very different impression compared to the original photograph, which is partially caused by different illumination and the halo covering the left handside of the outline (Figs. 3.5 a–d). Nevertheless, the tracheid remains at the top of the pollen (Figs. 3.3 and 3.4) and the characteristic shadow in the lower left corner and on the right handside of the pollen are still visible (Figs. 3.4 and 3.5, arrowhead), and permit identification of the specimen as the holotype with reasonable certainty. No other similar pollen grain could be found on the slide that could be the holotype. The labelling clearly identified the slide as the one containing the holotype, so we assume the above-described pollen to be the holotype.

Original Description. – Größe: 65 µm. Die Form bildet ein ziemlich regelmäßiges Ovaloid und erinnert an die früher beschriebene Form *Pollenites macroserratus Keuperianus.* Von dieser unterscheidet sie aber die Größe der Oberflächenskulpturelemente, die bei der Keuperform 2 µm beträgt, bei der Doggerform aber 5 µm übersteigt (Thiergart 1949, p. 17).

Translation of the Original Description. – Size: 65 µm. The shape forms a fairly regular ovaloid and is reminiscent of the previously described form *Pollenites macroserratus Keuperianus*. It differs from this, however, in the size of the sculptural elements of the ornamentation, which is 2 µm in the Keuper form, but exceeds 5 µm in the Dogger form.

Re-description. – The pollen grain is ca. 64.2 µm long and 41 µm wide. The distal side is directed at the viewer, the proximal side with the sulcus is shining through and much clearer visible than in the original photograph. It is roughly 30 µm long. Although the sculptural elements appear rather big on the original microphotograph, differentiated focusing back and forth through the specimen reveals that these are densely arranged winding and rounded muri with a length up to 8 µm and a width of 3–6 µm. These elements are not very high, ca. 1.5 µm. Depending on the angle, and especially at the outline these elements appear bigger, because one is looking at a section through the width or part of the longitudinal view of the sculptural element. The arrangement of these muri is probably best described as rugulate, creating a maze-like pattern, but with very little space in between them. An equatorial fringe is not visible. The muri protruding at the equator give the impression of a sinuate or corrugated outline, but there is no real fringe in the sense of a saccus present. (Figs. 2.5 a–d)

3.1.6. Holotype for *Pollenites macroserratus Keuperianus* Thiergart 1949

Syntypes (no holotype designated). – Pollenites macroserratus Keuperianus Thiergart 1949, p. 7, Pl. 1 Figs. 5, 6, 8, 9

Condition. – All syntypes lost. The syntypes described from Hohenwestedt (Pl. 1, Figs. 5, 6) could not be recovered and are assumed to be lost. The slide from Magdala (a) (Pl. 1, Figs. 8, 9) that is still available and should contain the two remaining syntypes was searched for palynomorphs resembling the original photographs and original description but could not be relocated. Except for some spores complying with the circumscription of *Polypodiisporites polymicroforatus*, we could not find any specimen that remotely resembles the depicted specimen. However, we could relocate a specimen from slide ‘Helmstedt’ which Thiergart does not mention in the protologue but depicts in plate II figure 1 (Fig. 2.12). The glycerin gelatin of the original slide was strongly desiccated. To re-embed the material, the cover slip was partially lifted to reinject new glycerin gelatin, which was only partially successful. Now two different prismatic lines are visible: a darker one of the younger embedding medium and a less prismatic edge from the old embedding medium. Despite re-embedding the specimen, this does not prevent prismatic effects of the primary layer of glycerin gelatin at the outline of the specimen (Figs. 2.13 and 2.15). Nevertheless, re-embedding slightly improved visibility and the specimen is in reasonable condition for study.

Original Description. – Hier wurde absichtlich die Potoniésche Bezeichnung für den kranzlosen *Tsuga*pollen gewählt, weil diese mesozoische Form am besten durch den Vergleich mit jenem charakterisiert wird, wenn auch die Feinheit der Oberflächenstruktur nicht völlig übereinstimmt. Die Helmstedter Rhätformen und diejenigen aus dem unteren Keuper von Blatt Magdala sind grobwarzig; die Gestalt oval, zum Unterschied von den später zu beschreibenden Doggerformen, die ihre ursprüngliche kugelige Form nicht beibehalten, sondern sich einfalten. Auch unterscheidet sich die Oberflächenskulptur von der Keuperform. Auch die Formen aus dem mittleren Keuper der Bohrung Hohenwestedt falten sich ein (Thiergart 1949, p. 7).

Translation of the Original Description. – Potonié's name for the fringeless *Tsuga* pollen was deliberately chosen here because this Mesozoic form is best characterised by comparison with that one, even if the fineness of the ornamentation does not completely match. The Rhaetian forms from Helmstedt and those from the lower Keuper from Magdala have coarse warts; the shape is oval, in contrast to the Dogger forms that will be described later, and which do not retain their original spherical shape, but are folded. The ornamentation also differs from the Keuper form. The forms from the middle Keuper of the Hohenwestedt borehole are also folded.

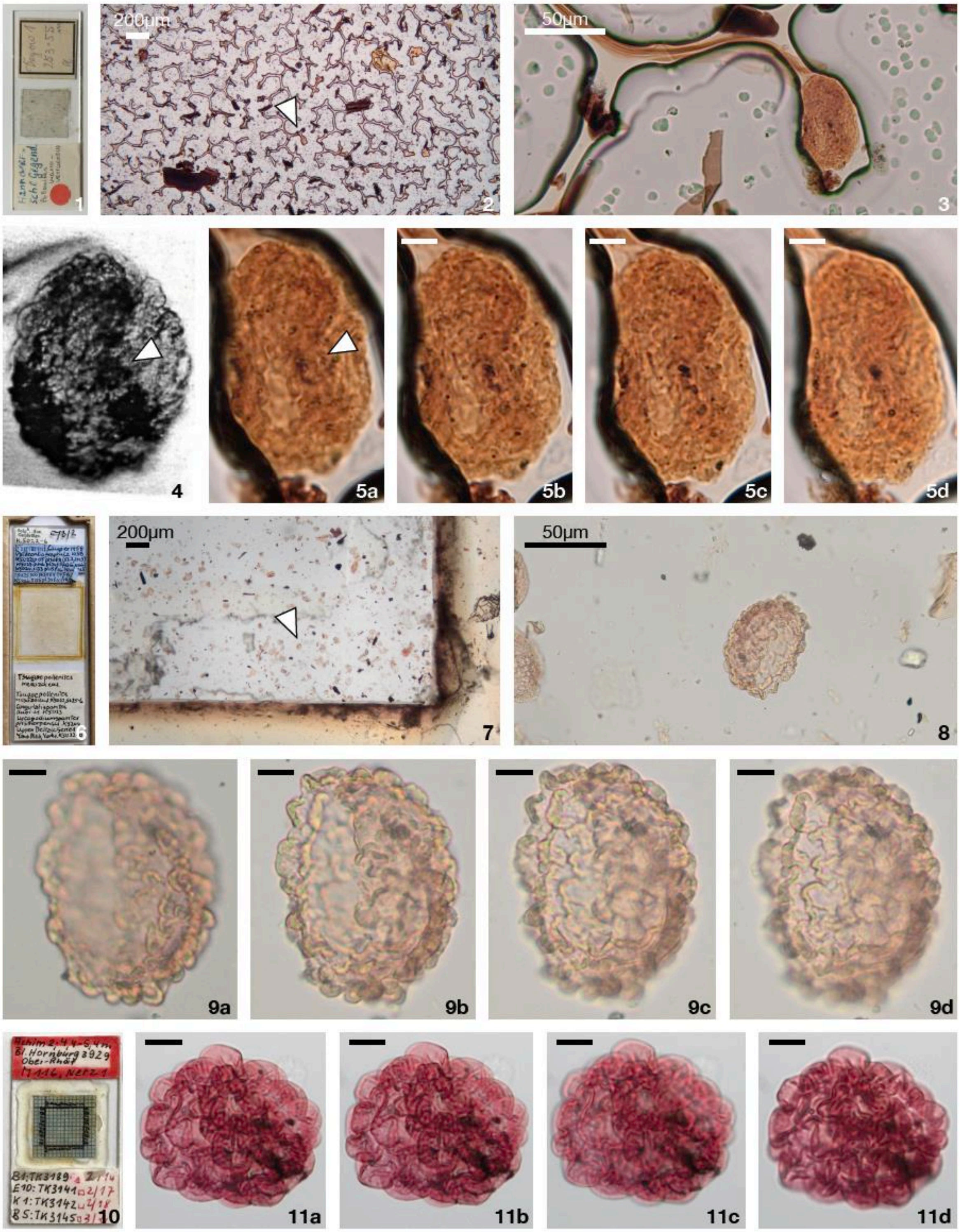
Description. – The only available specimen figured by Thiergart (none of the syntypes), is about 46 µm long and 42 µm wide, i.e. oval to subcircular. The exine is ca. 1.5–2 µm thick and the surface is covered by many small verrucae that give a sinuate impression when looking at the outline. The laesura permits identification as a spore. The laesura consists of one long slit with one shorter perpendicular slit at the middle (Fig. 2.13, arrowhead). The type of the laesura, ornamentation and overall shape is very compliant with the description of *Polypodiisporites polymicroforatus*.

3.1.7. Holotype for *Pollenites macroserratus doggerensis* Thiergart 1949 (Figs. 4.10 and 4.11)

Syntypes (no holotype designated). – Pollenites macroserratus doggerensis Thiergart 1949, p. 18, Pl. 2, Figs. 26, 29, 30 (remaining syntype refigured in Fig. 4.11)

Condition. – The preservation of the only remaining syntype is like that of *Cerebropollenites macroverrucosus* which is contained on the same slide (Figs. 3.1 and 4.9). The specimen is rather bleached, the characteristics are therefore hard to identify (Figs. 4.10–11). Digital contrast enhancement can help to improve this (compare Fig. 7.14).

Fig. 3. **Holotypes of *Pollenites macroverrucosus* THIERGART 1949, *Tsugaepollenites mesozoicus* COUPER 1958 and *Camerosporites pseudomassulae* MÄDLER 1964. 1–5**. Holotype for *Pollenites macroverrucosus;* **1.** strew mount slide without cover-slip seal. The red dot and indication of the type was added; **2**. Overview of the preservation of the slide. Glycerine gelatine has desiccated to dendritic remains; **3**. Partial embedding of the holotype causing prismatic effect at the edge; **4**. Original photograph from Thiergart (1949) (Pl. II, Fig. 19) reprinted with permission from Schweizerbart Science Publishers http://www.schweizerbart.de/journals/palb, *Pollenites macroverrucosus* in different focal planes. **5–8**. Holotype for *Tsugaepollenites mesozoicus;* **5.** strew mount slide; **6**. Location of the holotype at the very corner of the cover slip; **7.** Embedding of the holotype is still intact; **8.** Holotype for *Tsugaepollenites mesozoicus* in different focal planes; **9**. Smaller slide with an embedded net with coordinates with several single–grain mounts; **10.** Holotype for *Camerosporites pseudomassulae.* Scale = 10 µm (unless indicated otherwise).



Original Description. – Größe: 55–80 µ. Die Form zeigt mit der unserer heutigen *Tsuga canadensis* weitgehende Übereinstimmung. Die Oberflächenstruktur der Doggerform ist etwas feiner als die der Pollen der lebenden *Tsuga*-arten. Die meisten Stücke tragen durch die Einbettung bedingte, sekundäre Quetschfalten im Gegensatz zu den ähnlichen Rhätformen, die ihre ursprüngliche ovale Form beibehalten haben. Die genannte Übereinstimmung sagt natürlich nicht, daß die heutige Gattung schon damals existiert hat (Thiergart 1949, p. 18).

Translation of the Original Description. – Size: 55–80 µm. The form roughly corresponds to our present-day *Tsuga canadensis*. The ornamentation of the dogger form is slightly finer than that of the pollen of the extant *Tsuga* species. Most of the specimen have secondary folds as a result of the embedding, which is contrasting to the similar Rhaetian forms, which have retained their original oval shape. The explained similarity with extant forms, of course, does not mean that today's genus existed back then already.

Re-description. – The specimen is circa 88 µm long and 66 µm wide and oval. However, the original shape is probably subcircular if secondary folds are taken into consideration the. A distinct germination area is not visible but the area enclosed by the secondary folds depicts less distinct ornamentation and is interpreted as a sulcus. The sculptural elements are more or less spherical and up to 1.5 µm in size (Fig. 4.10–11).

3.1.8. Holotype for *Camerosporites pseudomassulae* Mädler 1964 (Fig. 3.10)

Holotype. – Camerosporites pseudomassulae Mädler 1964, p. 183, Pl. 2, Fig. 17

Condition. – The holotype is mounted in a cell E 10 of a mesh used for several single grain mounts. The embedding medium is preserved perfectly, permitting a clear view on the holotype.

Original Description. – Die fast kugeligen Sporen mit einem Durchmesser von 40–50 µ sind mit dicken, halbkugeligen Papillen dicht besetzt. Die 12–14 µ breiten und 8–10 µ hohen Papillen scheinen im Innern hohl zu sein, da sie teilweise zusammengesunken sind. Ein dunkler gefärbtes Dreieck deutet die Keimstelle an. Obwohl keine Y-Strahlen sichtbar sind, werden die Sporen vorläufig zu den trileten Formen gerechnet (Mädler 1964, p. 183).

Translation of the Original Description. – The almost spherical spores with a diameter of 40–50 µm are densely covered with thick, hemispherical protrusions [Papillen]. The protrusions [Papillen] are 12–14 µm wide and 8–10 µm high, and appear to be hollow inside, as they are partially collapsed. A darker coloured triangle indicates the germination area. Although no laesurae are visible, the spores are provisionally considered as trilete forms.

Note that the translation avoids the term ‘papillen’ which is not used in the sense of either definition of ‘papillae’ found in Punt et al. (2007), but rather in the sense of a spherical, hollow protrusions. Hence the use of ‘protrusion’, which is a necessary interpretation to find an adequate translation for the term used by Mädler.

Re-description. – The specimen measures ca. 52 x 46 µm. It is stained red with fuchsin (Mädler 1964a), which does not allow an impression of the original colour of the specimen, except for the generally hyaline character of the exine. There is no clear corpus visible, the specimen instead gives the impression of an aggregation of rounded protrusions of circa 7–12 µm in diameter that form an overall unit that appears circular. The protrusions appear wrinkled, rather thin (exine thickness ca. 0.5–0.7 µm), hollow which allows the other protrusion in layers behind the one in question to shine through.

3.1.9. Holotype for *Cerebropollenites thiergartii* Schulz 1967 (Fig. 4.8)

Holotype. – Cerebropollenites thiergartii Schulz 1967, p. 603, Pl. 11, Figs. 7–8

Condition. – When the holotype was studied for the first time in 2018, the slides were in very poor condition and became increasingly worse over the next two years. The majority of the glycerine gelatine had desiccated already. By chance a tiny pocket of embedding medium was left and the very edge of the cover slip, and in exactly that pocket the holotype was preserved (Fig. 3.1). Nevertheless, the progressing desiccation was already evident in the near vicinity, coming closer to the holotype every year (Figs. 4.1–4.7), which left the specimen partially without embedding in 2020 (Fig. 3.7).

Original Description. – Größe 40–80 µm (Holotypus 56 µm). Kontur rundlich, Exine etwa 1 um dick, allseitig dicht mit Warzen besetzt, die an der Basis miteinander verschmolzen sind. Größe der Warzen durchschnittlich 1–3 µm. Sulcus nicht immer sichtbar (oder vorhanden?), bis 36 µm lang, Exine oft mit Sekundärfalten (Schulz 1967, p. 603).

Translation of the Original Description. – Size 40–80 µm (holotype 56 µm). Outline subcircular, exine about 1 µm thick, densely covered on all sides with warts fused together at the base. The size of the warts measures 1–3 µm on average. Sulcus not always visible (or present?), up to 36 µm long, exine often with secondary folds.

Re-description. – The holotype is circa 60 µm long and 53 µm wide and overall subcircular. The sulcus is clearly visible, directed at the observer and ca 34 µm long and 11 µm wide. The exine is 1–2 µm thick and covered with many densely arranged verrucae, in contrast to Schulz description we cannot confirm, that the individual verrucae are merged at the base, they appear rather distinct, but where very densely arranged certain focal planes can give the impression that they are merged, when they are simply close together. The verrucae are about 1–2 µm wide and high. (Fig. 3.8)

3.1.10. Holotype for *Sciadopitys multiverrucosus* Sachanova et Ilyina 1968 (Fig. 4.14)

Holotype. – Sciadopitys multiverrucosus Ilyina 1968, p. 42, Pl. 5, Figs. 1, 2

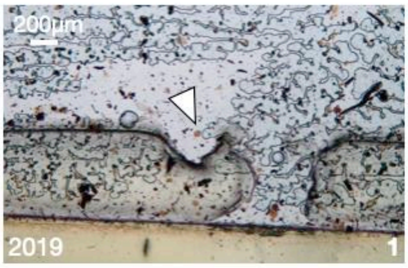
Condition. – The location of the holotype was clearly indicated by a red square (Fig. 4.12, 4.13). Although the holotype is located at the edge of the coverslip, it is still in excellent condition and fully embedded.

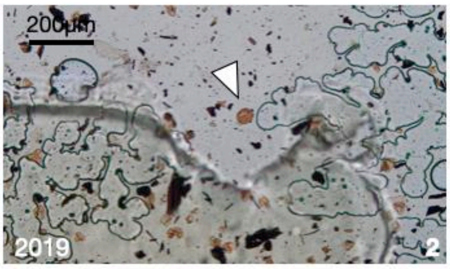
Re-description. – The holotype is circa 53 µm long and 45 µm wide and subcircular. The sulcus is a bit indistinct, but visible as a more hyaline oval area and approximately 27 µm long. The exine is circa 1 µm thick and covered with many densely arranged rounded verrucae similar to those in the holotype of *Cerebropollenites thiergartii*, but on average, have a bit bigger size of 1–4 µm (in diameter).

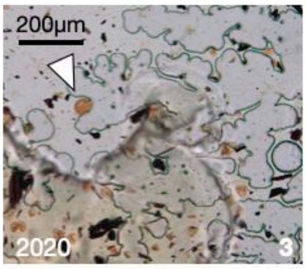
3.2. Taxonomy: Inter- and Infraspecific variation

At first, the diversity and variation of species associated with *Cerebropollenites thiergartii* can be overwhelming. Even more so as they can often be linked by intermediate forms forming a continuum between the taxa, especially when poor preservation makes characteristics ambiguous. However, sorting of the observed forms shows several typical distinctive characteristics, and consistent features. The most distinctive variation observable in the ornamentation. Forms can be arranged a long a continuum of sculptural elements that grow in size, ranging from forms with very small to very large and protruding sculptural elements. Because genus assignations are highly disputed and on top of that confusing because of the many different recombinations of the basionyms for the taxa we discuss, we refer to the different names only by their specific epithets when possible and appropriate.

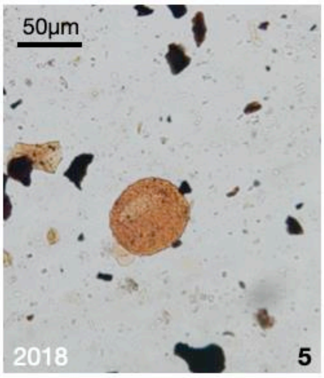
Fig. 4. Holotypes of *Cerebropollenites thiergartii* Schulz 1967, *Pollenites macroserratus doggerensis* Thiergart 1949. 1–8. Holotype for *Cerebropollenites thiergartii;* **1-3.** Location and preservation of the holotype in a remaining (but narrowing) pocket of glycerine gelatine indicated with an arrowhead**; 4.** strew mount slide with cover-slip seal (which is severely cracked), **5-7.** Decay of the holotype over three years, the continuous desiccation of the last pocket of gelatine is evident; **8.** Holotype for *Cerebropollenites thiergartii* in different focal planes; **9.** strew mount slide without cover-slip seal. The red dot and indication of the type was added; **10**, **11.** Holotype for *Pollenites macroserratus doggerensis.* **12**–**13.** Location and preservation of the holotype (indicated with an arrowhead) at the edge of the cover slip indicated in red. **14.** Holotype for *Sciadopitys multiverrucosus.* Scale = 10 µm (unless indicated otherwise).

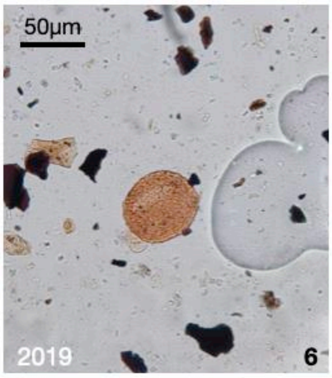

200µm
2019
1

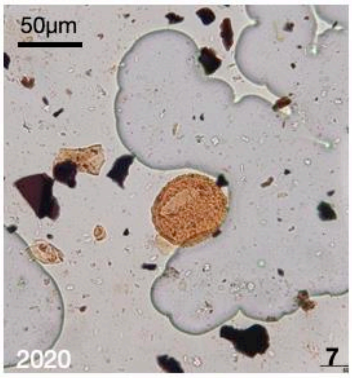

200µm
2019
2

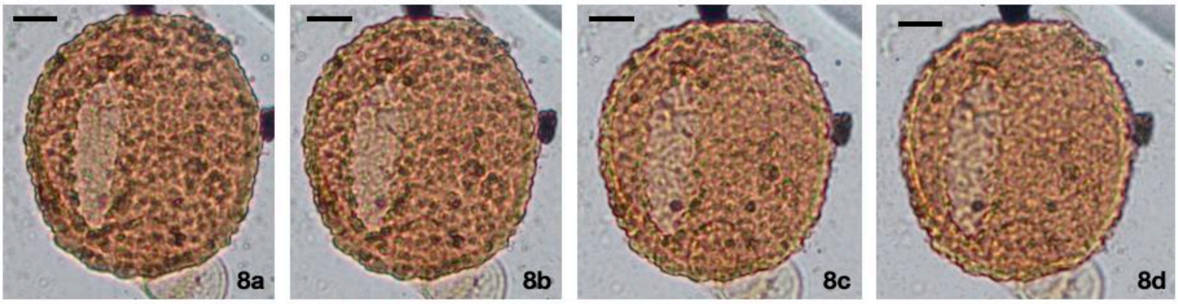

200µm
2020
3


Harnitz 3so
59/2
37-9,4 m
K11251
K11364
4


50µm
2018
5


50µm
2019
6


50µm
2020
7


8a
8b
8c
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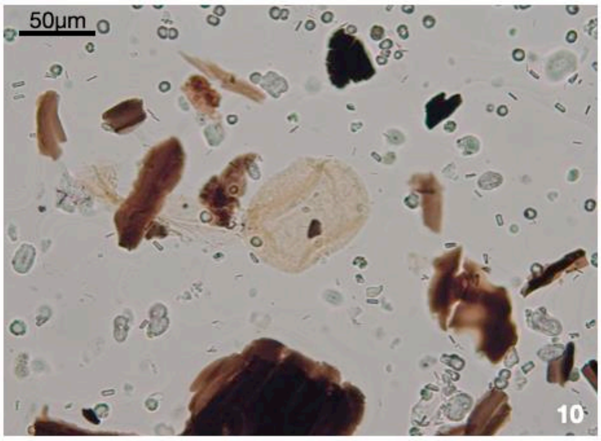
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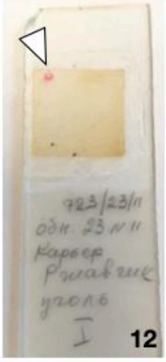
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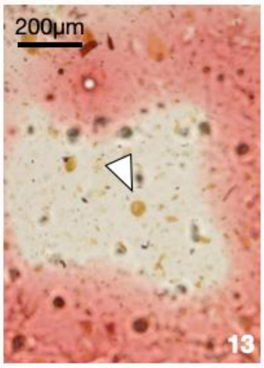
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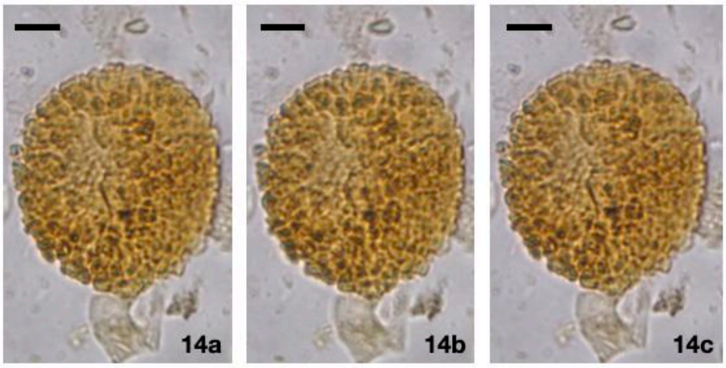
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3.2.1. Forms with small ornamentation

Specimen with very fine infrareticulate to diffusely granulate ornamentation (Figs. 4.1–4.10) can be sometimes mistaken with *thiergartii.* These are however assignable to *Chasmatosporites apertus* and have a fairly thick exine (2–3 µm). Due to their thicker exine, individuals of this taxon are less likely secondarily folded, and the thickening clearly delimits the sulcus. Although *Chasmatosporites apertus* can appear similar, it is not yet verrucate like *thiergartii.*

The holotype of *Cerebropollenites thiergartii* (Fig. 5.11) looks rather iconic, but most of the specimens we could find on the same slide that comply with the description look slightly different (Figs. 5.12, 5.13 and 5.18), although generally characterised by the typical ornamentation of small verrucae. The specimen that is most compliant with the holotype is lying on the side, preventing the view on the sulcus (Fig. 5.13). Some grains are much bigger and more folded (Fig. 5.12), smaller with a more circular sulcus (Fig. 5.18), and some (Fig. 5.14) are not clearly identifiable as a pollen at all and could be a *Polypodiisporites polymicroforatus*, especially due to the size, or a *Chasmatosporites apertus* with a slightly thinner exine, or in fact a poorly preserved and rather small *thiergartii.*

The Swedish material (Höllviken) contains only few specimens that are directly comparable to the holotype (Fig. 5.21 and Fig. 6.2 – proximal view and Fig. 5.23 – distal view). In the vast majority of cases, however, the exine appears partially dissolved, with mainly the ornamentation remaining to varying degrees (Figs. 5.15 and 5.16). The ornamentation and thinner sulcus area usually allow identification, even when the overall shape varies from the typical oval-subcircular (e.g., Figs. 5.11, 5.15, 5.21), and is more spindle shaped probably as a result of compression and folding (Figs. 5.17, 5.22). Some specimens are much smaller (around 40 µm) and more circular (Figs. 5.18 and 5.19 from Bonenburg), while others appear much bigger (up to 70 µm) and more ‘pancake’-shaped (Fig. 5.20). Common in all these specimens is a very fine ornamentation consisting of sculptural elements that are less than 1.5 µm in diameter.

In addition, we found forms more similar to the holotype of *Sciadopitys multiverrucosus* (Fig. 6.19) with slightly bigger sculptural elements ranging from 1.5 µm up to 2 µm (Figs. 6.3–6.4), and even up to 3 µm (Figs. 6.5–6.15). One can make a progradational series of increase in size (Figs. 6.1–6.6). The lower half of the spectrum includes the holotype of Schulz and the intraspecific variation observed in his material. The upper half is most similar to the holotype for *Pollenites macroserratus* f. *doggerensis*. (Fig. 5.14). With increased size of the verrucae (Figs. 7.17–7.19), some specimen can appear a bit evocative of *Sciadopityspollenites serratus* (Figs. 7.1–

7.16). However, the pollen *Sciadopityspollenites serratus* is usually smaller, the sculptural elements more distant from each other, and the verrucae themselves are often a bit dumbbell or irregular or angular shaped (Figs. 7.1–7.16).

In addition, we also observed other intermediate forms with very big and round verrucae (Figs. 6.21–24), in a size range much beyond previously described forms. In comparison to forms assignable to *mesozoicus* or *macroverrucosus,* the protrusions in these forms are much more massive and solid, and perfectly rounded. SEM images from existing literature have also illustrated such forms before (Fig. 7.23). Although the authors assigning them to *mesozoicus,* they are unlike any of the other holotypes documented in this study.

It should also be noted that almost all depicted forms in figures 5 and 6 derive from Jurassic samples. Only the specimen (Fig. 6.9) originates from the Rhaetian, i.e., from the transition from the Contorta to the Triletes Beds and could be also classified as *Ricciisporites tuberculatus*. It was unusual to find this specimen so perfectly preserved as a single grain. Normally, *Ricciisporites tuberculatus* pollen occur in tetrads and when found as singular grains, partial tetrad remains are still attached. Its resemblance with other depicted specimens (Fig. 6, especially between Figs. 6.9 and 6.10) is uncanny. The only perceivable difference is that the muri shining through from the back in the sulcus area are bigger, merged, and look like the remains of where the pollen was once attached in a tetrad in one of them (Fig. 6.9), indicating the typical tetrad condition of *Ricciisporites tuberculatus*.

3.2.2. Forms with intermediate-sized ornamentation

Comparison of the holotypes of *Pollenites macroverrucosus* (Fig. 8.1) and *Tsugaepollenites mesozoicus* (Figs. 9.1a and 9.1b) shows that they are overall similar but differ in the size and density of their sculptural elements. The observed variation in all studied material can then be categorised to belong mostly to one of the two specimens.

The sculptural elements in specimens similar to the holotype of *Pollenites macroverrucosus* (specimens in Fig. 8) all show a very dense arrangement of sculptural elements (compare Figs. 8.2 and 8.5). Their muri are very variable in length and shape, but rather uniform in thickness (ca. 1.2–1.5 µm). These muri are touching each with little space in between and are thus very reminiscent of the arrangement of the gyri in a brain. This ornamentation is best illustrated by an existing SEM image (Fig. 8.8). As a result of the ornamentation, the outline of these individuals is only slightly.

Specimens which are best compared with the holotype of *Tsugaepollenites mesozoicus* are clearly identifiable by their bigger and more loosely arranged muri. The contrast of the density of their sculptural elements is best illustrated by an SEM image (Fig. 9.12), which corresponds perfectly with a specimen from Couper's material (Fig. 9.11). Due the stronger contrast of muri and free intra-mural spaces the outline is much more sinuate due to strong differences in height (e.g. Figs. 9.4, 9.8, 9.9). This becomes especially obvious when comparing two SEM images one with a looser arranged ornamentation as in *mesozoicus* (Fig. 9.12) and one with much denser ornamentation as in *macroverrucosus* (Fig. 9.13).

It should be noted that most of *mesozoicus* specimen appear much more hyaline than those depicted in figure 8. This is partially an effect of observation with different objectives. While the Höllviken material could be studied with a 100x objective, the holotype material was only viewed at 40x in most cases because of its position at the very edge of the slide). The objective with the lesser magnification used for this study generally gives a more hyaline and less saturated image (compare Fig. 9.3 a taken with 100x and Fig. 9.3 b taken with a 40x objective). However, this does not compensate for the fact that the specimen here assigned to *mesozoicus* from the Couper material are generally more hyaline, although this effect is heightened by the objectives used for study. The more hyaline character appears to be the result of the less dense packing of the sculptural elements, with bigger empty spaces in between them and the bigger elements which are themselves fairly hyaline as well.

When focusing on the equator of the observed *mesozoicus* specimen, the rather big protrusions create an illusion of a fringe which is observable in the holotype, and even stronger in others (e.g. Fig. 9.11) This is not, however, comparable with the fringe in *Tsugaepollenites igniculus* (Figs. 10.11–10.13), which is the result of the contrast of two types of different ornamentations. In *mesozoicus* specimens, it is merely an optical effect of the overlying protrusions creating a darker impression than on the corpus, which is necessarily a bit lighter in colour because the sulcus area is without protrusions. It is therefore necessarily lighter in colour and enhances the impression of a fringe. In less well-preserved specimen for example (Fig. 9.9), there is no indication of a fringe. In contrast, in poorly preserved specimen of *Tsuagaepollenites igniculus* (Fig. 10.12) the poor preservation even permits a better view on the fringe. SEM images from literature further confirm the absence of a fringe in species comparable to the holotype of *Tsugaepollenites mesozoicus*, and also confirm the bigger spaces in between the sculptural elements (Fig. 9.12) in comparison to species that are better comparable to *Pollenites macroverrucosus* (Fig. 9.13 and Fig. 8.8)

The studied material was each dominated by either *macroverrucosus* (Höllviken) or *mesozoicus* (Couper) forms, but in both a small number of the respective other form could be found as well (e.g. Figs. 8.5–8.7), even in Thiergart's holotype slide (Fig. 9.10). The Swedish material from Höllviken also contained many specimens in varying degrees of preservation that are best compared to Thiergart's holotype (Figs. 8.2–8.4 and 8.9–8.16). The preservation can have an effect on how the sculptural elements are perceived (compare Figs. 8.13–8.16), but the density of packaging of the sculptural elements and the less wavy outline is still perceivable and characteristically different from poorly preserved *thiergartii* specimens (Figs. 5.16 and 6.14) or poorly preserved *mesozoicus* representatives (Fig. 9.9).

We can also document a third kind of specimens that are smaller, usually more circular and have muri that are similarly as high as in other specimens of *mesozoicus*, but much shorter, at most making a loop (Figs. 9.1, 9.6), rather than the meandering as in *mesozoicus* (Fig. 9.11). Again, SEM images from existing literature document specimens with this morphology (Fig. 9.7).

3.2.3. Forms with large and hyaline protrusions

While the previous described forms show a relative large infraspecific variation in their sculptural elements, the forms with the largest and on top of that very hyaline protrusions that can be assigned to *pseudomassulae,* do not. Although these pollen can vary greatly in size (45–63 µm in diameter), their overall appearance is rather uniform and mostly influenced by preservation, i.e. pyrite impressions (e.g. Figs. 10.4, 10.7) or thermal maturation, especially towards the Rhaetian 'dark zone' (van de Schootbrugge et al. 2009) (compare Fig. 10.3 from the Contorta Beds, to Fig. 10.4 from the Triletes Beds). Increased thermal maturation can mask the otherwise strongly hyaline yellow-brown impression of the palynomorph wall, and it becomes clear, especially when looking at the very hyaline representatives (e.g., Figs. 10.5–10.7), that these specimens do not have a fringe but a collection of rather large and simple convolutions that are 5–20 µm in diameter (compare fringe in Figs. 10.11–10.13). These convolutions are usually rounded, but can appear a bit sharper edged at times (Figs. 10.5, 10.10), but are never angular. In some specimens mounted between two cover-slips that could be turned to investigate both proximal and distal side equally well, a germinal area could not be identified, and instead, protrusions are equally well developed on either side of the palynomorph (Figs. 10.5, 10.6).

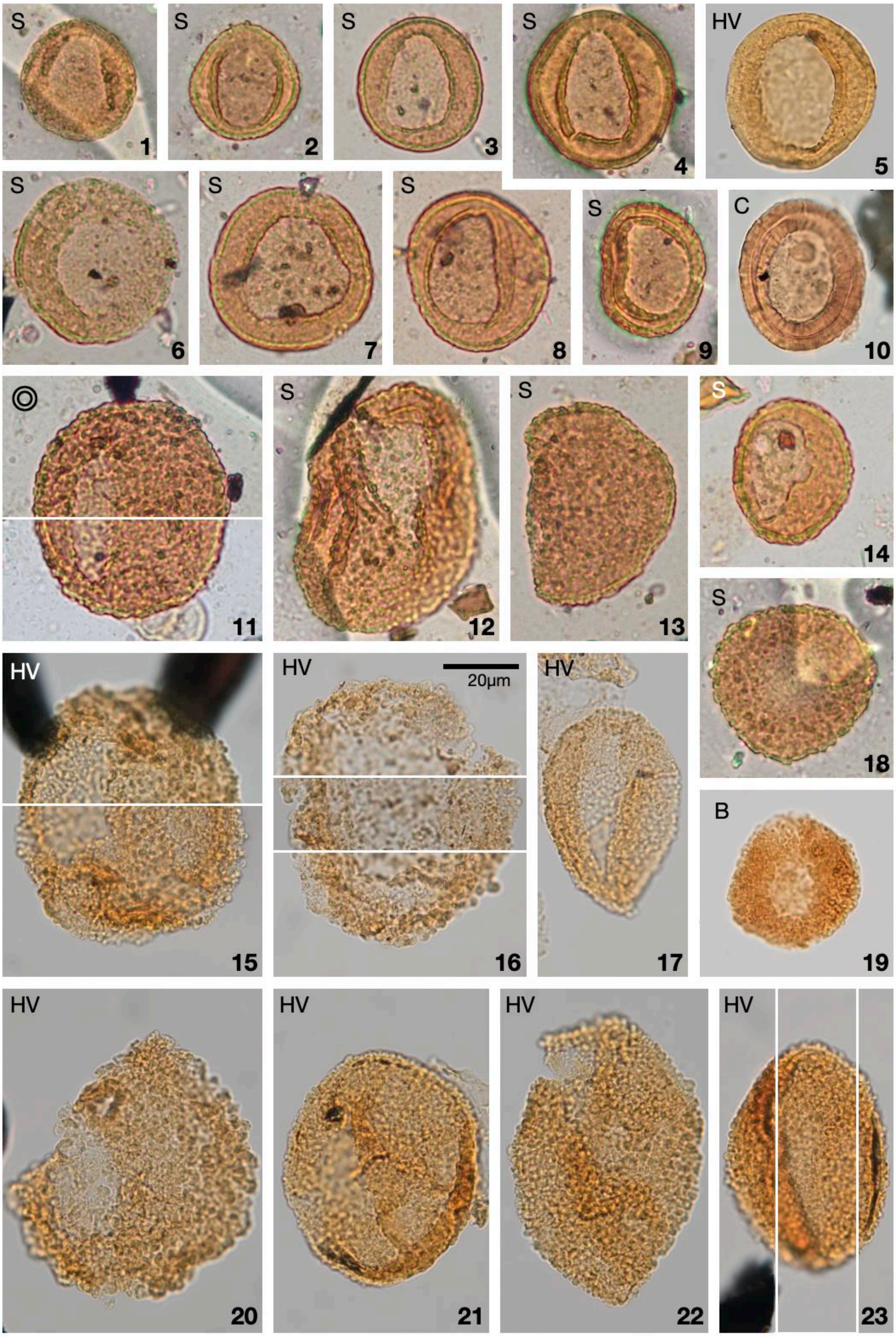


Fig. 5. Intraspecific variation of forms with small ornamentation I. 1–10. *Chasmatosporites apertus;* 11–23. *Cerebropollenites thiergartii*. B = Bonenburg, C = Couper; HV = Höllviken; S = Schulz ◎ = holotype.

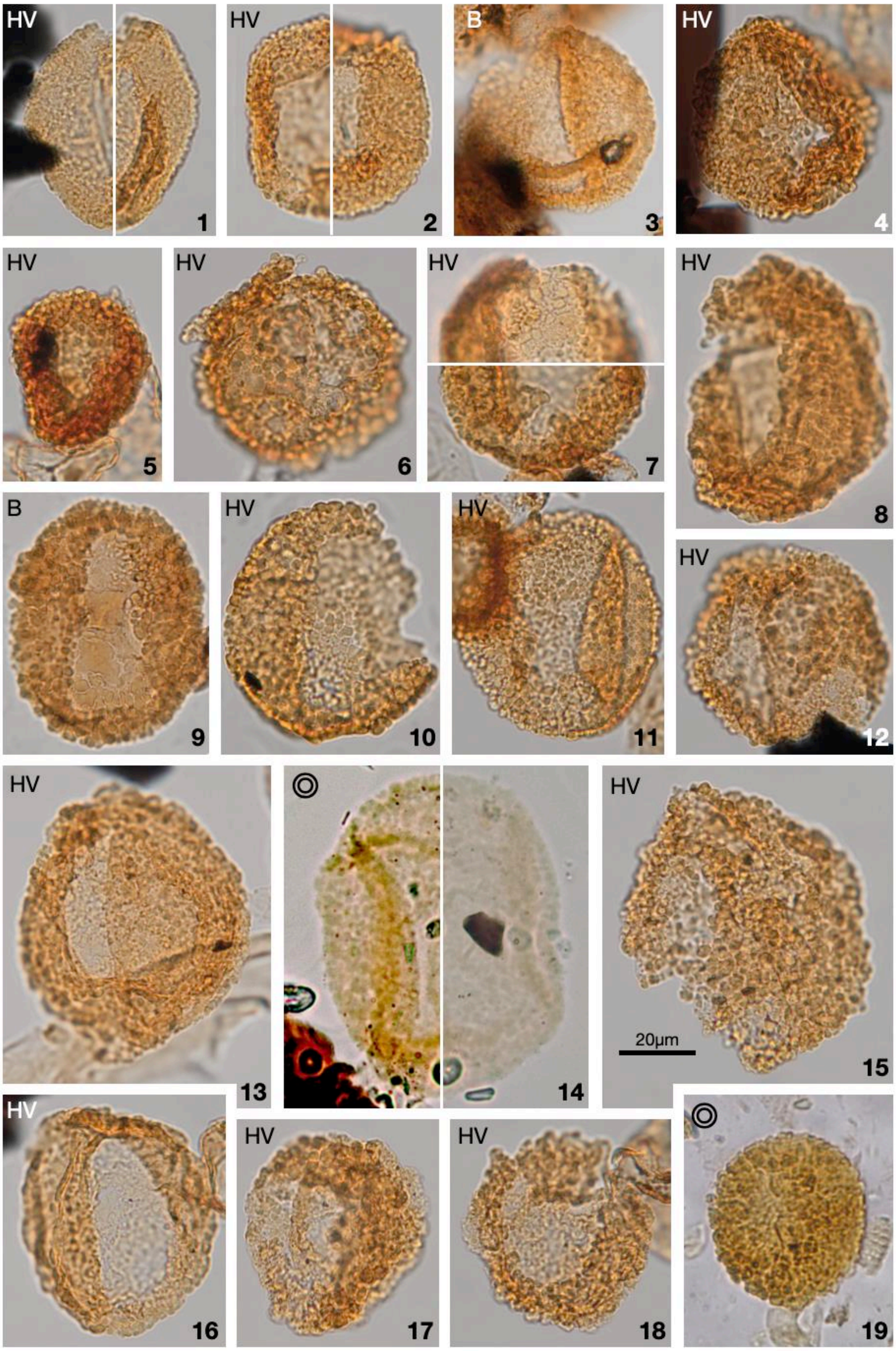


Fig. 6. Intraspecific variation of forms with small ornamentation II. 1–13. Variation in *Cerebropollenites thiergartii*; **14.** Holotype for *Pollenites macroserratus doggerensis,* left half contrast enhanced; **15–18.** Variation in specimens with poorer preservation tentatively assigned to the epithet *thiergartii* but showing transitionary ornamentation to *macroverrucosus*. **19.** Holotype for *Sciadopitys multiverrucosus*. **B** = Bonenburg, **HV** = Höllviken; **◎** = holotype.

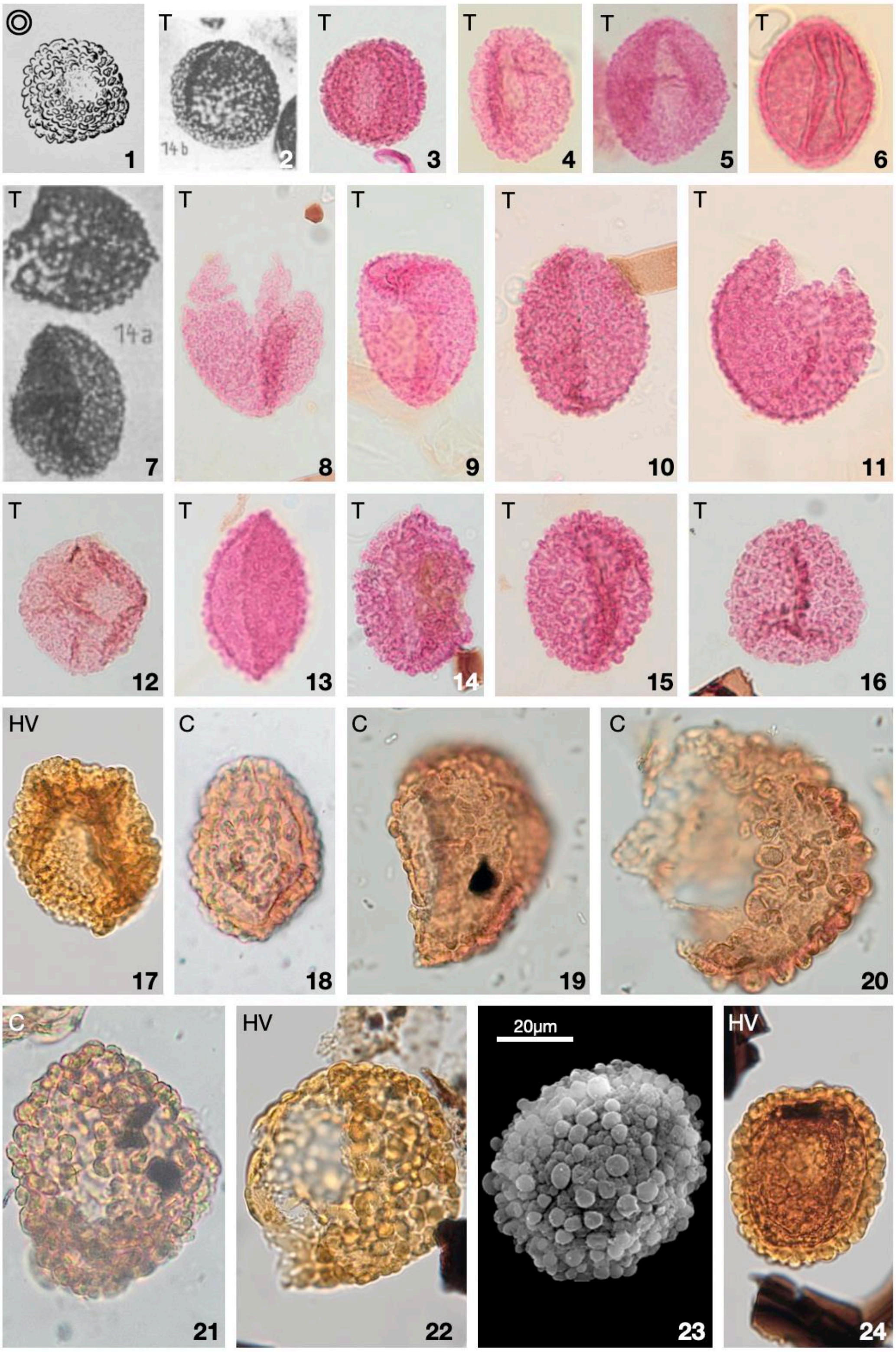


Fig. 7. Intraspecific variation in *Sciadopityspollenites serratus* (1–16) and variation in *Cerebropollenites sp.* (17–24). **1.** Drawing of the holotype for *Sciadopityspollenites serratus* reprinted with permission of the LBEG/BGR from Potonié (1958); **2 and 7.** Original photographs reprinted from Thiergart (1938) with permission of LBEG/BGR. **23.** SEM image reprinted from Shang and Zavada (2003) (Fig. 5) with permission of Taylor and Francis, there assigned as '*Cerebropollenites mesozoicus*'. Locality of the material is indicated in the top left corner (**C** = Couper; **HV** = Höllviken; **T** = Thiergart)

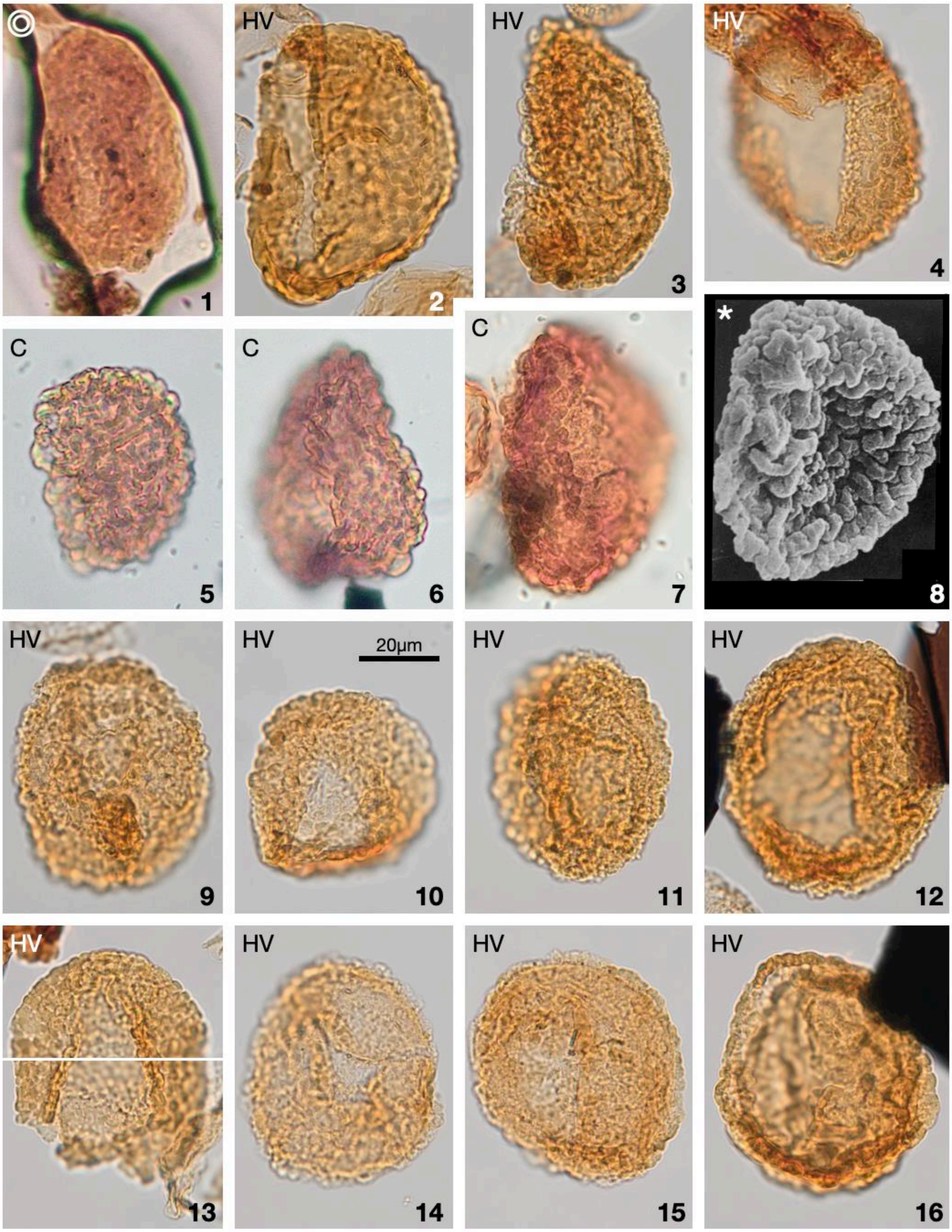
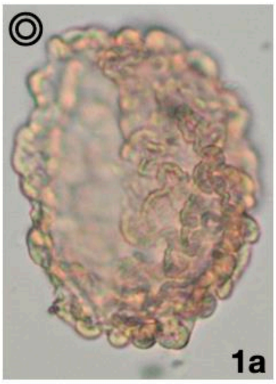


Fig. 8. Intra- and interspecific variation in rugulate forms most similar to *macroverrucosus*. 1. Holotype for *Pollenites macroverrucosus* Thiergart 1949. **2–7.** Variation in densely rugulate forms. **8.** SEM image of '*Cerebropollenites* sp.' from plate 3, figure F in Guy-Ohlson and Malmquist (1985), reprinted with permission of the Geological Survey of Sweden. **9–16.** Variation in densely rugulate forms. Locality of the material is indicated in the top left corner (**C** = Couper; **HV** = Höllviken). Specimens indicated with an asterisk (*) are not so scale.



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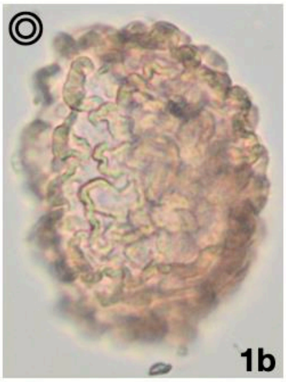

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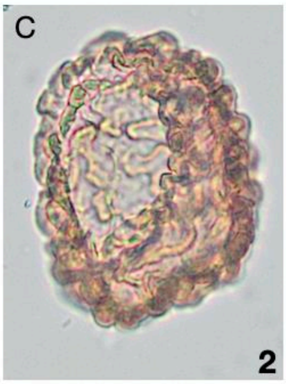

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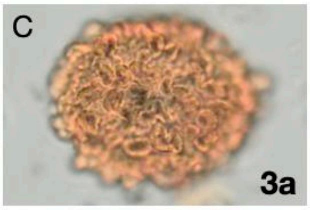

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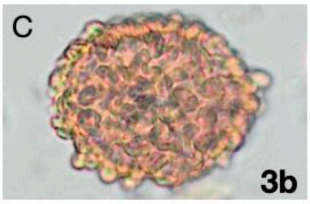

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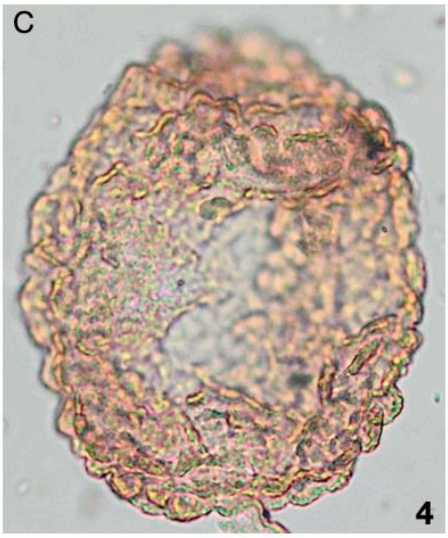

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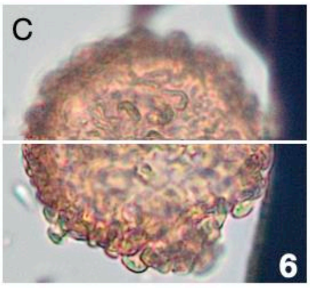

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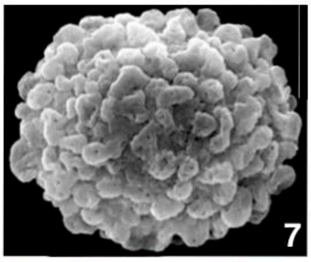
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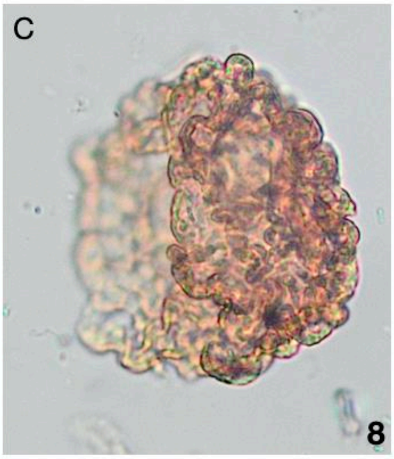

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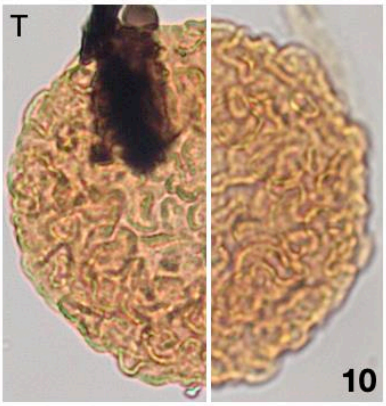

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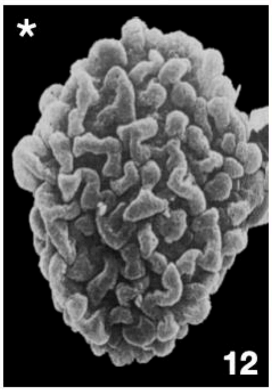

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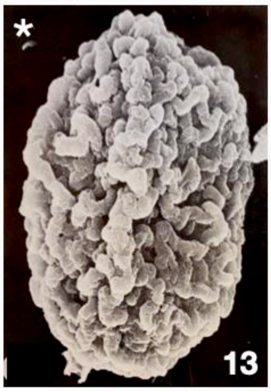

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Fig. 9. Intra- and interspecific variation in rugulate forms II. 1. The holotype for *Tsugaepollentes mesozoicus* in two focal planes (a+b); **2.** Form conspecific with the holotype; **3a.** Specimen considered conspecific with *Cerebropollenites carlylensis*, photo taken with 100x oil immersion objective; **3b.** the same specimen photographed with a 40x objective; **4–5.** Specimens with intermediate ornamentation in size of the protrusions, but density more similar to *mesozoicus*; **6.** Specimen as intermediate form between epithets of macroverrucosus and *carlylensis*, type of the ornamentation considered conspecific with *carlylensis;* **7.** SEM image reprinted from Shang and Zavada (2003) (Fig. 3) with permission of Taylor and Francis. There assigned as '*Cerebropollenites mesozoicus'* but with ornamentation closer to specimen from figure 3 and 6 in this plate; **8.–11.** Intraspecific variation of forms conspecific with *Tsugaepollentes mesozoicus;* **12**. SEM image altered after Guy-Ohlson (1989) (Fig. 34) with permission of the Micropaleontological Society. There assigned as '*Cerebropollenites mesozoicus'*, which complies very well with specimen shown on its left; **13.** SEM image reprinted from (Guy-Ohlson 1986) (plate 14, Fig. 1) with permission of the Natural History Museum Sweden. There assigned as '*Cerebropollenites mesozoicus'*, which complies best with specimen presented in Fig. 8 especially in direct comparison with SEM image on its left. Locality of the material is indicated in the top left corner (**C** = Couper). Specimens indicated with an asterisk (*) are not so scale.

3.3. Nomenclature – name usage statistics

The name *Cerebropollenites* with 16 described species is used exclusively for taxa occurring in the Mesozoic, whereas *Sciadopityspollenites* with at least 26 species is used from the Mesozoic to the Cenozoic (Fig. 11). However, there is a notable gap between Mesozoic *Sciadopityspollenites* species reaching until the Albian and species described from the Paleogene onwards. Only a few Cenozoic species, amongst them *Sciadopityspollenites serratus,* might already occur in the Mesozoic (Fig. 11 dotted line). Several of the Mesozoic *Sciadopityspollenites* names are recombinations of epithets otherwise combined with *Cerebropollenites* and are mostly used in studies from Russia (*macroverrucosus*, *mesozoicus*, *carlylensis,* Fig. 11). Calculating citations for all species per genus together amounts to roughly 500 citations for *Sciadopityspollenites* and about a thousand for *Cerebropollenites*, partially because *Cerebropollenites mesozoicus* alone has almost as many citations (430) as all *Sciadopityspollenites* species together.

Despite the large number of species, only few names are used more than twice per decade, i.e. have a citation rate (CR) of 0.2 or more. Some names have never been recombined with either *Cerebropollenites* or *Sciadopityspollenites* (e.g. *Cerebropollenites thiergartii*, *Cerebropollenites Sciadopityspollenites multiverrucosus*, *Sciadopityspollenites osmundaeformis)* or have not been adopted afterwards even though recombined (*Sciadopityspollenites carlylensis*). On the other hand, some recombinations of epithets (*mesozoicus, macroverrucosus,* and *pseudomassulae*) are used so frequently (here we apply a threshold of once every two years, i.e. CR around 0.5; Fig. 11) that their inconsistent recombinations can cause nomenclatural and taxonomic confusion.

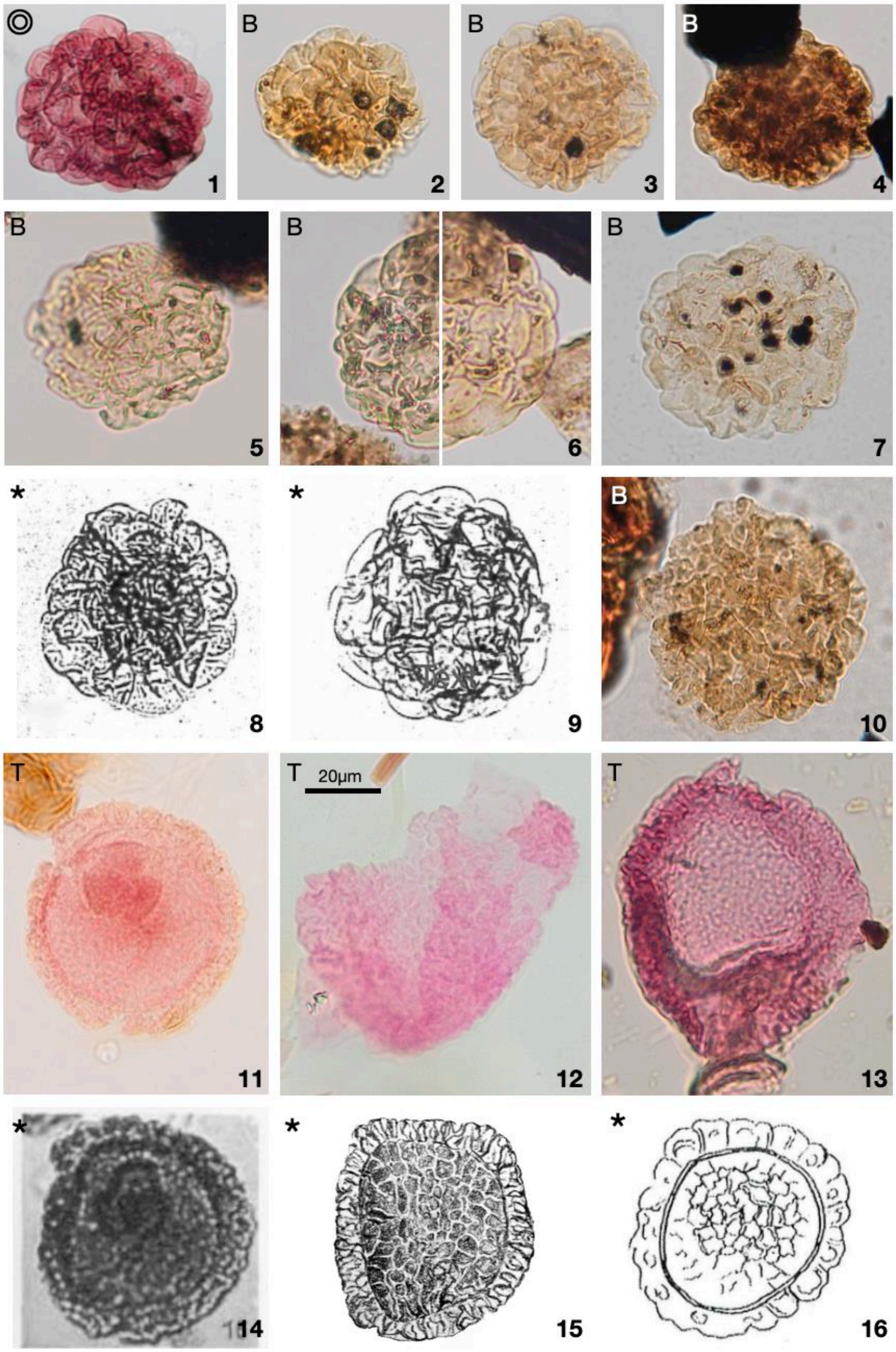
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Fig. 10. Intra- and interspecific variation of *Camerosporites* (≡ *Tsugaepollenites*) *pseudomassulae* and *Tsugaepollenites igniculus*. 1. Holotype for *Camerosporites pseudomassulae* Mädler 1964b; **2–10**. Intraspecific variation for *Camerosporites* (≡ *Tsugaepollenites*) *pseudomassulae;* **8.** and **9**. Specimens from Orbell (1973) there assigned as '*Cerebropollenites mesozoicus*', reprinted with permission of the British Geological Survey; **11.** Rephotographed *Tsuga-pollenites igniculus* from Thiergart (1938); **12.–13.** *Tsugaepollenites igniculus*; **14.** Original photograph for *Tsuga-pollenites igniculus* from Thiergart (1938) reprinted with permission from LBEG/BGR; **15.** Drawing for *Tsuga-pollenites igniculus* from Potonié and Venitz (1934) reprinted with permission from LBEG/BGR; **16.** Drawing for *Tsuga-pollenites igniculus* reprinted from (Potonié 1931). Locality of the material is indicated in the top left corner (**B** = Bonenburg; **T** = Thiergart). Specimens indicated with an asterisk (*) are not so scale.

Comparing the use of these frequently combined epithets with the use of *Cerebropollenites thiergartii* also shows that the epithets have variable popularity over the decades (Fig. 12). The epithet *mesozoicus* is the most popular in general, with increasing use up to the 1980s, after which it declines in favour of *macroverrucosus* which is less often, but relatively consistently often over the decades from the 1980s onwards (Fig. 12 A). The epithets *pseudomassulae* and *thiergartii* are used similarly often until the 2000s, whereas*thiergartii* gets increasingly used (Fig. 12 A). In the 2010s citations of *thiergartii* increase further and are six times higher than *pseudomassulae* and circa a third more than *mesozoicus* (Fig. 12 A). This increase is mainly constituted by number of citations that cannot be assigned regionally, i.e., reviews or meta-analytical studies that reference the name, but do not document it for a particular region (Fig. 13). It is striking, that the name does not occur in any studies on Russian material and absent in Asian studies in the 1990s and 2000s.

Apart from the interspecific change of name usage, the intraspecific change of the different recombinations of both *mesozoicus* and *macroverrucosus* is significant. The epithet *mesozoicus* was first combined in the basionym as *Tsugaepollenites mesozoicus* (Fig. 12 B). While the recombination with *Tsugaepollenites* was still more favoured in the 1960s, the recombination with *Cerebropollenites* took over in the 1970s, which then peaked in the 1980s before declining use thereafter. It is noteworthy, that the trend of *Sciadopityspollenites mesozoicus* usage increases until the most recent decade (2010s) although the overall number of citations is very low (CR=0.46; Fig. 11 and 12 B). Amongst the three competing recombinations, the name *Cerebropollenites mesozoicus* is clearly the most common (CR=6.95) and established name (Establishment Index (EI) value = 1.2). The use of names in the different regions of the world was mixed until the 1980s, after which the recombination with *Sciadopityspollenites* appears to be preferred in studies with material from Russia.

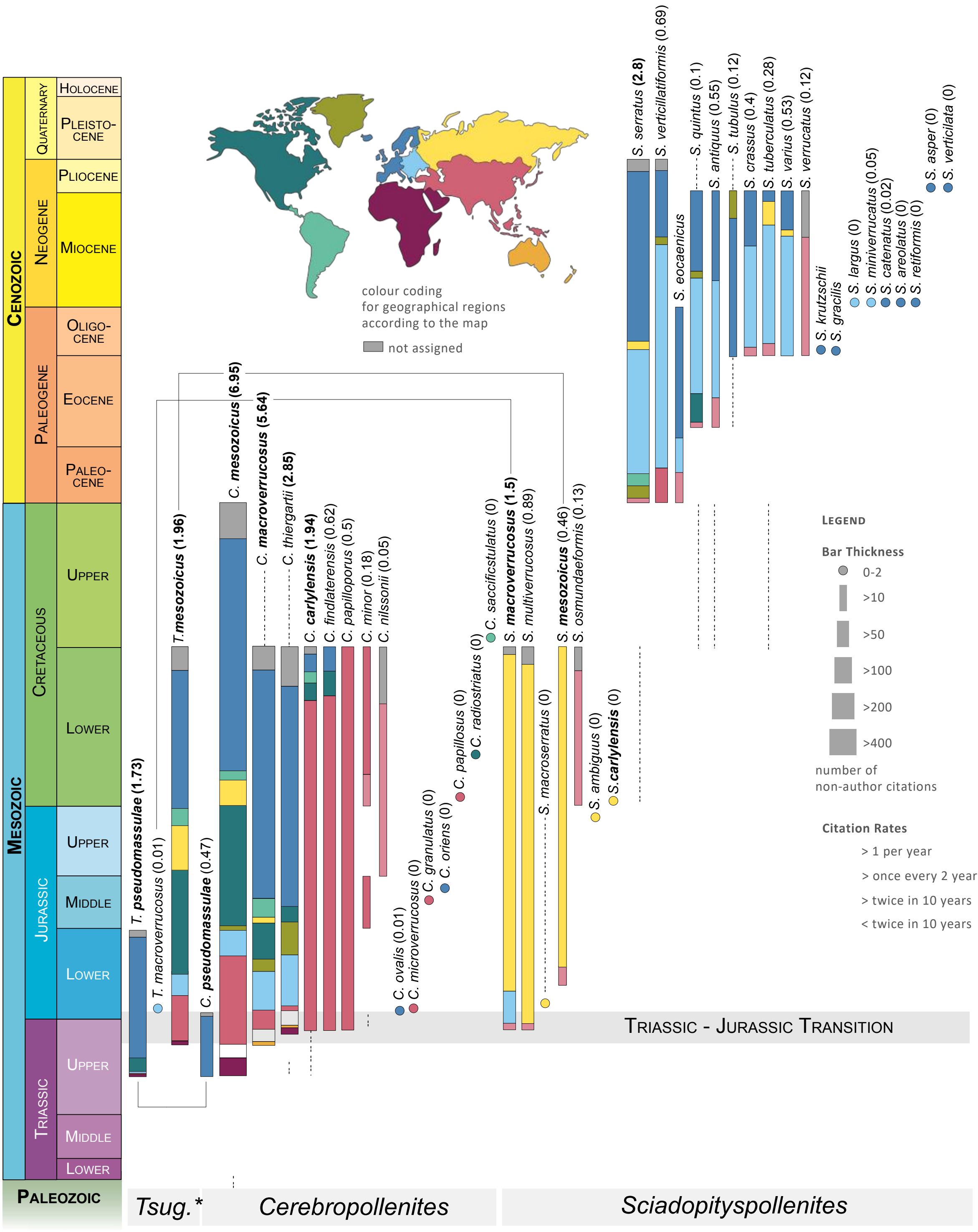
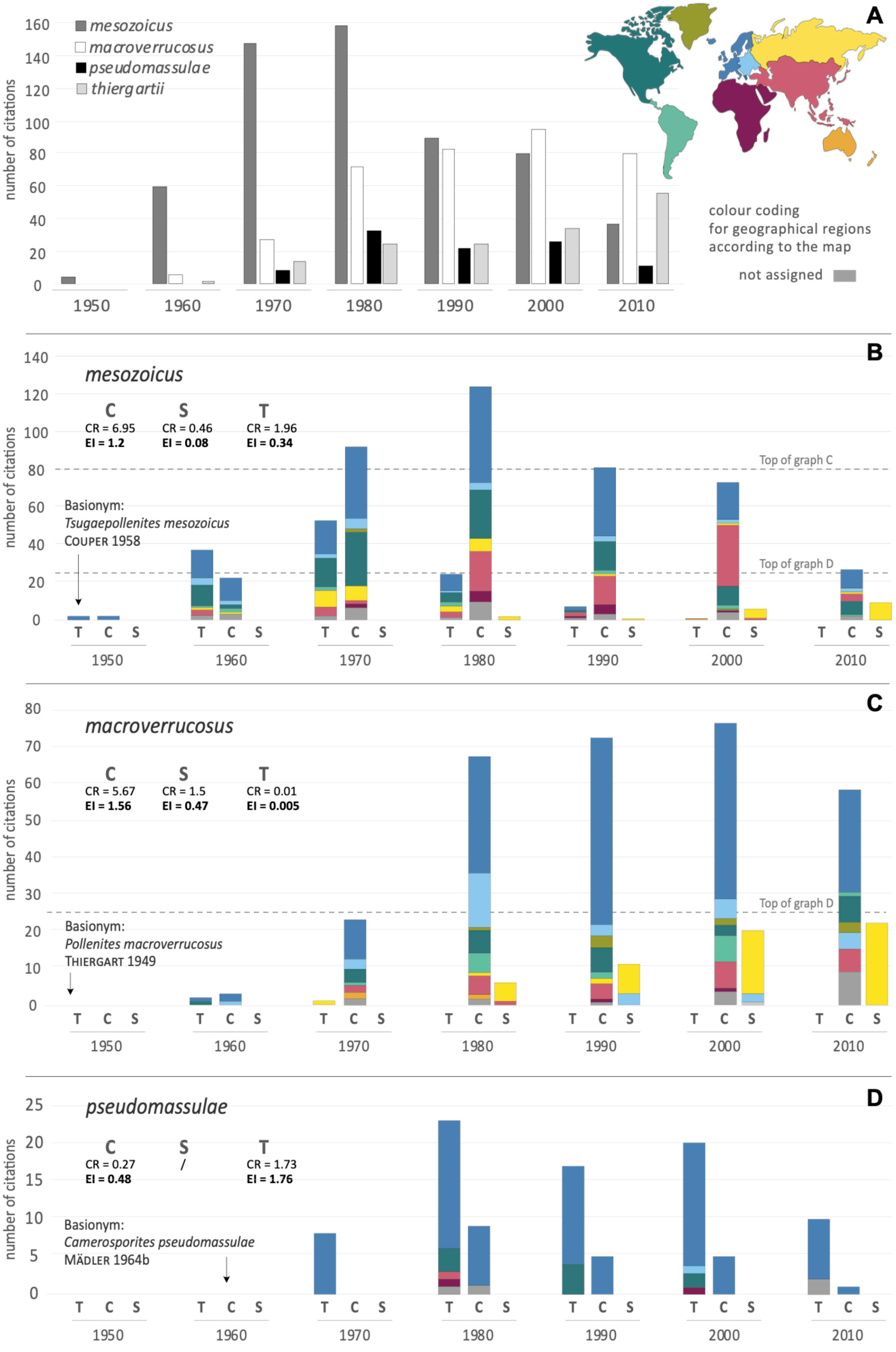


Fig. 11. **Stratigraphic ranges of *Cerebropollenites* and *Sciadopityspollenites* and all described taxa, colour-coded according to country of origin.** Thickness of the bars indicates the number of citations. Length of the bars indicate stratigraphic range. Additionally, the full length represents100% of the citations of each taxon, colour coded subdivisions, represent percentage share of citations from the geographical region represented by that colour.

The very same pattern is visible for the recombination of *macroverrucosus* with *Sciadopityspollenites*, yet with higher amplitude, i.e., higher Citation Rate (CR=1.5) and much higher Establishment Index value (EI=0.47) of *Sciadopityspollenites macroverrucosus* in comparison to *Sciadopityspollenites mesozoicus* (EI=0.05) (Fig. 12 C). In addition to studies for Russian material, a number of studies from Eastern Europe use this recombination too (especially in the 1990s and 2000s (Fig 12 C). All in all, the most favoured recombination for the epithet *macroverrucosus* is *Cerebropollenites* (CR=5.67; EI=1.56), and in contrast to the epithet *mesozoicus*, the recombination with *Tsugaepollenites* is neglectable (CR=0.01) (Fig. 12 C).

This epithet *pseudomassulae* is used much less frequently than the previous two and it has never been recombined with *Sciadopityspollenites* (Figs. 11 and 12 D). Since its original description with the basionym *Camerosporites pseudomassulae* in 1964 there is a significant time gap until its recombination as *Tsugaepollenites pseudomassulae* in 1975. Consequently, the number of citations is still low in the 1970s before having more than 15 citations per decade in the 1970s–2000s (Fig. 12 A). The recombination with *Cerebropollenites* occurs concurrently from the 1980s onwards, but with decreasing values from decade to decade till today (CR=0.27). *Tsugaepollenites pseudomassulae* is in comparison the most favoured recombination (CR=1.73, EI=1.76), but it is striking that the names occur almost exclusively in European and North American studies (Fig. 12 D).

Fig. 12. User statistics for the epithets *mesozoicus*, *macroverrucosus*, *pseudomassulae*. Historically each epithet is most commonly assignable to either **T** (*Tsugaepollenites*), **C** (*Cerebropollenites*) or **S** (*Sciadopityspollenites*). **A.** Overview of number of citations per epithet (irrespective of its genus assignation). The data for *Cerebropollenites thiergartii* is given for comparison. **B.** Number of citations for the epithet *mesozoicus* per genus per decade. **C.** Number of citations for the epithet *macroverrucosus* per genus per decade. Note the different scale in comparison to the other graphs (see A for comparison of taxa). **D.** Number of citations for the epithet *pseudomassulae* per genus per decade. Note the different scale in comparison to the other graphs (see A for comparison of taxa).


A
number of citations
160
140
120
100
80
60
40
20
0
mesozoicus
macroverrucosus
pseudomassulae
thiergartii
1950
1960
1970
1980
1990
2000
2010
colour coding for geographical regions according to the map
not assigned
B
mesozoicus
C
CR = 6.95
EI = 1.2
S
CR = 0.46
EI = 0.08
T
CR = 1.96
EI = 0.34
Basionym:
Tsugaepollenites mesozoicus
COUPER 1958
Top of graph C
Top of graph D
T C S
C
macroverrucosus
C
CR = 5.67
EI = 1.56
S
CR = 1.5
EI = 0.47
T
CR = 0.01
EI = 0.005
Basionym:
Pollenites macroverrucosus
THIERGART 1949
Top of graph D
D
pseudomassulae
C
CR = 0.27
EI = 0.48
S
/
T
CR = 1.73
EI = 1.76
Basionym:
Camerosporites pseudomassulae
MÄDLER 1964b
25
20
15
10
5
0

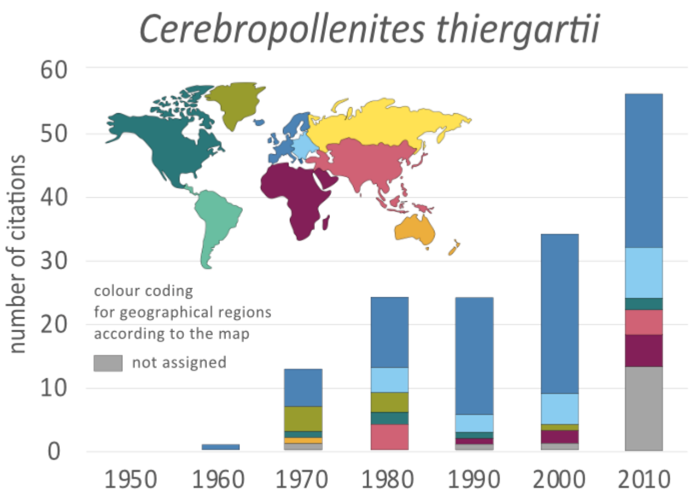


Fig. 13. User statistics for *Cerebropollenites thiergartii.* Number of citations of the name *Cerebropollenites thiergartii* per decade per geographical region of the world.

4. Discussion: Commentated Literature Review

4.1. For the genera *Tsugaepollenites*, *Sciadopityspollenites* and *Cerebropollenites*

4.1.1. Genus *Tsugaepollenites* (Potonié & Venitz 1934) Potonié 1958

Type: *Sporonites igniculus* Potonié 1931, p. 556, Fig. 2 (drawing after V80a)

Original genus description. – Genotypus 35 µm, Äquator ± kreisförmig, mit äquatorständigem Velum, das sehr schmal sein kann, dieses krausenartig radial gefältelt, extrema lineamenta unregelmäßig gewellt bis gekerbt. Exine des Zentralkörpers rugulat, d.h. mit unregelmäßigen kurzen ± geschlängelten Muri bis Warzen bedeckt (Potonié 1958, p. 48).

English translation. – Genotype 35 µm, equator more or less circular, with an equatorial velum, which can be very narrow, this fringe is radially folded, outline irregularly convoluted to sinuate. Exine of the central body rugulate, i.e., covered with irregular short more or less winding muri to warts.

Discussion. – Without making a formal emendation, Manum (1962) adds or clarifies two important diagnostic features for the genus:

> 1. The corrugated protrusions forming the conspicuous sculpturing are hollow. This may easily be observed both in surface view and in optical section of the exine. […] 2. The grains are heteropolar […]. The ventral side has a central area which has a less "puffy" and corrugated sculpturing than the dorsal side, and it is usually depressed. Protrusions of a more puffed-out nature than those of the dorsal side surround the

> area and are present in the equatorial region where they produce a more or less prominent equatorial fringe, noticeable in polar aspect of the grains. German examples of Tsugaepollenites which I have seen possess these characters. (Manum 1962, p. 45)

Manum's additions are very important and appear very adequate in view of our own study of the type for the genus name, and as will be pointed out below, especially in distinguishing species assigned to *Cerebropollenites* and *Sciadopityspollenites*. Manum's clarified diagnostic features are additionally supported by an SEM study on pollen assigned to *Tsuga* from the Middle Miocene (Grímsson & Zetter 2011), which highlights the very same distinguishing characteristics pointed out by Manum (1962), and illustrates that a monosaccus, heteropolarity through the difference in sculpture on the proximal and distal face, and the large subcircular germinal area which almost encompasses the entire proximal face, are crucial distinguishing characteristics.

4.1.2. Genus *Sciadopityspollenites* Raatz 1937 ex Potonié 1958

Type: *Sporites serratus* (Potonié & Venitz 1934), p. 15, Pl. 1 Figs. 6–7

Original (?) genus description. – Gestalt rund bis oval bis spindelförmig. Infolge der warzigen Oberflächenstruktur erscheint die Umrißlinie unregelmäßig gewellt. Eine Dehiszenz ist niemals zu erkennen (Raatz 1937, p. 13).

English translation. – Shape round to oval to spindle-shaped. As a result of the verrucate ('warty') ornamentation, the outline appears irregularly undulated ('wavy'). Dehiscence never perceivable.

Discussion. – Interestingly, were very ambiguous in their systematic section (p.15), and while they refer to it as a spore (*Sporites*) in the text, the legend of plate 1 uses *Pollenites*, probably because they named *Ophioglossum* and *Tsuga* as potential affiliations. Raatz (1937) also calls attention to this, and references Thiergart in Gothan (1936), who has shown that pollen compliant with the taxon *Pollenites serratus* is produced by *Sciadopitys*. Raatz subsequently uses the new genus name *Sciadopitys-pollenites*. He does not provide a clearly lablled genus diagnosis/description, but does provide the above given genus or species description. According to Art. 38.5 *Code* this would suffice for valid publication of the genus, since the genus was monotypic at the time.

Potonié (1958) later provided a more elaborate description, clearly identifiable genus description. Our English translation thereof reads:

> "Equator more or less circular; germinal area not always recognizable, sometimes partly covered by secondary folds, not like a colpus (as stated by Thomson & Pflug 1953) but roughly circular to slightly oval; when it [germinal area] has opened, it

> appears as a more or less triangular gap. The exine is ornamented with small warts, which in the type of the genus protrude over the equator with mostly over 30 more or less irregular protrusions. The warts are rather homogenious in size and have a slightly uneven but rounded surface; their diameter is about half their height; their outline is irregularly circular to polygonal, also rugulate elongated or irregularly triangular. The verrucae cover the whole exine except for the area of germination."
>
> (translated after Potonié (1958), but also compare translation in Jansonius and Hills (1976) (card 2547):

Based on the lack of a genus diagnosis in 1937, Jansonius & Hills (1976) argue that the genus was not valildly published until this criterion was fulfilled in January 1958 by Potonié. Therefore they cite the genus as *Sciadopityspollenites* Raatz ex Potonié 1958. Potonié appears to think differently, as indicated by his later citations as *Sciadopityspollenites* (Raatz 1937) R. Pot 1958 (Potonié 1966). Even if one disagrees with this interpretation, the name would have been effectively and validly published the latest as of January 1958 by Potonié (1958).

4.1.3. Genus *Cerebropollenites* Nilsson 1958

Type: *Tsugaepollenites mesozoicus* Couper (1958) designated by Nilsson (1958)

Original genus description. – Inaperturate, azonate Pollenkörner von mehr oder weniger eckig ovalem oder kreisförmigen Umriss. Exine nicht besonders verdickt; besonders dünn und fast ganz eben in einer kreisförmigen Fläche an der distalen Seite. Oberfläche im übrigen grob und unregelmäßig gefaltet; Längskontur der einzelnen Falten mehr oder weniger tief gewellt (Nilsson 1958, p. 155).

English translation. – Inaperturate, azonate pollen grains with more or less angular, oval or circular outline. Exine not very thick; especially thin and almost without ornamentation in a circular area on the distal face. Surface of the other areas big and irregular folds; the folds more or less deeply sinuous seen from longitudinal view (altered after Jansonius and Hills 1976; card 443).

Discussion. – Potonié (1960) considers the new genus superfluous based on his implied interpretation that Couper's holotype is saccate and should be incorporated in the genus *Tsugaepollenites*. Similarly, yet more formally, Dettmann (1963) reinterprets the equatorially protruding ornamentation of Couper's holotype as having several 'intercommunicating vesiculate protrusions' leading her to synonymise the younger *Cerebropollenites* with the senior synonym *Tsugaepollenites*. Oblivious to this interpretation and recombination, Schulz (1967) retains the assignation to *Cerebropollenites* and indicates without formal emendation that the genus *Cerebropollenites* is, in fact, monosulcate and not inaperturate as described by Nilsson. A year later, Singh and Kumar (1968) emend to counter the merging of *Cerebropollenites* with *Tsugaepollenites* (Jansonius and Hills 1976; card 443) as follows:

> "Pollen grains oval to circular in flattened condition, numerous vesiculae of variable size present on both the faces, distal exine marked by a thinner polar region small, circular or of variable shape having smooth to granulose ornamentation, the remaining surface being rough and covered by vesiculae, individual vesiculae variable in size and shape, *extrema lineamenta* usually deeply corrugated." (Singh & Kumar 1968)

Pocock (1970) provides another genus diagnosis, which partially differs from the previous ones, but also adopts the interpretation of *Cerebropollenites* as saccate. Pocock's new diagnosis (1970) is not indicated as a formal emendation, however, and is subsequently not referenced in Jansonius and Hills (1976) or later authors citing the genus. Pocock (1970) is a very relevant publication that does not only conduct the first broader study on inter- intraspecific variation, but also describes two new species based on the size distribution patterns he observes, and stating that the conventional practice of assigning all Jurassic grains of the genus to *Cerebropollenites mesozoicus* would be an oversimplification. It is most likely due to his 1970 and Schulz' 1967 publication, that the name *Cerebropollenites macroverrucosus* is used more often from the 1970s onwards (Fig. 13 C).

A very important observation on Couper's holotype made by Mädler (1963), however, is not mentioned in the previously cited publications, not even in Schulz. Mädler (1963) distinguishes Couper's type from *Tsugaepollenites* based on the lack of a "equatorial velum" and the clearly visible sulcus in comparison to the obscure germinal area in *Tsugaepollenites.* He argues that due to these differences the holotype of Couper should be rather assigned to *Sciadopityspollenites*, but notes the conventional use of for Mesozoic taxa, it should be assigned to *Cerebropollenites* as the equivalent Mesozoic predecessor of *Sciadopityspollenites* (Mädler 1963).

All in all, the questions that underlie all these arguments is whether the type of the genus *Cerebropollenites* (1) is compliant with the description of *Tsuagepollenites* and if not, whether (2) *Cerebropollenites* or *Sciadopityspollenites* is the correct genus name to adopt.

When Couper (1958) described his new species *mesozoicus* from the Middle Jurassic, he compared it with extant *Tsuga* pollen which he also studied for his publication. Reissinger (1950) had already depicted pollen like Couper's holotype and speculated about an affinity with *Tsuga* or *Sciadopitys*. Reissinger notes that the pollen he documented (Pl. 17, Figs. 33 and 34) are size-wise in between the size ranges of extant representatives of the two genera. Based on a not-depicted specimen that he describes as slightly different than the two depicted pollen, i.e., with a bigger and rounder sulcus area, he interprets all three pollen to be most likely representatives of *Tsuga* (Reissinger 1950). From the present perspectives, it seems most likely that the two pollen that Reissinger depicted in plate 17 are more similar to the holotype of Couper, while the one grain he only describes might be in fact related to *Tsuga*.

Reissinger's very expressed view of a relation with *Tsuga* might have influenced later workers like Couper, who explicitly cites him to support his own interpretation of his newly described species after he also studied pollen grains of extant *Tsuga*. Couper's interpretation of the new taxon appears strongly influenced by the interpretation of these grains as *Tsuga*-related, which is reflected in his phrasing of the diagnosis stressing particularly the existence of a fringe, i.e., a monosaccus in this context. After considering Couper's and other representations (of light and SEM microscopy) (Couper (1958) Pl. 30, Figs. 6,7; Grímsson & Zetter (2011); Figs. 23, 24, 26, 27) of *Tsuga* and *Sciadopitys* pollen, we must stress the difference between Couper's new holotype and younger *Tsuga* pollen, as well as the type specimen for the genus *Tsuagepollenites* (see Figs. 10.11–10.16). Typical for *Tsuga* and *Tsugaepollenites* pollen is the existence of a monosaccus, which morphologically appears like a fringe at the equator of the pollen grain (see also Grímsson & Zetter 2011; Figs. 23, 24). After re-examination of Couper's holotype, we cannot document such a fringe. Depending on the focal plane, the hyaline protrusions overlaying each other, especially at the equator, can give the impression of a fringe, but change of focus does not perpetuate that impression (see Fig. 9, section 3.1.7).

It should be noted that some *Tsuga* pollen species with a very narrow monosaccus (*Tsuga* sp. 2 or '*T. canadensis* type'-type, see Grímsson & Zetter (2011), can appear similar to Couper's type with light microscopy. Yet, in contrast to Couper's holotype, the very round sulcus area posesses a very distinct ornamentation in *Tsuga* pollen and *Tsugaepollenites* pollen. Assignation to *Tsugapollenites* might have been an effect of priming, since Couper only studied extant material from *Tsuga* but not of *Sciadopitys*. However, pollen of the latter are much more similar to the holotype of Couper in shape, size, sulcus, and absence of a saccus (Grímsson & Zetter 2011; Uehara & Saiki 2011; Bykowska & Klimko 2016).

Ultrastructural studies on various *Cerebropollenites* grains from the Late Jurassic and Cretaceous further corroborate the absence of a saccus in *Cerebropollenites* as a distinctive feature compares to *Tsugaepollenites* (Batten & Dutta 1997; Shang & Zavada 2003). Both studies stress that the convoluted protrusions give the impression of a fringe or saccus, but that *Cerebropollenites* is missing the tectum and alveolate structure typical of saccate pollen and instead, possess (still) at least, a partially fused sexine and nexine. In addition, the degree of the fusion of sexine in nexine is varying from species to species and might be an ancestral stage in the development of a monosaccus, like in extant *Tsuga*. So far the ultrastructural studies on late Mesozoic *Cerebropollenites* pollen show that these pollen types do not have a vesiculate saccus but consist of more massive and solid structures, i.e. not saccate (Batten & Dutta 1997; Shang & Zavada 2003). While our observations of early Mesozoic taxa of this pollen group discussed in the present paper suggest the lack of a vesiculate saccus, additional ultrastructual studies still need to verify the nature of their pollen wall structure.

Since all genus diagnoses are inspired by and contain aspects from comparisons with extant pollen, it is worth noting, that SEM and ultrastructural studies on fossil extant asaccate *Sciadopitys* pollen suggest much greater similarity of *Cerebropollenites* with *Sciadopitys* than with *Tsuga* (Surova & Kvavadze 1988; Grímsson & Zetter 2011; Uehara & Saiki 2011). Waksmundzka (1981) pointed out in her SEM study of fossil *Sciadopityspollenites mesozoicus* (Couper 1958) Waksmundzka 1981, that the verrucae are ornamented with small clavate elements (compare Pl. 24, Fig. 5 in Waksmundzka, 1981). The same feature was documented by Shang and Zavada (2003), and is particularly pronounced in the species *Cerebropollenites papilloporus*, which posesses distinct "pappilae" on the verrucae (compare Figs 12-14 in Shang and Zavada, 2003). The very same chracteristic is visible in fossil *Sciadopitys* pollen from the Miocene (compare Fig. 28 in Grímsson & Zetter 2011), and in pollen grains of extant *Sciadopitys verticillata* (Pl. 3, Fig. 14 in Ho and Sziklai 1973; Fig. 4 in Bykowska and Klimko, 2016). The latter studies refer to this microornamentation as microechinate, which is rather a semantic difference, as all studies demonstratively show the same typical morphological feature.

So the answer to the first question, i.e. whether the type for *Cererbopollenites* is compliant with the genus diagnosis of *Tsugaepollenites* is 'NO'. We dismiss this assignation based on lack of different type of ornamentation on the proximal and distal face, as would be typical for *Tsuagepollenites* and on the absence of a saccus supported by ultrastructural studies of fossil *Cererbopollenites* species (Batten & Dutta 1997; Shang & Zavada 2003) and extant *Sciadopitys* pollen (Uehara & Saiki 2011). It should also be noted, that the lack of differentiation of proximal and distal face typical for *Tsuagepollenites* was already pointed out by Nilsson (1958), and was the main reason for the erection of the new genus *Cerebropollenites*. Despite the intial increase of the name *Tsugaepollenites mesozoicus* that was stil observed in the 1970s, the recombination with *Cererbopollenites* took over, and suggests that the majority of the scientific community is acknowledging the above laid out differences.

The subsequent question is whether *Cerebropollenites* or *Sciadopityspollenites* is the correct genus assignation for the various species assigned to either or both of the two genera. In other words, are they conspecific and if yes, which one has priority? In his genus diagnosis for *Cerebropollenites*, Nilsson (1958) does not describe any morphology that would not be already circumscribed by the earlier diagnosis of *Sciadopityspollenites*. Mesozoic (*Cerebropollenites*) as opposed to Cenozoic (*Sciadopityspollenites*) occurrences is an artificial, rather than a morphological difference, as pointed out by Mädler (1963), and was introduced by conventional use as such over the decades. The negative consequence of this practice is that it masks the continuity and evolution of the pollen and its mother plant. Since extinction and origination rates are often calculated at the genus level, artificial separation based on different stratigraphic ranges potentially increases interpretations of extinction and origination. To prevent this, synonymisation is not only advisable but a necessity. Since *Sciadopityspollenites* was described first (either 1937 or the latest by January 1958), *Cerebropollenites* (published April 1958) has to be considered the junior synonym. Although this practice is numerically underrepresented in name use, it should be adopted to adhere to the principle of priority, like many Russian workers have for many years.

4.2. For the specific epithets *thiergartii*, *macroverrucosus* vs. *mesozoicus*, and pseudomassulae

4.2.1. The epithet *thiergartii*

Already before and shortly after Schulz (1967) described the new taxon *Cerebropollenites thiergartii*, authors documented pollen that occurred together with *Pollenites macroverrucosus* but with a much finer ornamentation. Thiergart himself already erected *Pollenites macroserratus doggerensis* for such forms and unfortunately, the relatively poor images and similar forma (*Pollenites serratus* f. *helmstedtensis* and *Pollenites serratus macroserratus* f. *keuperianus*) might have reduced the impact of these new taxa, even more so, as they were only distinguished on a subspecies level and with very similar names. Following or re-evaluation of the type material we believe the latter two forms to be conspecific with *Ricciisporites lundbladii* and *Polypodiisporites* sp. The similarity with *Pollenites macroverrucosus* has however caused other authors to use these names to refer to forms conspecific with *thiergartii*. Rogalska (1954) reports specimens differing from *Pollenites macroverrucosus*, by much smaller verrucae and describes that they in turn differ in the size of their verrucae (compare Pl. 6, Figs. 13–14 in Rogalska (1954)). She assigns them to cf. *Pollenites serratus* f. *helmstedtensis*. Bóna (1969) shortly after Schulz also depicts such a specimen (Pl. 8, Fig. 7 in Bóna (1969)), but assigns it to the newly recombined *Tsugaepollenites macroserratus* f. *doggerensis* (Thiergart 1949) Bóna 1969. These uses show the ambiguity and inconsistent application of the names for the different *forma* of *Pollenites serratus* or *macroserratus* erected by Thiergart, and might explain why they were hardly used, especially not after Schulz' revision. The use of *Cerebropollenites thiergartii* quickly rose after its description (Fig. 13). The lesser overall number of citations in comparison to *Cererbopollenites mesozocius/macroverrucosus* reflects the abundance patterns of these taxa. The rise of citations for *Cererbopollenites thiergartii* after the turn of the century is then driven by the evaluation of its stratigraphic value in the disccussion of the new GSSP section for the base of the Jurassic and its role as the palynofloral marker for it (Morton 2012; von Hillebrandt et al. 2013) (see increase if not geographically assigned citations in Fig 13).

Striking is the entire absence of citations for *Cerebropollenites thiergartii* from Russia, even more so as there is no recombination with *Sciadopityspollenites* as for the other *Cerebropollenites* taxa (e.g. *Sciadopityspollenites mesozoicus*). This might be explained by the usage of the taxon *Sciadopityspollenites multiverrucosus*, the second most used taxon of the genus in the Mesozoic after *Sciadopityspollenites macroverrucosus*. Since *Sciadopityspollenites multiverrucosus* is reversely not recombined with *Cerebropollenites* and has the same stratigraphic range (Fig. 11), it appears to be the vicarious name for *Cerebropollenites thiergartii* in many Russian studies. It was erected as *Sciadopitys multiverrucosus* (Ilyina 1968) and later on recombined with *Sciadopityspollenites* (Ilyina 1985). With her recombination, Ilyina shows a brightfield image together with an SEM image of a pollen that looks very similar to the holotype of *Cerebropollenites thiergartii,* only with slightly bigger verrucae (Fig. 6). Although Ilyina (1985) speculates on a potential synonymy with *Cerebropollenites carlylensis*, probably because of the relatively small size, we believe, based on our observations on intra- and interspecific variation, that the two taxa are conspecific even though the holotype itself was not available for study. Since they are believed to be conspecific, the geographic isolation of the two taxa is not the result of biological speciation but rather a result of literary isolation, likely fostered by different languages and alphabets. This would also imply that the one-year younger name *Sciadopityspollenites multiverrucosus* is the junior synonym of *Cerebropollenites thiergartii*.

The majority of publications documents *Cerebropollenites thiergartii* from the Jurassic onwards. Due to its occurrence within the turn to more negative δ^{13}C values in the lower part of the main carbon-isotope excursion, well above the extinction level of Triassic biota, but significantly below the lowest occurrence of the first Jurassic ammonite (Kürschner et al. 2007; Bonis et al. 2009; von Hillebrandt et al. 2013). Bonis et al. (2010) reported *Cerebropollenites thiergartii* and *Ischyosporites variegatus* about 4 m above the base of the Blue Lias Formation in St. Audrie's Bay Fisher and Dunay (1981)). Moreover, *Cerebropollenites thiergartii* has been reported from lowermost Liassic sediments in the Germanic Triassic basin in the Mariental core 1 (van de Schootbrugge et al. 2009; Heunisch et al. 2010) and the Bonenburg outcrop (Schobben et al. 2019; Gravendyck et al. 2020c), in the Kamien Pomorski core in Poland (Pieńkowski et al. 2012), as well as in Greenland (Pedersen & Lund 1980; Mander et al. 2010), the Sverdrup Basin (Suneby & Hills 1988), from Kong Karls Land near Svalbard (Smelror et al. 2019), and in the Eastern Tethys realm and the Alborz Mountains in Iran (Achilles et al. 1984).

Based on detailed palynological studies in the Northern Calcareous Alps, previous studies (Kürschner et al. 2007; Bonis et al. 2009) proposed *Cerebropollenites thiergartii* SCHULZ 1967 found 2 m below the entry level of *Ps. spelae* as a palynological marker close to the base of the Jurassic (see also discussion in Hohman and Stadtman (1978); Cirilli (2010)). It is a particular relevant taxon because of the paucity of other palynofloral markers. Yet, the documentation of this taxon as early as the Rhaetian (Lund 1977) challenges the application as a marker fossil Lindström et al. (2017b). Lund (1977) reported a singular occurrence of *Cerebropollenites thiergartii* in his stratigraphic table already from the Middle and Upper Rhaetian in cores (Rødby 1 and Maasbüll 1) from the Danish basin. However, Lund's findings are questionable as the illustrations of his pollen do not show the typical morphological features of *Cerebropollenites thiergartii*. Lund's report of a potentially much earlier appearance of *Cerebropollenites thiergartii* has thus created doubt to the stratigraphic significance of this taxon, despite its continued use as such. Intriguingly, only 3 years after the publication of his monography, Lund defined together with K.R. Pedersen the base of the Hettangian in the Triassic–Jurassic boundary deposits on Greenland by the first occurrence of *Cerebropollenites thiergartii* (Pedersen & Lund 1980).

The less clearly defined species boundaries and the often poor quality of images, or representation of a single focal plane, can make it difficult to distinguish *Cerebropollenites thiergartii* from forms assigned to the epithet *macroverrucosus*, with relatively smaller and more densely packed sculptural elements. Although *macroverrucosus* possess muri rather than verrucae, this is not always easily discernible from a photograph only, and has surely complicated identification of *Cerebropollenites thiergartii*, especially of those specimens with relatively large verrucae (compare Fig. 5). This might explain Lund's documentation of *Cerebropollenites thiergartii* as low as the Rhaetian (Lund 1977). The specimen he depicts in plate 7 figure 15 as *Cerebropollenites thiergartii* is probably better assigned to the epithet *macroverrucosus*. We attempted to consult the original slide to confirm this interpretation based on the photograph, but the slides in question were not available and are considered as being "lost". Other original material from Lund (1977) studied from the same interval depicted several specimens that comply with the holotype of *Pollenites macroverrucosus,* but none that complied with *Cerebropollenites thiergartii*. Indeed, forms assigned to the epithets *macroverrucosus* were also reported in the Rhaetian in Bonenburg (Gravendyck et al. 2020c). Additionally, the misapplication of *Cerebropollenites mesozoicus* for *Tsugaepollenites pseudomass*ulae of Orbell (1973), i.e. a taxon that occurs most commonly and is probably limited to the Rhaetian, has further complicated the stratigraphic range of all involved taxa. Further studies using the herein presented classification will be needed to confirm the exact ranges of the respective taxa, and although we cannot entirely resolve the documentation of *Cerebropollenites thiergartii* in the Rhaetian, it seems most likely to be the result of a taxonomic confusion, neglectable in correlation schemes, unless other studies can confirm such early occurrence.

4.2.2. The epithets *mesozoicus* and *macroverrucosus*

Nilsson (1958) points out that Thiergart's *Pollenites macroverrucosus* might be related, but refrains from a final judgment as the description and photograph would be insufficient. Nevertheless, he argues that a pollen shown by Rogalska (1956) (Pl. 19, Fig. 4) classified as *Pollenites macroverrucosus* would be identical with his specimens. After examination of Rogalska's photograph, we think that the density of sculptural elements is higher and the elements generally smaller with the outline much less undulated than in Nilsson's photographs, and therefore, not identical. The same opinion is expressed by Mädler (1963), who opposes synonymisation of *mesozoicus* and *macroverrucosus* based on the differences in ornamentation, and considering the latter to possess more 'wart-like' structures.

Schulz (1967), however, expressed the opinion that Thiergart's type, which he had re-examined and the type of Couper, which he did not re-examine, would be conspecific and therefore, synonymized them in favour of *macroverrucosus*, i.e. the older name having priority. The strong increase in use of the name *macroverrucosus* from the 1960s to the 1970s might have been fostered through Schulz' recombination (Fig. 12 C), which brought it back into the spotlight and was followed by the majority of authors (e.g. Bóna 1969; Lund 1977; Pedersen & Lund 1980; Ilyina 1985; Dybkjær 1991; Batten & Dutta 1997). Few express their doubt, whether synonymisation of *mesozoicus* and *macroverrucosis* is justified (e.g. Mädler 1963; Tralau 1968; Morbey 1975). The fact that the use of the epithet *mesozoicus* still increases until the 1980s might be owed to Pocock's judgment of such a synonymized treatment as an 'oversimplification'

(Pocock 1970), leading to separate and continued use of *mesozoicus* by some auhtors thereafter (Tralau 1968; Fisher & Dunay 1981; Waksmundzka 1981; Guy-Ohlson & Malmquist 1985; Guy-Ohlson 1986; Song et al. 2000; Shang & Zavada 2003) (Fig. 12 B).

One very problematic use of the name *Cererbropollenites mesozoicus* is found in Orbell (1973). Under this name he figures two specimens with very hyaline protrusions which are clearly conspecific with the holotype for *Camerosporites pseudomassulae* (Figs. 10.8 and 10.9). Dybkjær (1991) explicitly clarifies this as an erroneous assignation prior to her establishment of the *Cererbopollenites macroverrusous* zone. Indeed, Morbey (1975) already implies the same by listing Orbell's use in his synonym list for *Tsugaepollenites pseudomassulae*. However, as this is rather a misapplication than a true synonym, this might have even enhanced the taxonomic and nomenclatural confusion around the epithets *macroverrucosus* and *mesozoicus*, and even *pseudomassulae*.

In the most extensive revision of *Cerebropollenites* to date, Pocock (1970) analysed the size distribution of different *Cererbopollenites* species and observed four distinct peaks leading him to keep *mesozoicus* and *macroverrucosus* apart, and describing two addional species, i.e., *carlylensis* and *findlaterensis.* He considers *findlaterensis* to be the largest and most convoluted species, while *macroverrucosus* is the second largest, more ovoid in shape than the others and with a very longitudinal sulcus. He also considers *mesozoicus* to be the second smallest although noting a considerable size overlap between *mesozoicus* and *macroverucosus*, and more spherical and *carlylensis*, to be the smallest species.

We agree that the general lumping of *mesozoic* and *macroverrucosus* is possibly oversimplistic considering the variation we observed and described above. Nevertheless, size as the main sorting crieterion as practiced by Pocock is difficult as well, especially as preservation, perspective on the pollen grain and maturity might influence it. Sorting the observed variation on a gradient of sculptural elements of increasing size and according to the density of their arrangement permits to distinguish the two holotypes for *Pollenites macroverrucosus* and *Tsugapollenites mesozoicus*. We can also confirm that observed variation of the sculptural elements is independent of the pollen grain size, and to some extent, independent of their preservation.

Although not using size as the sorting criterion, it should be noted that we also observed a series of grains with slightly elongate more hook-shaped verrucae, which are generally rounder with a rounder sulcus, and might represent specimen best addressed as *carlylensis* (Figs. 9.3 and 9.6). They are generally smaller and whether this is an immature form (with not as elaborately developpoed muri as in *macroverrcuosus* or *mesozicus*), or whether it is a taxon that is more consistent in size and shape, remains unclear. Either way, addressing these smaller, rounder forms with a separate name will help to lump or separate them later, depending on the paleobiological interpretation of the author and the study question.

4.2.3. The epithet *pseudomassulae*

More than 10 years after description of the basionym, Morbey (1975) recombined it, tentatively, with *Tsugaepollenites* and in his synonymy he lists *Cerebropollenites mesozoicus* (Couper 1958) Nilsson 1958 in (Orbell 1973). Later in the text Morbey's distinguishes forms assignable to this epithet from *Tsugaepollenites mesozoicus/macroverrucosus*. Nevertheless, his listing of Orbell's misidentification (which is strictly speaking not a synonym) in the synonymy might have inspired confusion amongst other workers who considered the *mesozoicus*/*pseudomassulae* to be synonymous (e.g. Achilles 1981; Brenner 1986; Holstein 2004).

When Mädler (1964) described the new species as *Camerosporites pseudomassulae*, he assigned it to the genus mainly because of an alleged trilete mark, which would distinguish the genus also from Maljavkina's *Rubinella*. In our re-investigation we found no trilete mark, and only what appears like an artefact due to the folding in the preparation of Mädler's holotype. Our re-interpretation is supported by the absence of such character in all other investigated species, including those that were investigated from both sides on a double-coverslip mount. An assignation to *Rubinella*, a fern spore with much smaller verrucate structure, can also be excluded.

The ample discussion about the taxon mixed into the discussion around the epithet *mesozoicus* (see section 4.2.2), also shows that the assignation to *Tsugaepollenites* is problematic. Despite the apparent consensus amongst workers to assign it to *Tsugaepollenites* (Fig. 12.D), however, this might be the result of being the lesser evil due to lack of other options. The alleged 'fringe' of *pseudomassulae* is usually the characteristic on which the assignation to *Tsuagepollenites* is based on. Although the protrusions give the impression of a fringe, they lack the internal alveolate structure and an interpretation as a saccus has to be rejected on the same terms as for the holotype for *Tsugaepollenites mesozoicus* (see section 4.1). Further, the lack of heteropolarity and differences on ornamentation on either side of the palynomorph prevents justifiable assignation to the genus *Tsugaepollenites*. Lacking an aperture, e.g. a sulcus like in *Cerebropollenites* and *Sciadopityspollenites* also prevents assignation to either of these genera or any other taxon known to us. Further ultrastructural studies will be needed to better understand the structure, morphology, and potential botanical affinity, of the holotype for *Camerosporites pseudomassulae* and conspecific specimens.

It is noteworthy that the hyaline character of this taxon is somewhat reminiscent of the outer layer of *Perinopollenites*, but whether it is a pollen at all is not self-evident at all. Heunisch et al. (2010) pointed out that due to their similar hyaline colour and surface, together with the convolutions, taxa identified with the epithet *pseudomassulae* can resemble *Cymatiosphaera* (compare Pl. 9 Fig. 11 in Heunisch et al. (2010)). Since the compressed septa of *Cymatiosphaera* result in a more angular appearance of the convolutions, it can be still differentiated however. Heunisch et al. (2010) also argue that the newly described *Tsugaepollenites schlimmii* (Achilles 1981) is in fact a specimen of *Cymatiosphaera*. We concur with this view and note that this is a good example how the hyaline impression of specimens assigned to *pseudomassulae* appear relatively similar to the exine of various aquatic palynomorphs which are also often isopolar. Without any visible aperture, an unambiguous assignation to extant gymnosperm pollen taxa thus cannot be made, nor can a potential relationship with an algae group be excluded.

It is remarkable that the taxon is mostly documented from Central Europe (Fig. 12.D). Since some reports, however few, are from beyond Europe (e.g. Olsen and Sues 1986; Lachkar et al. 2000), this is not necessarily attesting for a limited geographical occurrence. Yet, not all references can be checked for their adequacy and since there has been some confusion concerning the distinction with *mesozoicus*, it will be interesting to see whether future work can confirm upon clarified distinction of the taxon, its occurrence beyond Europe. Given that it is most common and probably limited to the Rhaetian, disappearing latest in the Early Jurassic (Herngreen et al. 2003; Cirilli 2010; Heunisch et al. 2010; Gravendyck et al. 2020c), an unambiguous naming is desirable for stratigraphic and paleoecological purposes. Since the species cannot be clearly assigned to any existing genera that stand to reason, we propose erecting the new genus *Pseudomassulites* below.

5. Revision: Systematic Palynotaxonomy

The above given literature review showed that problems distinguishing the different taxa associated with *Cerebropollenites thiergartii* did not only arise by the lack of distinguishing characteristics. Poor photographic documentation, including only isolated focal planes being reproduced, together with a few, but nevertheless impactful misapplications, likely fostered confusion. The recombination with different genera and isolated use of recombinations and revisions of *Sciadopityspollenites* for Mesozoic taxa in Russia also make it difficult to have a good overview. Following our re-evaluation of holotype material and intra- and interspecific variation we now clarify typical features and distinguishing characteristics for the variation of forms in and around *Cerebropollenites thiergartii* in a series of nomenclatural novelties that will be described in the following (see overview in Fig. 14).

5.1. Names to be limited to the holotypes

After our re-evaluation of Thiergart's holotype material, we consider the taxa described as ***Pollenites serratus*** f. ***helmstedtensis***, ***Pollenites macroserratus*** f. ***keuperianus*****,** and ***Pollenites macroserratus*** f. ***doggerensis*** to be conspecific with *Ricciisporites lundbladii*, *Polypodiisporites cf. polymicroforatus*, and *Cerebropollenites thiergartii,* respectively. All of them are typical for the time interval from which they are described (e.g., Lindström 2016; Lindström et al. 2017), but Thiergart's material has not been considered in the erection of these later names.

The original holotypes for these names, however, cannot always be relocated beyond doubt. To not make taxonomy and nomenclature even more difficult with names of ambiguous circumscription that might potentially have priority over the younger, but much more common and less ambiguous names, we encourage not to use these three names by Thiergart anymore, i.e. to limit the names to the respective holotypes (Fig. 14). Note that this practice is commonly applied in the Lentin and Williams Index of Fossil Dinoflagellates (Fensome et al. 2019), and is adopted here, accordingly.

5.2. Categorising the intra- and interspecific variation

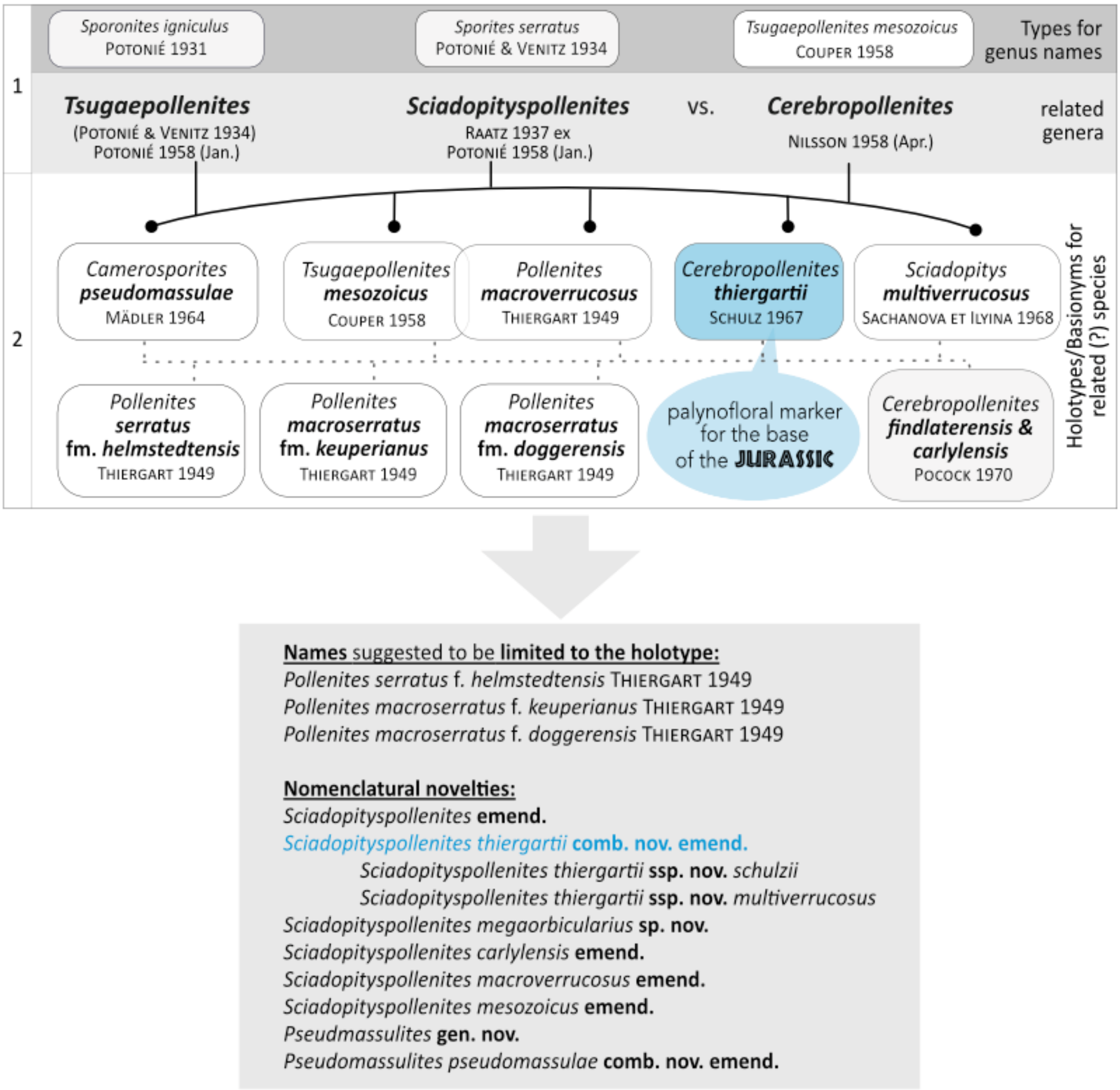
Traditional characteristics that are used to distinguish the diversity in *Cerebropollenites thiergartii* and associated taxa, i.e., grain or sulcus shape and size, are very variable (see for example the variation in the holotype slide for *Cerebropollenites thiergartii* from Schulz, Figs. 5.11–14, 5.18). They are therefore, contrary to the practice of Pocock (1970), not considered to be the most useful criteria to categorised diversity. Even more so, as the sulcus is not always clearly discernible.

Here, we thus propose to categorise the variation we observed in *Cerebropollenites thiergartii* and associated taxa in 6 main categories (Figs. 15 A–F). In addition, we proposed that all forms that have been previously assigned to the epithet *pseudomassulae* (Fig. 15 G), and which in contrast to the other forms typically do not depict an aperture, nor a differentiation in ornamentation on either side of the specimens, be therefore assigned to a new genus ***Pseudomassulites*** **gen. nov.** described below.

We found the ornamentation to be the most distinctive feature to separate the different categories of forms we observed. The relatively poor images (especially in older literature), and poor preservation of many specimens partially hampers clear characterisation of the ornamentation. This might have tempted earlier workers to rely on less subjective criteria such as size. This has been especially complicated as printed photographs often only depict one focal plane. The precise nature of the ornamentation of *Cerebropollenites/Sciadopityspollenites* species makes it necessary to study various focal planes to determine how big, how sinuate the sculptural elements are and how much space they possess in between. This has likely complicated comparison of photographs and specimens in the past, which is probably one source of the rather inconsistent use of names (compare the (mis-)application list of names in supplementary Table 2 and classification presented here).

Throughout the years, several authors have provided SEM images of *Cerebropollenites* species (Guy-Ohlson 1978; Waksmundzka 1981; Guy-Ohlson & Malmquist 1985; Ilyina 1986; Batten & Dutta 1997; Shang & Zavada 2003), but the specimens were classified rather inconsistently. Nevertheless, some of the documented specimens very well illustratate the categorisation presented here (Fig. 15). The SEM images provide the best view on the shape, size, arrangement, and density of the sculptural elements. With these images in mind, it is also easier to discern the crucial chracteristics in brightfield view. Following our observations on the holotype specimens and the observed inter- and intraspecific variation, we categorise the observed variation in categories A–F, which are sorted according to the increasing size of their sculptural elements, ornamentation type (from verrucate to rugulate), and the density of their arrangement. It should be considered, however, that there are many transitionary and intermediate forms, and unfavourable preservational states, that can make assignation to one or the other categories more difficult. Nevertheless, the categories presented here are considered the endmembers of morphological variation to aid more consistent use of the names.

Categories A and B (Fig. 15) encompass what we assign to the epithet *thiergartii*, which will be, according to the discussion above, be recombined as *Sciadopityspollenites thiergartii* comb. nov. Schulz in his original description noted that that verrucae can be up to 3 µm in size. Reviewing the variation of forms assignable to *thiergartii* (compare transition from smaller to bigger verrucae in Figs. 6.1–6.4), we found that they either have smaller sculptural elements (more on the 1 µm size range, Figs. 5.11–5.23), or much bigger elements (more towards the 3 µm size range, Figs. 6.5–6.15). Lund (1977) and Heunisch et al. (2010) already noted, that *Chasmatosporites apertus* can be hard to distinguish from *Sciadopityspollenites thiergartii* comb. nov., which is especially true for the forms with smaller ornamentation. Ilyina (1985) described the new *Sciadopityspollenites multiverrucosus* and although we believe them to be conspecific, her photograph depicts a specimen with relatively big verrucae. Many taxa have been distinguished for less, and if there is stratigraphic or paleoecological desire to distinguish these forms, we propose to treat them as different *subspecies*, those with smaller verrucae (Fig. 15.1) more similar to Schulz' specimen as ***Sciadopityspollenites thiergartii* comb. nov. ssp. nov. *schulzii*,** and those with bigger verrucae (Fig. 14 B), using Ilyina's junior synonym, as ***Sciadopityspollenites thiergartii* comb. nov. ssp. nov. *multiverrucosus*.**



<u>Names</u> suggested to be <u>limited to the holotype:</u>
Pollenites serratus f. *helmstedtensis* Thiergart 1949
Pollenites macroserratus f. *keuperianus* Thiergart 1949
Pollenites macroserratus f. *doggerensis* Thiergart 1949

Nomenclatural novelties:
Sciadopityspollenites **emend.**
Sciadopityspollenites thiergartii **comb. nov. emend.**
    Sciadopityspollenites thiergartii **ssp. nov.** *schulzii*
    Sciadopityspollenites thiergartii **ssp. nov.** *multiverrucosus*
Sciadopityspollenites megaorbicularius **sp. nov.**
Sciadopityspollenites carlylensis **emend.**
Sciadopityspollenites macroverrucosus **emend.**
Sciadopityspollenites mesozoicus **emend.**
Pseudmassulites **gen. nov.**
Pseudomassulites pseudomassulae **comb. nov. emend.**

Fig. 14. Problem overview of related taxa relevant for the distinction of *Sciadopityspollenites thiergartii* comb. nov. et *emend*. and other proposed nomenclatural novelties.

Category C contains specimens with exceptionally large verrucae. Focusing through the different focal planes, as well as the SEM image (Fig. 15.12) confirms, that these elements are not rugulate (and rather hollow looking) muri like in the holotype for *Tsugaepollenites mesozoicus*, but solid and very rounded verrucae. Forms of this kind were relatively rare but were found in Couper's material (Fig. 7.21) and in the Höllviken material (Fig. 7.22) alike. It is not trivial to distinguish these from forms probably better assigned to *Sciadopityspollenites mesozoicus* (Fig. 7.20) or forms more similar to *Sciadopityspollenites thiergartii* comb. nov. ssp. nov. *multiverrucosus* (Fig. 7.17), especially when encountering rather smaller and compact specimen (Fig. 7.24). Nevertheless, these forms stand out and are here assigned to the new species ***Sciadopityspollenites megaorbicularius*** **sp. nov.**

Category D are specimens that a considerably smaller, rounder with an ornamentation that represents a transition between verrucate and rugulate forms (Fig. 15 C). The verrucae are more elongate and more looped, through which they also appear to have rounded verrucate elements in bright field view, yet the SEM image, and more detailed focussing through different focal planes gives a more adequate impression of the looped or hook–shaped elements for specimen depicted in Fig. 7.18 and Figs. 15.15–15.16). These forms can be best addressed as ***Sciadopityspollenites carlylensis*** although we find Pocock's descriptions, which is mainly based on size-differences, insufficient and will be emended below. Forms referred to as *Sciadopityspollenites osmundaeformis* are probably conspecific (Song et al. 2000).

Categories E and F contain specimens with rugulate ornamentation and are assigned to *Sciadopityspollenites macroverrucosus* and *Sciadopityspollenites mesozoicus* respectively based on their different size and density of muri. The forms assigned to ***Sciadopityspollenites macroverrucosus*** possess smaller muri, which are more densely packed (Figs. 15.20–15.23), which creates a less corrugated outline (Fig. 15.24). Forms assigned to ***Sciadopityspollenites mesozoicus*** possess the biggest muri of all forms studied here, and variation in Couper's slide and SEM images show, that the spaces in between these sculptural elements are relatively large (Figs. 15.26–15.27). Although we acknowledge that there are a number of intermediate forms (especially when preserved poorly), but it is noteworthy that the samples from Couper were dominated by *Sciadopityspollenites mesozoicus,* while samples from Höllviken were dominated by *Sciadopityspollenites macroverrucosus* with a considerable number of *Sciadopityspollenites thiergartii.* This might suggest stratigraphic and/or paleoecological differences. Potential differences are particularly relevant, because Dybkjær (1991) described the *Cerebropollenites macroverrucosus* Zone (now better *Sciadopityspollenites macroverrucosus* Zone) for the Sinemurian to the Pliensbachian (Lower Jurassic), and because the *Cerebropollenites* palynofloral province (i.e. now the *Sciadopityspollenites* province) is described for the boreal region of the Early Cretaceous (Herngreen et al. 1996). It will be interesting to see by which taxa exactly this zone and province are constituted of. Seen the previous inconsistent use, this cannot be evaluated with existing data yet. It will depend on future studies to disentangle potential differences between these two species, or lack thereof, to better evaluate their respective temporal and geographic distribution and stratigraphic value.

5.3. Classification key

The distinctive characteristics given above can be summarised in the following classification key. Note that this key is not a conclusive classification key for palynology at large but intends to help distinguish the various taxa discussed in this paper.

1a. Isopolar palynomorph with very large (> 6µm high and wide), hyaline protrusions covering the entire grain on either side and without visible germinal area. _______***Pseudomassulites*** gen. nov.

1b. Heteropolar palynomorphs with small verrucae to rugulate muri (max. 6 µm high) that can have equatorial protrusions that appear as a fringe. ____________________________________2

2a. Monosaccate Pollen. Saccus appears as a wide to very narrow fringe of hollow, vesiculate equatorial protrusions that can or may not be radially folded. Pollen heteropolar, with larger sculptural elements (verrucae to regulate muri) on one side and smaller sculptural elements on the other side, which is usually more depressed in a dehydrated state and takes up more than half of one side of the pollen grain. ____***Tsugaepollenites*** (consults relevant literature)

2b. Asaccate pollen. The sculptural elements can however give the impression of an equatorial fringe, especially when sculptural elements are large (<2–3 µm). Ornamentation can vary from verrucae to more or less regulate muri but do not vary on either side of the grain, yet are not visible in the sulcus area. Sulcus round to oval taken up less than half of the area on one side of the grain, often only partially shining through as a more hyaline area when changing the focal plane. ____*Sciadopityspollenites* – 3

3a. Pollen ornamented with verrucae. ____4

3b. Pollen ornamented with muri (focus on the corpus) that can appear as large (<2–3 µm) verrucae at the equator. ____8

4a. Ornamentation verrucae that are very small and not elongate. Verrucae less than 2 µm in in size. ___________________________***Sciadopityspollenites thiergartii*** comb. nov. ssp. nov. ***schulzii***

4b. Ornamentation with verrucae bigger than 2 µm in in size, that can but may not be elongate._5

5a. Verrucae evenly rounded. ____6

5b. Verrucae not evenly rounded, with slightly uneven surface and shape that can be partially elongate.

____7

6a. Spherical verrucae up to 4 µm in diameter. _______________ ______________________***Sciadopityspollenites thiergartii*** comb. nov. ssp. nov. ***multiverrucosus***

6b. Spherical verrucae bigger than 4 µm in diameter. ______________________________________***Sciadopityspollenites megaorbicularius*** sp. nov.

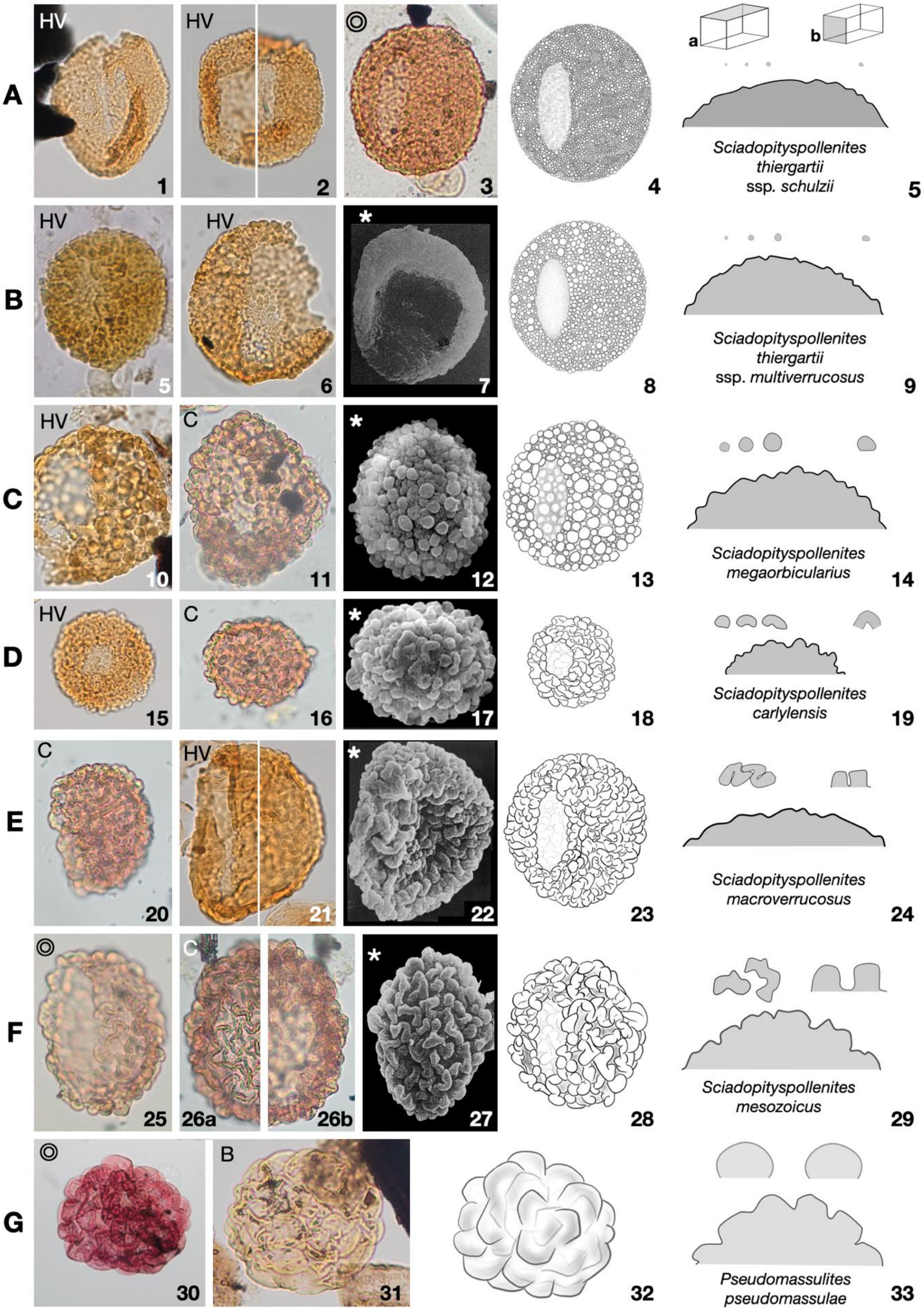
7a. Verrucae more or less rounded, sometimes a bit elongate appearing barbell shaped. Surface of these verrucae rounded to angular; never looped. Pollen subcircular to spindle-shaped. ____***Sciadopityspollenites serratus***

7b. Verrucae a bit elongate but not stretched out lengthwise, but rather looped and thereby appearing rounded. Pollen circular to sub-circular. _____***Sciadopityspollenites carlylensis*** *emend.*

8a. Pollen outline weakly corrugated (Fig. 14.24). Dense arrangement of the sculptural elements (most similar to the densely packed gyri of a brain); little empty space in between the sculptural elements max. ¼ of the width of the rugulate muri. ***Sciadopityspollenites macroverrucosus*** emend.

8b. Pollen outline strongly corrugated (Fig. 14.29). Looser arrangement of the sculptural elements (more similar to the windings of a walnut embryo); larger spaces in between the sculptural elements ca. $^1/_2$–$^1/_3$ of the width of the rugulate muri.__***Sciadopityspollenites mesozoicus*** *emend.*

Fig. 15. Overview of the newly defined categories (A–G) for observed intra-and interspecific variation. Each row (**A–G**) depicts images and idealised drawings and newly applied names for that category. The last column shows the outline of specimens from the respective category, and shows sculptural elements as seen from above (a) or as seen in a section view (b) as an analogue to similar overview for Cenozoic taxa found in (Krutzsch 1971). Locality of the material is indicated in the top left corner (**C** = original material from Couper (1958); **HV** = Höllviken (van de Schootbrugge et al. 2009); **B** = Bonenburg (Schobben et al. 2019; Gravendyck et al. 2020c). Holotypes are indicated with a double circle (◎). SEM images reprinted from previous literature indicated with an asterisk (*). SEM images reprinted with permission: 7–Ilyina (1985); 12 and 17– Shang & Zavada (2003); 22–Guy-Ohlson & Malmquist (1985); 27–altered after Guy-Ohlson (1989).


A
HV
1
HV
2
◎
3
4
a
b
Sciadopityspollenites thiergartii ssp. schulzii
5
B
HV
5
HV
6
*
7
8
Sciadopityspollenites thiergartii ssp. multiverrucosus
9
C
HV
10
C
11
*
12
13
Sciadopityspollenites megaorbicularius
14
D
HV
15
C
16
*
17
18
Sciadopityspollenites carlylensis
19
E
C
20
HV
21
*
22
23
Sciadopityspollenites macroverrucosus
24
F
◎
25
C
26a
26b
*
27
28
Sciadopityspollenites mesozoicus
29
G
◎
30
B
31
32
Pseudomassulites pseudomassulae
33

5.4. Revised descriptions

5.4.1. ***Sciadopityspollenites*** (Raatz 1937) Potonié 1958 ***emend***.

Type. – *Sporites serratus* Potonié & Venitz 1934, Arbeiten aus dem Institut für Paläobotanik und Petrographie der Brennsteine, vol. 5, pp. 1-54, p. 15, Pl. 1, Fig. 6, specimen in sample VII 17 (lost)

Synonyms. – = *Cerebropollenites* Nilsson 1958 in Publications from the Institutes of Mineralogy, Paleontology and Quaternary Geology, University of Lund, 53: 72.

Emended description. – Asaccate pollen with a (sub)circular, oval to spindle-shaped outline. Circular to oval sulcus not always recognizable, when (partly) covered by secondary folds or due to the position of the grain. The exine is ornamented with small verrucae or muri, which protrude over the equator which can give it the impression of a fringe. The sculptural elements are varying in shape, size and densisty depending on the species. The sculptural elements are relatively homogenious around the pollen grain and cover the whole exine except for the area of germination.

Comparison. – The genus *Tsugaepollenites* is distinguished by a monosaccus, which appears as an equatorial velum. Although the ornamentation in the present genus can give a misleading impression of a vesiculate saccus, this should be identified as the protruding ornamentation through changing of the focal plane. Apart from that *Tsugaepollenites* is distinguished by differences in size on the proximal and distal face. The genus *Pseudomassulites* gen. nov. is distinguished by much larger, more hyaline protrusions and lack of a germinal area.

Stratigraphic range. – Mesozoic (maybe Upper Triassic, surely Jurassic) to Cenozoic (Pliocene).

Botanical affinity. – There are to date no known *in situ* finds in microsporangia. (Bose (1955) documented some possible male cone scales with *Sciadopitys*-like pollen complying with the genus diagnosis of *Sciadopityspollenites*, but he noted that because the shales in which they were found were so full of this type of pollen, the grains might have attached themselves to the scales in the process of maceration. However, one can also argue that concentration of this pollen was so high because they might all come from the male cone scales.

Later, Manum (1987) described *Sciadopitys*-like leaves from the Upper Jurassic. Similar finds associated with a palynoflora containing, amongst others, abundant "*Cerebropollenites macroverrucosus*" and "*Cerebropollenites thiergartii*", were also recorded from the Middle and Upper Jurassic from northern Norway (Bose & Manum 1990; Manum et al. 1991). However, these fossils were recombined as *Oswaldheeria* and assigned to a different and new family

(Miroviaceae) by the authors themselves (Bose & Manum 1990; Manum et al. 1991). Distinction of this genus from the Sciadopityaceae by erecting a new family was further supported and emphasised by later anatomical studies which drew comparisons to other groups (e.g. ginkgophytes and podocarps) based on the difference in vasculature and absence of brachyblasts in *Oswaldheeria* (Gordenko 2007; Taylor et al. 2009).

Macrofossils, including reproductive structures, assignable to Sciadopityaceae (e.g. *Sciadopitophyllum*, *Sciadopityostriobus*, *Sciadopityoides*) are generally known from the Upper Cretaceous onwards (Christophel 1973; Sveshnikova 1981; Ohsawa et al. 1991; Saiki 1992; Taylor et al. 2009). Due to the unique wood anatomy of Sciadopityaceae (Ohsawa 1994), wood of the *Protosciadopityoxylon*-type from the Middle Jurassic can be linked to the family and suggests much older occurrences (Jiang et al. 2012, 2019). Given the hypothetical relative age of the family of circa 225–200 My based on molecular clock data (Crisp & Cook 2011), findings of this type of wood and pollen of Sciadopityaceaen affinity in the Jurassic appear plausible.

Despite the lack of certain *in situ* finds that definitely link *Scidadopityspollenites*, the circumstantial evidence, together with the overall compliant morphology, surface and ultrastructure of fossil *Sciadaopityspollenites* with extant *Sciadopitys* pollen, further supports affiliation with the Sciadopityaceae. Although many authors have favoured a potential affinity with extant *Tsuga* (Couper 1958; Nilsson 1958), this is not supported when comparing surface and ultrastructural characteristics (Ho & Sziklai 1973; Grímsson & Zetter 2011).

Through the basionym *Tsugaepollenites mesozoicu*s Couper 1958, the genera *Cerebropollenites/Sciadopityspollenites* have been historically linked to *Tsuga*, but these studies only considered the suggested similarities with *Tsuga* and completely omitted potential association with *Sciadopitys* (e.g. Couper 1958; Nilsson 1958; Batten and Dutta 1997; Shang and Zavada 2003). However, others studies based on SEM and TEM for both taxa corroborate early assumptions based on morphology visible in light microscopic studies and that the name *Sciadopityspollenites* rightly suggest an affiliation with Sciadopityaceae (Raatz 1937; Kirchheimer 1938; Thiergart 1938; Zauer & Mchedlishvili 1966; Ilyina 1968, 1985).

Remarks. – Forms formerly assigned to *Cerebropollenites* are considered conspecific and therefore, as a junior synonym, do not demand distinction. The nomenclatural type is lost. A new type, i.e. a lectotype, could be chosen from Thiergart’s material which was cited by Potonié (1958) and might be interpreted as original material. If it is not considered original material, there is currently no original material known to remain and yet, current phrasing of the *Code* prevents the possibility of a neotype unless and until the recent proposal to alter the *Code* to rectify this is accepted (Gravendyck et al. 2020b).

Sciadopityspollenites thiergartii **Schulz 1967 comb. nov. et *emend*.**

Holotype/Basionym. – *Cerebropollenites thiergartii* Schulz E. (1967). Paläontologische Abhandlungen Abteilung B 2: 541–633; p. 603, Pl. 11, Figs. 7–8 (here Fig. 3.8)

Synonyms. – = *Pollenites macroserratus* f. *doggerensis,* Thiergart 1949 in Palaeontographica Abteilung B, 89: 18.

= *Tsugaepollenites macroserratus* f. *doggerensis* (Thiergart 1949) Bóna 1969 in Annales Instituti Geologici Publici Hungarici 51: 695.

= *Sciadopitys multiverrucosus* Ilyina 1968 in Comparative analysis of spore-pollen complexes of Jurassic deposits of the Southern Part of Western Siberia [in Russian]: 42, Pl. 5, Figs. 1–2.

= *Sciadopityspollenites multiverrucosus* (Sachanova et Ilyina 1968) Ilyina 1985 in Jurassic Palynology of Siberia [in Russian]: 97, Pl. 9, Figs. 1–2.

Emended description. – Asaccate pollen with a subcircular to oval outline. Size range variable from smaller (usually more circular) grains of 40 µm to grains larger usually less rounded grains of up to 80 µm in length. Oval or sometimes subcircular sulcus that measures approximately half to $^{2}/_{3}$ the length of the pollen and is visible as a thinning of the pollen grain. The exine is 1–(2) µm thick and covered with many densely arranged verrucae. The size of the warts measures 1–4 µm on average in width and height. Due to the protrusion of the verrucae at the equator the specimens show a finely serrated outline. (Figs. 14 A and B)

Comparison. – From all *Sciadopityspollenites* species the one with the smallest sculptural elements (compare overview for Cenozoic taxa in Krutzsch (1971)). *Sciadopityspollenites megaorbicularius* has also verrucae but much larger in size (>3 µm). *Sciadopityspollenites carlylensis* has more elongate sculptural elements. *Sciadopityspollenites mesozoicus* and *Sciadopityspollenites macroverrucosus* are distinguished by muri instead of verrucae.

Stratigraphic range. – Base of the Jurassic to upper Lower Cretaceous.

Remarks. – We have observed two kinds of specimen that can be differentiated by the size of their verrucae. Since both of them are included in the size range originally given by Schulz and since there is (currently) no stratigraphic need to divide them on species level, the two forms are divided only in infraspecific rank. Using the two varieties separately might show by application in the future, whether there is stratigraphic and/or ecological difference or not.

Sciadopityspollenites thiergartii Schulz 1967 ssp. nov. *schulzii*

Holotype/Basionym. – *Cerebropollenites thiergartii* Schulz 1967, p. 603, Pl. 11, Fig. 7–8 (here Fig. 3.8)

Description. – Forms with verrucae in the lower size range; verrucae around 1.5 µm, max. up to 2 µm in hight and width. (Fig. 14 A)

Remarks. – Forms of only this kind were found in Schulz' original material, hence the name.

Sciadopityspollenites thiergartii Schulz 1967 ssp. nov. *multiverrucosus*

Holotype/Basionym. – to be determined upon effective publication

Description. – Forms with verrucae in the bigger size range; verrucae around <1.5 µm, max. up to 4 µm in hight and width. (Fig. 14 B)

Remarks. – Ilyina (1965) depicted forms of this kind and in honour of the name multiverrucosus which is widely used in Russian publications the epithet of this conspecific taxon is used to delimit forms with verrucae of a bigger size range.

Sciadopityspollenites megaorbicularius sp. nov.

Holotype/Basionym. – to be determined upon effective publication

Description. – Asaccate pollen with a subcircular to oval outline. Size range variable from smaller (usually more circular) grains of 40 µm to grains larger usually less rounded grains of up to 70 µm in length. Oval or sometimes subcircular sulcus that measures approximately half to $^2/_3$ the length of the pollen and is visible as a thinning of the pollen grain. The exine is 1–2 µm thick and covered with many large and densely arranged verrucae. The size of the verrucae measures >4 µm in width and height. Due to the protrusion of the verrucae at the equator the specimens show a corrugated outline. The verrucae are solid, not hollow or hyaline. (Fig. 14 C)

Comparison. – Differs from *Sciadopityspollenites thiergartii* by having much larger verrucae. *Sciadopityspollenites carlylensis, Sciadopityspollenites macroverrucosus* and *Sciadopityspollenites mesozoicus* have elongate sculptural elements or rugulate ornamentation instead of verrucae.

On top of the that sculptural elements of the new species more solid and less hyaline than protrusions in *Sciadopityspollenites macroverrucosus* and *Sciadopityspollenites mesozoicus*

Stratigraphic range. – Lower Jurassic, potential range beyond will demand further investigation.

Remarks. – The name is derived from the size and shape of the verrucae that are reminiscent of very large orbicules.

Sciadopityspollenites carlylensis (Pocock 1970) Fedorova et al. 1993 _emend_.

Holotype/Basionym. – *Cerebropollenites carlylensis* Pocock 1970 in Palaeontographica Abteilung B, 130: 98, Pl. 21 Fig. 10

Lectotype. – Lectotypification necessary. Although the holotype is assumed to be lost, original material is available at the Geological Survey of Canada (Krista Boyce, March 2021, personal communication)

Synonyms. – ? = *Sciadopityspollenites osmundaeformis* (Zhang 1965) Wang et al. 1981 Acta Palaeontologica Sinica, 20: 533.

Emended description. – Asaccate pollen with a subcircular to oval outline. Grains usually rather sub-circular than oval, 25–50 µm in diameter. Subcircular to oval sulcus that measures approximately half the length of the pollen and is visible as a thinning of the pollen grain. The exine is 1–(2) µm thick and covered with slightly elongate sculptural elements that are no verrucae but rather muri that can be a bit looped (2–3 µm high). Due to these protrusion of the sculptural elements at the equator the specimens show a finely corrugated outline. (Fig. 14 D)

Comparison. – Differs from *Sciadopityspollenites thiergartii* and *Sciadopityspollenites megaorbicularius* by not having verrucae, but rather more elongate sculptural elements. Differs from *Sciadopityspollenites macroverrucosus* and *Sciadopityspollenites mesozoicus* by not having windy and rugulate ornamentation

Stratigraphic range. – Lower Jurassic – upper Lower Cretaceous. Probable occurrences in the Rhaetian (Upper Triassic) should be confirmed upon these new, clearer defined categories.

Remarks. – Tentative synonymisation of *Sciadopityspollenites osmundaeformis* is based upon expressed opinion in Song et al. (2000) that we concur with upon re-investigation of the available photographs in Li (1984). Given the few citations of the name (Fig. 11) this appears likely although it could not be confirmed due to unavailability of the holotype.

Sciadopityspollenites macroverrucosus **(Thiergart 1949) Ilyina 1985 *emend*.**

Holotype/Basionym. – *Pollenites macroverrucosus* Thiergart 1949 in Palaeontographica Abteilung B, 89: 17, Pl. 2, Fig. 19

Synonyms. – ≡ *Cerebropollenites macroverrucosus* (Thiergart 1949) Schulz 1967 in Paläontologische Abhandlungen Abteilung B, 2: 603.

= *Tsugaepollenites macroverrucosus* (Thiergart 1949) Bóna 1969 in Annales Instituti Geologici Publici Hungarici, 51: 694–965.

Emended description. – Asaccate pollen with a subcircular to oval outline. Size range variable from 40 µm to larger grains of up to 80 µm in length. Oval or sometimes subcircular sulcus that measures approximately half to $^2/_3$ the length of the pollen and is visible as a thinning of the pollen grain. The exine is up to 1.5 µm thick, ornamentation rugulate. Dense arrangement of the sculptural elements (most similar to the densely packed gyri of a brain); little empty space in between the sculptural elements max. ¼ of the width of the rugulate muri. The large sculptural elements (up to 4 µm high) protruding at the equator can give an impression of a fringe; the outline is corrugated (Fig. 14 E).

Comparison. – *Sciadopityspollenites thiergartii* and *Sciadopityspollenites megaorbicularius* are distinguished by verrucate ornamentation. *Sciadopityspollenites mesozoicus* has larger and more loosely arranged muri. *Sciadopityspollenites carlylensis* as less elongate and less winding sculptural elements.

Stratigraphic range. – Lower Jurassic – upper Lower Cretaceous. Probable occurrences in the Rhaetian (Upper Triassic) should be confirmed upon these new, clearer defined categories.

Remarks. – The distinction with *Sciadopityspollenites mesozoicus* is maintained and the two taxa regarded as morphological endmembers of intermediate forms. After preliminary observation of variation in Bonenburg (Schobben et al. 2019; Gravendyck et al. 2020c) and in the original material from Lund (1977) for the Rhaetian, *Sciadopityspollenites macroverrucosus* might occur in the Rhaetian while *Sciadopityspollenites mesozoicus* joins the assemblages in the Jurassic. Whether or not there is such a stratigraphic and/or ecological difference remains to be further evaluated upon usage of the newly defined categories.

Sciadopityspollenites mesozoicus **(Couper 1958) Waksmundzka 1981 *emend*.**

Holotype/Basionym. – *Tsugaepollenites mesozoicus* Couper 1958 in Palaeontographica Abteilung B 103: 155, Pl. 30, Fig. 8 (here Fig. 2.8)

Synonyms. – ≡ *Cerebropollenites mesozoicus* (Couper 1958) Nilsson 1958 in Publications from the Institutes of Mineralogy, Paleontology and Quaternary Geology, University of Lund 53: 72, Pl. 6, Figs. 10-12.

Emended description. – Asaccate pollen with a subcircular to oval outline. Size range variable from smaller (usually more circular) grains of 40 µm to grains larger usually less rounded grains of up to 90 µm in length. Oval or sometimes subcircular sulcus that measures approximately half to $^{2}/_{3}$ the length of the pollen and is visible as a thinning of the pollen grain. The exine is up to 1 µm thick, ornamentation rugulate. Looser arrangement of the winding m12uri with larger spaces in between the sculptural elements ca. $^{1}/_{2}$–$^{1}/_{3}$ of the width of the muri. The large sculptural elements (up to 6 µm high) protruding at the equator give an impression of a fringe; the outline is strongly corrugated (Fig. 14 F).

Comparison. – *Sciadopityspollenites thiergartii* and *Sciadopityspollenites megaorbicularius* are distinguished by verrucate ornamentation. *Sciadopityspollenites macroverrucosus* has less high and more densely arranged muri. *Sciadopityspollenites carlylensis* as less elongate and less winding sculptural elements.

Stratigraphic range. – Lower Jurassic – Upper Cretaceous, probably occurrences in the Rhaetian (Upper Triassic) should be confirmed upon these new, clearer defined categories.

Remarks. – see remark for *Sciadopityspollenites macroverrucosus*

5.4.2. *Pseudomassulites* gen. nov.

Type. – *Camerosporites pseudomassulae* Mädler 1964 in Fortschritte in der Geologie von Rheinland und Westfalen 12: 169–200, p. 183, Pl. 2, Fig. 17 (here Fig. 2.10)

Description. – Palynomorphs consisting entirely of an aggregation of large hyaline protrusions. A distinct corpus is not visible except for the space deliminated by the protrusions. No differentiation on either side of the palynomorph, protrusions equal in size all around, no germinal area or other features visible. Protrusions rounded, compression can make them appear more angular, but never with clear straight septa.

Comparison. – *Tsugaepollenites* is distinguished by a saccus and heteropolarity of the grain with different types of ornamentation on one grain. *Sciadopityspollenites* is distinguished by a sulcus and by different and more solid ornamentation.

Botanical affinity. – Unknown, given the above expressed doubts concerning the isopolar appearance, it is not even clear whether this is in fact a pollen at all.

Remarks. – The new genus is erected as a monotypic genus, to prevent assignation of the only species to other genera (with features that the present species does not show; e.g. saccus, heteropolarity) because of lack of other options. Given Mädler's description of the protrusions to give the impression of massula, i.e. an aggregation of pollen as a dispersal unit (Mädler 1964a; Punt et al. 2007), the genus name is alluding to the same characteristic, because it is the crucial distinguishing factor. It is currently not clear whether the taxon is a spore, pollen or aquatic element.

Pseudomassulites pseudomassulae (Mädler 1964) comb. nov. et *emend*.

Holotype/Basionym. – *Camerosporites pseudomassulae* Mädler 1964 in Fortschritte in der Geologie von Rheinland und Westfalen 12: 169–200, p. 183, Pl. 2, Fig. 17 (here Fig. 2.10)

Synonyms. – ≡ *Tsugaepollenites ? pseudomassulae* Morbey 1975 in Palaeontographica Abteilung B, 152: 30–31, Pl. 10, Figs. 9-12.

≡ "*Cerebropollenites pseudomassulae*" Taugourdeau-Lantz et al. 1984 in Documents du Bureau des Recherches Géologiques et Minieres 81: 70, Pl. 3, Fig. 2;

note that the name was not properly recombined, because it is missing the necessary full and direct reference to the basionym (Art. 41.5 *Code*).

Emended description. – (Sub)circular palynomorph with large, hyaline and hollow protrusions. Specimen Diameter ranges from (35) – 55 – (65) µm. No differentiation in ornamentation on either side of the grain. Protrusions semicircular, circa twice as broad as high (5–10 µm high and 10–18 µm wide), usually rounded or slightly folded, other protrusions are shining through the other due to the very hyaline and otherwise laevigate exine.

Comparison. – *Sciadopityspollenites mesozoicus* (and even more so *Sciadopityspollenites macroverrucosus* can be distinguished by the smaller, windy and less hyaline sculptural elements. *Sciadopityspollenites megaorbicularius* sp. nov. is likewise distinguished by a sulcus and more solid, i.e., not so hyaline, and much smaller verrucae. The taxon can resemble *Cymatiosphaera* (compare Pl. 9 Fig. 11 in Heunisch et al. 2010). The compressed septa of *Cymatiosphaera* result in more angular appearance of the convolutions, that differentiate it from *Pseudomassulites pseudomassulae*.

Stratigraphic range. – Typically, Rhaetian (Upper Triassic), possibly ranging until the Hettangian (Lower Jurassic). It is not clear at this point whether Jurassic occurrences might simply be reworked or owed to confusions with *Sciadopityspollenites mesozoicus* (≡ *Cerebropollenites mesozoicus, Tsugaepollenites mesozoicus*).

5.5. A note on nomenclature

According to the *Code*, dissertations are usually not considered effectively published unless they contain a statement that the content is considered effectively published under Art. 30.9 of the *Code*, or contain 'implied' evidence of the authors consideration of the content as effectively published, e.g. through an ISBN number (Turland 2019). Since the present paper has not undergone peer review yet, we do not deem the current paper as effectively published. Therefore, none of the above presented nomenclatural novelties take effect yet, and should be considered like a preprint. Only upon effective publication in a journal after peer review will the above made revisions take effect.

To prevent greater nomenclatural confusion than there is already, an additional proposal to reject the recombinations with *Cerebropollenites* will be formally made in Taxon (McNeill et al. 2018; Turland 2019). The analysis of name usage has shown that the very widespread and much more frequent use of *Cerebropollenites* threatens the correct recombinations with *Sciadopityspollenites* which are so far common in Russia but not beyond. Thereby the necessary minimal requirement for such an official proposal is fulfilled, but we encourage to adopt the herein proposed name use before such use might become binding by formal decision.

6. Conclusion

In the past, the numerous recombinations of names with *Tsugaepollenites*, *Cerebropollenites,* and *Sciadopityspollenites* caused inconsistent use and confusion around the marker fossil *Cerebropollenites thiergartii* (see problem overview in Fig. 14). Even more so as a part of the community consistently uses recombinations with *Sciadopityspollenites* (except for that marker fossil), whereas the majority uses recombinations with *Cerebropollenites.* The tentative and sometimes doubted assignation of the epithet *pseudomassulae* to the genus *Tsugaepollenites*, and the unclear boundaries not only between the epithets *mesozoicus* and *macroverrucosus* also made classification difficult.

The main objective of the present study was to clarify taxonomic and nomenclatural confusion (1) on a generic level between ***Cerebropollenites*** Nilsson 1958, ***Tsugaepollenites*** (Potonié & Venitz 1934) Potonié 1958 and ***Sciadopityspollenites*** Raatz 1937 ex Potonié 1958 and (2) on the species level for taxa relevant for the Triassic–Jurassic transition, especially *Cerebropollenites* ***thiergartii,*** *Cerebropollenites* ***macroverrucosus/mesozoicus*** and *Tsugaepollenites* ***pseudomassulae****.* We restudied the relevant holotype material to distinguish the genus and species defining characteristics, and evaluated the inter- and intraspecific variation in original and new material. Together with an analysis of name usage over the time and an extensive literature review, we identified sources of previous confusion and redefined species circumscriptions.

The lack of differentiation between *Cerebropollenites* and *Sciadopityspollenites* support previous synonymisation. The use of *Sciadopityspollenites* is not only taxonomically and nomenclaturally imperative because of priority, but will also unify previous disjunct use of *Cerebropollenites* for Mesozoic and *Sciadopityspollenites* for Cenozoic taxa or Mesozoic species in Russian studies.

The clarification of distinctive characteristics led to the revision of existing taxa and the following nomenclatural novelties: *Sciadopityspollenites thiergartii* nov. comb.; *Sciadopityspollenites thiergartii* nov. comb. nov. spp. *schulzii; Sciadopityspollenites thiergartii* nov. comb. nov. spp. *multiverrucosus*; *Sciadopityspollenites megaorbicularius sp. nov.; Sciadopityspollenites carlylensis emend.; Sciadopityspollenites macroverrucosus emend.; Sciadopityspollenites mesozoicus emend*.; *Pseudomassulites* nov. gen and *Pseudomassulites pseudomassulae* nov. comb. et emend.

These taxonomical and nomenclatural clarifications presented here are the most extensive review of *Cerebropollenites*/*Sciadopityspollenites* to date and provide a new basis to better evaluate the stratigraphic value of *Pseudomassulites pseudomassulae* nov. comb. et *emend*. as a Rhaetian marker, and to disentangle potential stratigraphic or regional differences between *Sciadopityspollenites macroverrucosus emend.* and *Sciadopityspollenites mesozoicus emend.* to better evaluate their respective temporal and geographic distribution and stratigraphic value.

Most importantly, the study provides clear differentiation of *Sciadopityspollenites thiergartii* nov. comb. from other species. Given the paucity of biostratigraphic markers for the base of the Jurassic, the presented clarification will be an important tool to resolve past confusion that potentially diminishes its stratigraphic value and to avoid future confusion. These clarifications are distinctive and should allow future workers to make full use of the stratigraphic potential of this important marker species.

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Chapter 9

General Discussion

The overarching aim of this thesis was to integrate the Bonenburg section within the existing framework of records end-Triassic records and describe and compare its paleoenvironmental changes and vegetation history during one of the five big mass extinction events.

Chapter 2 provided the overall stratigraphic framework of the Bonenburg section, combining palynostratigraphy with the biostratigraphy of invertebrates and chemostratigraphy of total organic carbon isotopes. **Chapter 3** investigated the paleoenvironmental changes through palynofacies and palynological analysis and discussed the vegetation history. It also provided a first glimpse of palynotaxonomy by documenting assemblage composition and aberrant pollen and spores. **Chapter 4** provided the nomenclatural and theoretical background for understanding the current issues linked to taxonomy especially in palynology. Following a review of rules, practices and problems recommendations were provided to inform better practices in more detailed palynotaxonomic studies. **Chapter 5** compared the suitability of the output of two important palynological databases for palynotaxonomic studies and provided the background for quantitative analyses of name usage over time and made recommendations when to use which database. **Chapter 6** introduced new metrics to describe how established names are, providing innovative tools for palynotaxonomic discussions supporting proposals for conservation, protection and rejection, especially for competing names such as those discussed in the following chapters. **Chapter 7** presented the systematic palynotaxonomy as it has evolved through this thesis, comparing type material with the palynomorphs from the Bonenburg section and identifying taxa in need of revision. It also integrated recommendations presented in the previous chapters, especially applying a new presentation style for synonymy and employing indices to measure name usage. Additionally, the chapter made a proposal to emend the *Code of Nomenclature for algae, fungi, and plants* to solve a current paradox when attempting to designate neotypes, which is an essential precondition to revise several ambiguous taxa which were identified in the previous chapter. **Chapter 9** revised the index fossil *Cerebropollenites thiergartii* and other associated taxa, which are relevant for the stratigraphy of the Triassic–Jurassic transition.

1. Palynostratigraphic framework

Stratigraphy is an essential component to better understand the sequence of events that lead to mass extinctions and in this case, the end-Triassic mass extinction. In Europe, correlations of existing sections are complicated by almost complete lack of fossils in the so called ‘Event Beds’, which are assumed to represent the extinction interval. Palynomorphs are the only biostratigraphic markers available to complement chemostratigraphy in the barren interval.

Chapter 2 presented qualitative palynological results which confirmed the Rhaetian age of *Rhaeticosaurus mertensii* based on palynostratigraphy. Together with geochemistry and other biostratigraphic markers outside the barren interval, this chapter provided a solid stratigraphic framework for the correlation of the new section with other important European sections from Austria (western Tethys shelf) to Scandinavia (Central European Basin) and Greenland. A core finding was that lithology, geochemistry, and palynomorphs, enable the tentative correlation of the reddish Triletes Beds (CEB) and the similarly red-stained Schattwald Beds of the Eiberg Basin, including the important GSSP section Kuhjoch.

Chapter 3 presented quantitative palynological data, documenting detailed assemblage changes, which lead to a refined palynological assemblage zonation that confirmed and elaborated on qualitative results from chapter 2. Compared to mere presence absence data of stratigraphic important taxa (chapter 2), assemblage zonation proved to be the most useful tool to correlate sections in between basins, due to some varying FOs of several stratigraphically important spores. Due to the hiatus at the base of the Psilonotenton Fm in Bonenburg, the new section cannot provide new evidence as to the FO of *Cerebropollenites thiergartii* beyond the fact that single individuals occur in the first samples lithologically assigned to the Psilonotenton Fm. It will be interesting for future studies to investigate the stratigraphic ranges of other associated taxa like *Pseudomassulites pseudomassulae* sp. nov. and *Sciadopityspollenites macroverrucosus* and *Sciadopityspollenites mesozoicus*, which occur already in the Rhaetian part of the section. After its detailed taxonomic revision (see chapter 8), further studies will be needed to document the stratigraphic ranges of their newly defined circumscriptions to evaluate their stratigraphic usefulness.

2. Paleoenvironment and vegetation history

Chapter 2 discussed potential causes for the clay mineralogy changes, preliminary palynofacies results of wood fragment abundance and a shift to ^{13}C-enriched TOC in the Event Beds. A change in the weathering regime, leading to an increased physical erosion on land and an elevated riverine influx, was proposed as a possible explanation and could be further supported by detailed palynofacies and palynological analysis. Especially reworked palynomorphs from the Paleozoic could tentatively support this interpretation, but more quantitative data is needed to further investigate this hypothesis.

Chapter 3 proposed a new approach to evaluate paleoenvironmental change. Rather than looking at richness values alone, analysis of diversity patterns, especially evenness values, was also estimated and proved to give a more insightful view. Based on this new approach, our palynofloral and environmental reconstruction indicate gradual changes rather than a dramatic turnover as suggested by previous studies based only on richness values, and our elevated evenness values further indicate three pulses of increased environmental disturbance, with the last two pulses shortly following each other. It is noteworthy that in fact, only few palynomorph taxa truely go extinct in Bonenburg, and that the observed vegetation changes suggest that plants are more resilient to environmental change than animals in the investigated interval. It will be interesting to compare these findings with diversity changes of other biota, especially molluscs, because preliminary qualitative results from chapter 2 indicate that the disappearance of many marine elements, especially bivalves and brachiopods, coincide with the first disturbance pulse documented in the vegetation. The few marine species that do continue to occur until the next pulse, then disappear coincidently with the gradual transition from Cheirolepidiaceae and Voltziales dominated Conifer forest, and after the second pulse of disturbance, into a shrubbier and more herbaceous assemblage of Cycads, ferns, and diverse cryptogams. More information on the changes in lithology and abundance patterns in marine biota is needed to further integrate the results of environmental change encoded in palynofacies and palynology. A core finding of chapter 3 was that the diversity patterns also coincide with trend changes in $\delta^{13}C_{TOC}$ isotope curves detected in Bonenburg, and also in the GSSP section Kuhjoch and the Hochalplgraben section, suggesting a supra-regional pattern of change. Comparison in between sections beyond the given examples proved to be difficult as most sections focus on the Triassic–Jurassic transition itself, therefore not providing enough datapoints for comparison of changes predating the extinction interval. It will be interesting for future sampling and analyses to focus in more detail on the interval leading up to the marine extinction to better understand the changes, and their geographical and temporal extent and magnitude.

An important side observation of chapter 3 was the occurrence of malformations in several different taxa coinciding with evenness peaks, i.e. supposed pulses of disturbance. For the first time, we documented that aberrant *Classopollis* and *Ricciisporites* tetrads occur already in the Rhaetian, together with aberrant spores in several other taxa like *Rhaetipollis*, *Triancoraesporites* and *Perinosporites*. Against expectations, we did not find similarly high numbers of malformed deltoid spores as documented for the CEB from recent studies (Barth et al. 2018; Lindström et al. 2019). This might have several potential reasons. Firstly, the interval that is characterised by a very high abundance of deltoid spores might be partially missing due to the hiatus in Bonenburg (compare chapter 2 and Barth et al. 2018). Secondly, there is no uniform understanding of what can be counted as aberrant versus secondarily folded, yet, despite a first attempt to categorise kinds of malformation by Lindström and coworkers (2019). It takes a lot of experiences to distinguish between normal and abnormal. Chapter 7 enlarged on preliminary observation on malformed spores from chapter 3, but obvious malformations, e.g. a square instead of a triangular spore outline, or alteration of the trilete mark to monolete mark remained rather rare. Less obvious malformations might have been counted as spores *indet* and might have been overlooked.

A more uniform counting scheme will be needed to evaluate this aspect of teratology for the Bonenburg, but also for other European sections, to produce comparable data of abundance changes of malformations. The temporally constrained occurrences of aberrations that were documented in Bonenburg in many different taxa at the same time (chapters 3 and 7) suggests already that this is not only a result of reproductive strategy (e.g. apomixis), but an indication of environmental stress. Despite potentially extreme culprits like heavy metals (Lindström et al. 2019), it will be important to identify the effect of different abiotic variables on microsporogenesis and palynomorph morphology, to evaluate the suitability of terratology as a potential disturbance proxy.

Additionally, it will be very interesting to further investigate the abundance patterns and size variation in aberrant *Classopollis* tetrads beyond the available pilot data (chapter 7). Finding *Classopollis* grains still attached in tetrads gives us a rare insight into paleogenetics through the immediate result of microsporogenesis. As laid out in chapter 7, one particular tetrad coordination can give way to potential unreduced pollen, and interestingly this coordination was documented in *Classopollis* to varying amounts, but not documented in *Ricciisporites*. It will be important, to follow up on abundance variance of the different tetrad coordinations in these two taxa with contrasting fates of diversification (*Classopollis*) and extinction (*Ricciisporites*). Size variation in pollen is often used to correlate with ploidy level (Gould 1957; De Storme et al. 2013; Marinho et al. 2014) and Kürschner and coworkers (2013) already suggested that unreduced pollen in *Classopollis* might provide evidence for potential polyploidy in the mother plant. Therefore, observations on size variation in single grains in *Classopollis* and *Ricciisporites* over time, paired with abundance of different tetrad coordination might reveal further evidence for a polyploidiisation event in the Cheirolepidiaceae and explain their success after the end-Triassic mass extinction.

Due to continous occurrence of *Classopollis* and frequent occurrence in tetrads and the newly documented malformations predating the end-Triassic mass extinction, they represent an ideal study object to understand the paleogenetic history of this extinct plant lineage and its Mesozoic success story. Chapter 7 provided preliminary results comparing palynomorphs in different sections and suggests that abberrant *Classopollis* tetrads occur not only in Bonenburg, but also in Kuhjoch (Austria), St. Audrey's Bay (UK), and Stenlillle (Denmark). Further qualitative and quantitative studies are needed to evaluate distribution patterns and their potential implications. If future studies can support that teratology can serve as a proxy for disturbance, *Classopollis* will represent an ideal model organism due to its wiedspread and long-lasting occurrence and recurrence of tetrads, and potential to trace and better understand environmental disturbance throughout the Mesozoic.

3. Revised palynotaxonomy

Taxonomy is the backbone of every subsequent palynological study. Yet, there is a shift towards more applied studies probably because of financial and temporal limitations of modern palynological studies, and/or page limitations in journals. This has made lengthy palynotaxonomic works unfashionable, at least in terrestrial palynology. Indeed, dinoflagellate indexes are still updated, containing many revisions, with comments and recommendations how to classify them and which names to adopt (compare the latest version of the Lentin and Williams Index for dinoflagellates; Fensome et al. 2019).

If paleopalynology is to remain competitive against other applied disciplines and approaches, e.g. from geochemistry, it will likely be important to keep updating one of the most important tools in the toolbox of paleopalynology, namely palynotaxonomy. During data acquisition for the results presented in chapter 2 and chapter 3, it became clear that many circumscriptions are ambiguous and often hard to ascertain in the original form. Lengthy long-distance book requests and literature exchange with colleagues are time consuming and not always successful.

Chapter 4 reviewed the existing rules and nomenclatural framework in which palynotaxonomy operates. It discussed current problems and made recommendations for new best practices for future palynotaxonomic works. Chapter 5 and 6 provided the theoretical background of what is here called "name usage statistics", i.e. the empirical study of name usage over time with the help of databases, that can be used for taxonomic revisions and potential proposals of rejection or conservation (McNeill et al. 2018). Riding et al. (2012) informed about the John Williams Index, a hand-written card index, currently only available on site at the Natural History Museum in London. They have illustrated its usefulness and higher number of references in comparison to Palynodata, a digitally available resource which was, however, discontinued 9 years before the John Williams Index. The main objective of chapter 5 was to compare the usefulness and output of references for several Rhaetian genera (including those revised in chapters 7 and 8) for each database. We showed that it depends very much on the study question which database is best to use, but for taxonomic revisions the (partially) random variance between the two databases makes it important to use both. Chapter 6 introduced simple metrics to represent name usage and establishment of names. Together, chapters 5 and 6 lay the groundwork for the use of these databases and applications of the metrics for taxonomic revisions in chapters 7 and 8 and will be important for future proposals for conservation and rejection amounting from revisions made in chapters 7 and 8.

The lucky discovery of the Schulz collection presented in Appendix I, provided a unique opportunity to assemble an elaborate collection of original descriptions and diagnoses. Additionally, it provided the possibility to study the type and original material for many Rhaetian key taxa. The results and synopsis of this study was summarized in chapter 7. This chapter represents the most up-to-date catalogue for a Rhaetian palynomorphs occurring in the Germanic Triassic. It allows an easy consult of the original circumscriptions, without the need to gather material from over 100 different, often only non-digitised hard-copy publications from the 1940s-1990s. The integrated study of type-material documented the changed location and condition of type material, suggesting the ample need for neo-, lecto-, and epi-typifications. However, neotypifications are in many cases not available due to a current phrasing in the *Code of Nomenclature for algae, fungi, and plants.*

Chapter 7 provided the most comprehensive and up-to date catalogue of terrestrial palynotaxonomy for the Rhaetian. The chapter compiled diagnoses for some of the most important and recurrent taxa of the Germanic Triassic observed in Bonenburg, and compared them with relevant holotypes to better understand their intraspecific variation. Where necessary, we made emendations, recombinations and new descriptions. Additionally, we proposed for the first time a solution for this fundamental problem, arising from a paradox in the current *Shenzhen Code* which currently prevents neotypification when no other type material, but the illustrations are left. However, such typification is often needed for taxonomic revisions, in paleopalynology as well as in paleobotany at large. It will depend on the decision of the scientific community at the next Botanical Congress whether the formally proposed solution published in TAXON is accepted or not. If it is accepted and comes into effect, the proposed new phrasing of the *Code* will make it possible to designate neotypes, which is currently, unintendedly, impossible.

Chapter 8 finally revised the prominent marker fossil for the base of the Jurassic *Cerebropollenites thiergartii* (von Hillebrandt et al. 2013) and its associated taxa. For many years the distinction of the genera *Cerebropollenites*, *Sciadopityspollenites* and *Tsugaepollenites* and the species *Cerebropollenites thiergartii* and the associated taxa *Cerebropollenites macroverrucosus/ mesozoicus* and *Tsugaepollenites pseudomassulae* was ambiguous and names were used inconsistently. A key finding of this chapter is that *Cerebropollenites macroverrucosus/ mesozoicus* depict overlapping morpho-spaces explaining their inconsistent use in the past. Nevertheless, we also showed that there are some distinctive characteristics. Arguing from a strictly taxonomic and nomenclatural point of view using the fossil-taxon concept, it does not matter whether or not they were produced by the same mother plant or not. It will depend on future studies using the newly defined circumscriptions to document the stratigraphic ranges of these forms and evaluate whether they have stratigraphic significance or not. Studies conducting vegetation reconstructions can then for their analyses lump or separate these taxa depending on the study question. Based on the redocumentation of the holotype, the study of inter and intraspecific variety, and the revised circumscriptions, it is now easier to discriminate *Cerebropollenites thiergartii.* This revision will hopefully restore taxonomic stability and help palynologists to make full use of its value as the marker for the base of the Jurassic.

4. Conclusion

The main focus of the thesis was to integrate the Bonenburg section within the existing framework of end-Triassic records and describe and compare its paleoenvironmental changes and vegetation history during the end-Triassic mass extinction. I provided a detailed palynostratigraphic framework, backed with detailed palynotaxonomic catalogue. This supports correlation of existing end-Triassic records in Europe, especially the correlation of the (except for palynomorphs) fossil-barren Triletes Beds in the CEB and the similarly red stained Schattwald Beds of the western Tethys shelf. I found that the palynofloral record in Bonenburg support best the interpretation of a gradual ecosystem change during the marine extinction of the end-Triassic. While there are potential signs of stress, such as increased evenness values and teratological occurrences, plants seem to be more resilient to change than animals and therefore might not depict the same dramatic extinction trends. Further studies on teratological abundance patterns and data acquisition on size variation over time will be needed, to better understand the cause and implications of teratological occurrences.

My data for the Bonenburg section provides the most detailed palynological record of the changes leading up to the end-Triassic mass extinction to date. For the first time, I could document, that teratological occurrences in several pollen (*Classopollis, Rhaetipollis*, *Ricciisporites*) and spores and (*Triancoraesporites*, *Perinosporites*) occur as early as the Rhaetian. Additionally, I provided a detailed catalogue of Rhaetian palynotaxonomy including the original descriptions (and their English translations). Together with the re-evaluation of corresponding type material, this provides valuable reference material for future palynological studies. I also made a long-needed revision of *Sciadopityspollenites thiergartii* comb. nov. and the associated taxa, proposing six nomenclatural novelties and emendations. This revision will aid, I hope, future correlations of European sections and provides the foundation for future evaluations of the stratigraphic value of associated taxa. Additionally, I highlighted several other taxa whose taxonomic revision is needed. Currently, their revision is still hindered by paradox in the *Code of Nomenclature for algae, fungi, and plants*. If the emendation we proposed is accepted and passed, this will make a crucial contribution not only to paleopalynology, but to palaeobotany at large.

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Chronological Publication List and Contributions

Published

1. Schobben, M.A.N., **Gravendyck, J.**, Mangels, F., Struck, U., Bussert, R., Kürschner, W.M., Korn, D., Sander, P.M., Aberhan, M., 2019. *A comparative study of total organic carbon-δ13C signatures in the Triassic–Jurassic transitional beds of the Central European Basin and western Tethys shelf seas*. Newsletters on Stratigraphy. 52, pp. 461-486.

https://doi.org/10.1127/nos/2019/0499

Contribution: conducting the palynofloral analysis of the paper and writing the respective part of the manuscript which is, after the isotope analysis, the most significant part of the paper

2. Gravendyck, J., Bachelier, J.B., Heunisch, C., 2020a. *A biography and obituary of W.H. Eberhard Schulz (1931–2017)*. Palynology. 44, pp. 453–459.

https://doi.org/10.1080/01916122.2019.1620894

Contribution: archive research; sorting out the inheritance of E. Schulz; idea and initiative, manuscript writing; corresponding author

3. Gravendyck, J., Bachelier, J.B., Kürschner, W.M., Herendeen, P.S., 2020b. (009) *A proposal to solve a paradox when neotypifying names of fossil-taxa*. Taxon 69, 628. (proposal to amend the code)

https://doi.org/10.1002/tax.12249

Contribution: identification of the problem; ideas for solution, manuscript writing; corresponding author

4. Gravendyck, J., Schobben, M., Bachelier, J.B., Kürschner, W.M., 2020c. *Macroecological patterns of the terrestrial vegetation history during the end-Triassic biotic crisis in the central European Basin: A palynological study of the Bonenburg section (NW-Germany) and its supra-regional implications*. Global Planetary Change 194, pp. . https://doi.org/10.1016/j.gloplacha.2020.103286

Contribution: sample collection of high-resolution sampling from the transition from the Contorta to the Triletes Beds, part of sample preparation (washing after HF treatment, heavy liquid separation, slide preparation), data acquisition and analysis; manuscript writing; corresponding author

Published Online

5. **Gravendyck, J**., Fensome, R. A., Head, M.J., Herendeen, P.S., Riding, J.B., Bachelier, J.B., Turland, N. J. *Taxonomy and nomenclature in palaeopalynology: Basic principles, current challenges and future perspectives.* Palynology. *Published Online*. https://doi.org/10.1080/01916122.2021.1918279

Contribution: archive research; idea and initiative, manuscript writing; corresponding author

In preparation

6. **Gravendyck, J**., Bachelier, J.B., Coiffard, C. *Name Usage Statistics I: Working with databases.* Palynology.

Contribution: idea and initiative, compilation and analysis of dataset, manuscript writing; corresponding author

7. **Gravendyck, J**., Coiffard, C., Bachelier, J.B. *Name Usage Statistics II: Indices to quantify name usage.* Palynology.

Contribution: idea and initiative, compilation and analysis of dataset, manuscript writing

8. **Gravendyck, J**., Bachelier, J.B., Coiffard, C., Kürschner. *Revisiting the Rhaetian: re-evaluation of types and diagnoses in view of Bonenburg's palynomorphs.* Palaeontographica Abteilung B.

Contribution: compilation and analysis of dataset, manuscript writing

9. **Gravendyck, J**., Bachelier, J.B., Coiffard, C., Kürschner. *Re-evaluation of Cerebropollenites thiergartii Schulz 1967 and related taxa: priority of Sciadopityspollenites and other nomenclatural novelties.* Grana.

Contribution: compilation and analysis of dataset, manuscript writing

Conference Proceedings

1. **Gravendyck, J**., Bachelier, J.B., Kürschner, W.M., 2018. *Detailed Insights into the end-Triassic biotic crisis with respect to its impact on palynofloral assemblages.* Conference Proceedings of the 10th Eurpean Paleobotany & Palynology Conference. Dublin. p. 28. https://www.researchgate.net/publication/334971540_Detailed_Insights_into_the_end-Triassic_biotic_crisis_with_respect_to_its_impact_on_palynofloral_assemblages

2. **Gravendyck, J**., Bachelier, J.B., Kürschner, W.M., 2019. *short story on the life of W.H. Eberhard Schulz (1931–2017)*. Conference Proceedings of the 52nd Annual Meeting of the AASP-The Palynological Society. Ghent. p. 28. https://www.researchgate.net/publication/335749962_A_short_story_on_the_life_of_WH_Eberhard_Schulz_1931-2017

3. **Gravendyck, J**., Bachelier, J.B., Kürschner, W.M., 2019. *Terratology in fossil spores and pollen – A result of chance, a genetic pattern or a result of ecological upheaval?* Conference Proceedings of the 52nd Annual Meeting of the AASP-The Palynological Society. Ghent. p. 29. https://www.researchgate.net/publication/335749985_Teratology_in_fossil_spores_and_pollen_-_A_result_of_chance_a_genetic_pattern_or_a_result_of_ecological_upheaval

4. **Gravendyck, J**., Bachelier, J.B., Kürschner, W.M., 2019. *Terratology in fossil spores and pollen – A result of chance, a genetic pattern or a result of ecological upheaval?* Conference Proceedings of the EGU Galileo Conferences – Mass extinctions, recovery and resilience. Utrecht. https://egu-galileo.eu/gc5-mass/GC5_abstracts.pdf

5. **Gravendyck, J**., Bachelier, J.B., Kürschner, W.M., P.S. Herendeen 2020. *Challenges of modern paleopalynotaxonomy: treasure hund of a PhD.* Palynology Short Talks. Online. https://nastrandberg.wixsite.com/palynology/post/program-for-session-3-student-research-showcase-sponsored-by-aasp-tps

Der Lebenslauf
ist in der Online-Version aus Gründen des Datenschutzes nicht enthalten.

Der Lebenslauf
ist in der Online-Version aus Gründen des Datenschutzes nicht enthalten.

Appendix I

A biography and obituary of W.H. Eberhard Schulz (1931-2017)

With Julien B. Bachelier, Carmen Heunisch

Published 2020 under the same title
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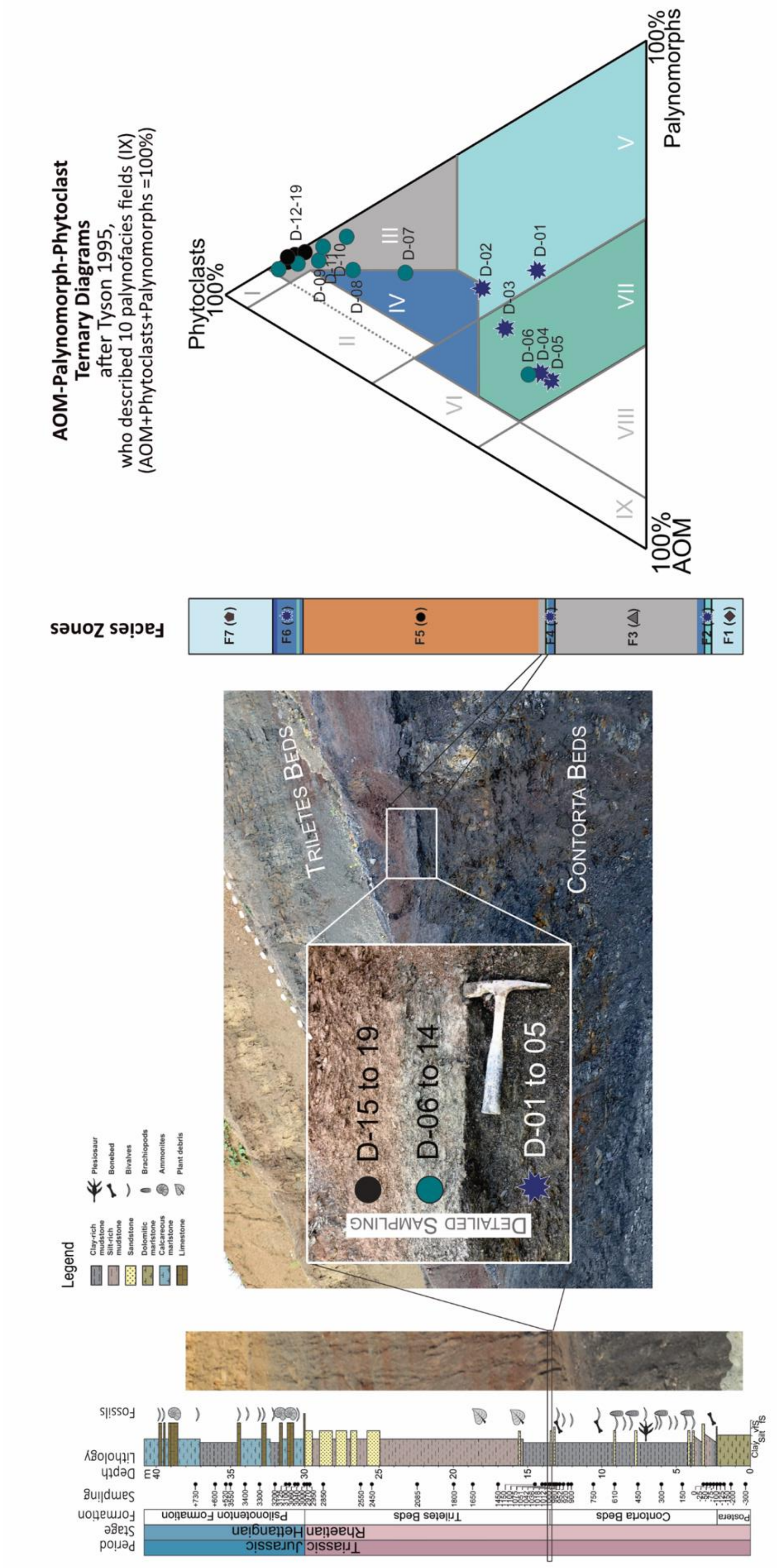
Appendix II

Supplementary material to chapters presented in this thesis

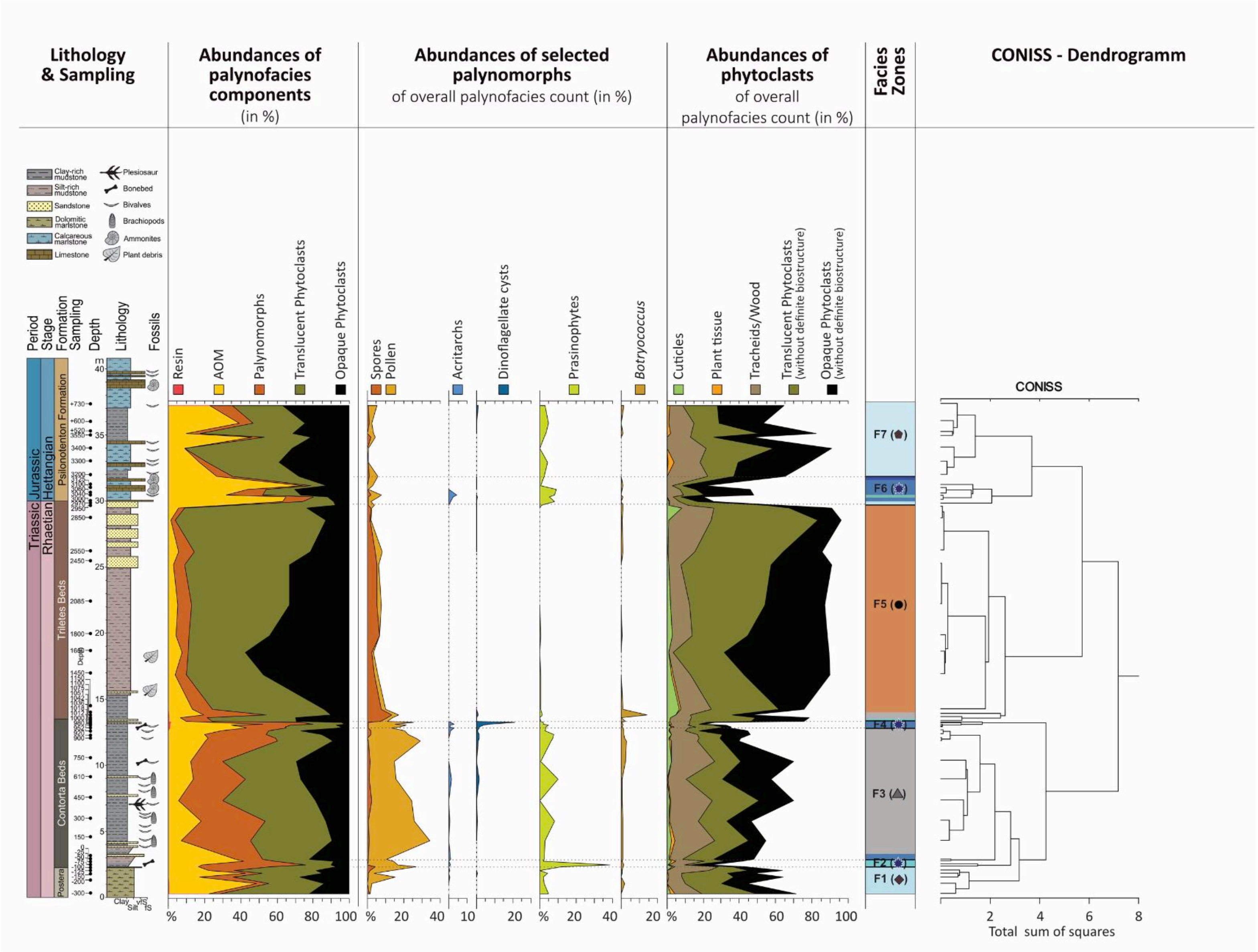
I. Supplements for Chapter 3 – Macroecological Patterns

I.i. Supplementary Figures

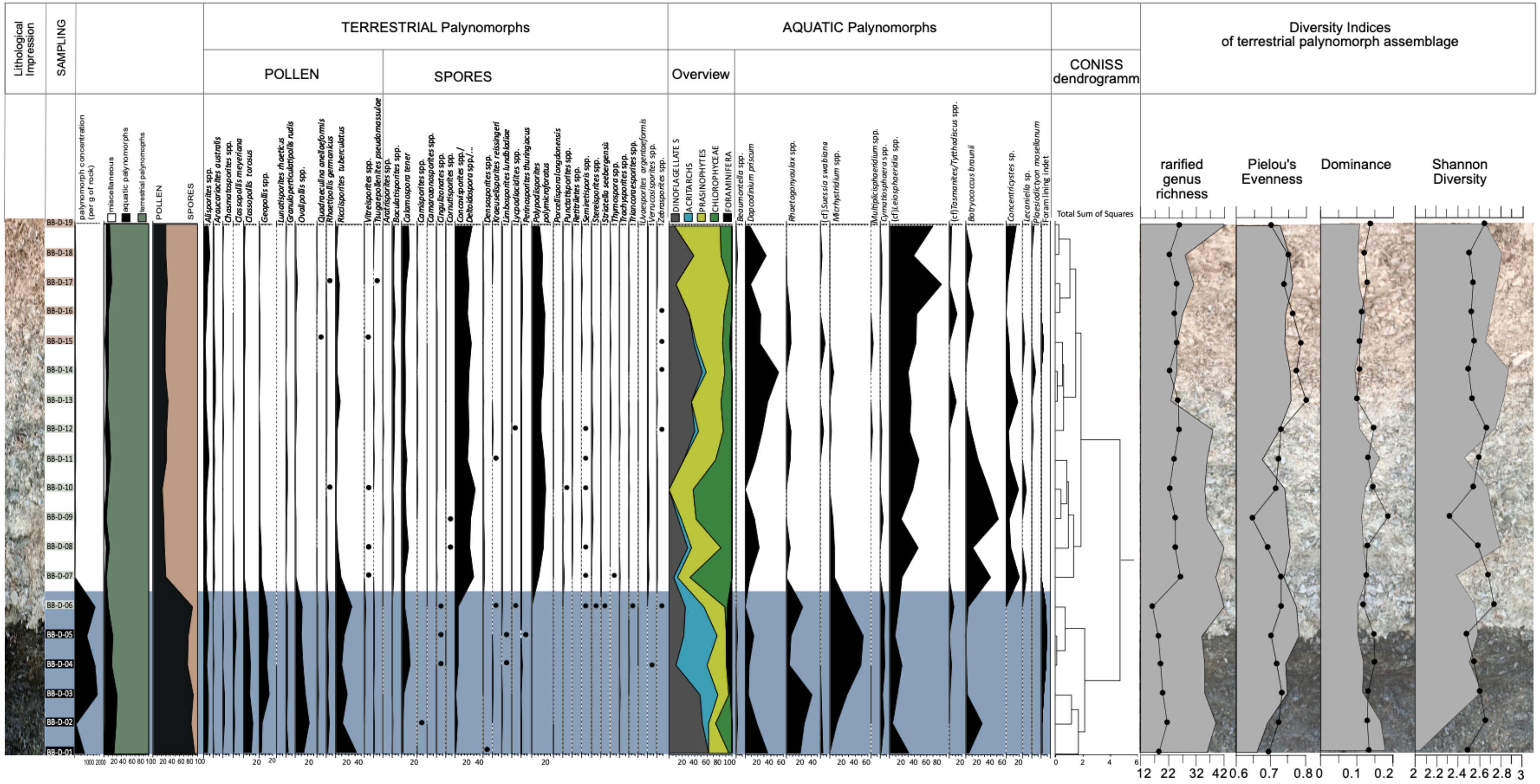


Supplementary Fig. 1. **Palynofacies and CONISS-Cluster analysis. Palynofacies** zones derived from CONISS-analysis (right; threshold of 3.5 total sum of squares (TSS) for the palynofacies zones). On the left abundances of palynofacies components.

Supplementary Fig. 2 Tyson-Plot from palynofacies analysis for detailed sampling. Origin of Detailed Sampling given on the left with AOM-Palynomorph-Phytoclast Ternary Plots (A-C) after Tyson (1995) on the right. Palynofacies fields refer to: **I**-highly proximal shelf or basin, **II** – marginal dysoxic-anoxic basin, **III**-heterolithic oxic shelf (‘proximal shelf’), **IV**-shelf to basin transition, **V**-mud-dominated oxic shelf (‘distal shelf’), **VI**-proximal suboxic-anoxic shelf, **VII**-distal dysoxic-anoxic ‘shelf’, **VIII**-distal dysoxic-oxic shelf, **IX**-distal suboxic-anoxic basin.

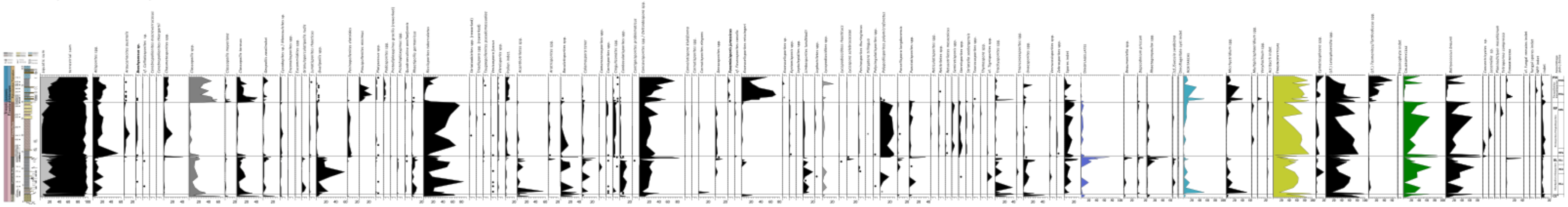

Lithology & Sampling
Abundances of palynofacies components (in %)
Abundances of selected palynomorphs of overall palynofacies count (in %)
Abundances of phytoclasts of overall palynofacies count (in %)
Facies Zones
CONISS - Dendrogramm
Clay-rich mudstone
Silt-rich mudstone
Sandstone
Dolomitic marlstone
Calcareous marlstone
Limestone
Plesiosaur
Bonebed
Bivalves
Brachiopods
Ammonites
Plant debris
Period
Stage
Formation
Sampling
Depth
Lithology
Fossils
Triassic
Jurassic
Rhaetian
Hettangian
Psilonotenton Formation
Triletes Beds
Contorta Beds
Postera
m
40
35
30
25
20
15
10
5
0
Clay
Silt
vfS
fS
Resin
AOM
Palynomorphs
Translucent Phytoclasts
Opaque Phytoclasts
Spores
Pollen
Acritarchs
Dinoflagellate cysts
Prasinophytes
Botryococcus
Cuticles
Plant tissue
Tracheids/Wood
Translucent Phytoclasts (without definite biostructure)
Opaque Phytoclasts (without definite biostructure)
% 20 40 60 80 100
% 20 40
10
20
% 20 40
20
% 20 40 60 80 100
F7 (⬟)
F6 (✱)
F5 (●)
F4 (✱)
F3 (▲)
F2 (✱)
F1 (◆)
CONISS
2 4 6 8
Total sum of squares

Supplementary Figure 3. Detailed palynology and diversity patterns along the transition from the Contorta to the Triletes Beds. Summarized results for the detailed sampling from the Contorta to the Triletes Beds: selected terrestrial and aquatic palynology, CONISS-Dendrogram and diversity indices: genus richness in grey; rarified genus richness (rarS) as dotted line. Other diversity patterns (Pielou's Evenness, Dominance and Shannon Diversity) are given for palynomorph clusters (e.g. tetrads) counted as individuals (i.e. 4) in grey, and counted as items (i.e. 1) in a dotted line. Palynomorph concentrations and pollen and spore ratio is given on the left. Marine ingression as identified through. Palynofacies analysis is indicated in blue.


Lithological Impression
SAMPLING
TERRESTRIAL Palynomorphs
POLLEN
SPORES
AQUATIC Palynomorphs
Overview
CONISS dendrogramm
Diversity Indices of terrestrial palynomorph assemblage
palynomorph concentration (per g of rock)
☐ miscellaneous
■ aquatic palynomorphs
🟩 terrestrial palynomorphs
POLLEN
SPORES
Alisporites spp.
Araucariacites australis
Chasmatosporites spp.
Classopollis meyeriana
Classopollis torosus
Geopollis spp.
Lunatisporites rhaeticus
Granuloperticulatipollis rudis
Ovalipollis spp.
Quadraeculina anellaeformis
Rhaetipollis germanicus
Ricciisporites tuberculatus
Vitreisporites spp.
Tsugaepollenites pseudomassulae
Aratrisporites spp.
Baculatisporites spp.
Calamospora tener
Camisporites spp.
Camarozonosporites spp.
Cingulizonates spp.
Cornutisporites spp.
Concavisporites spp./
Deltoidospora spp./...
Densosporites spp.
Kraeuselisporites reissingeri
Limbosporites lundbladiae
Lycopodiacidites spp.
Perinosporites thuringiacus
Polypodiisporites polymicroforatus
Porcellispora longdonensis
Punctatisporites spp.
Retitriletes spp.
Semiretisporis spp.
Stereisporites spp.
Striatella seebergensis
Thymospora spp.
Trachysporites spp.
Triancoraesporites spp.
Uvaesporites argentaeformis
Verrucosisporites spp.
Zebrasporites spp.
■ DINOFLAGELLATE S
■ ACRITARCHS
■ PRASINOPHYTES
■ CHLOROPHYCEAE
■ FORAMINIFERA
Beaumontella spp.
Dapcodinium priscum
Rhaetogonyaulax spp.
(cf) Suessia swabiana
Micrhystridium spp.
Multiplicisphaeridium spp.
Cymatiosphaera spp.
(cf) Leiosphaeridia spp.
(cf) Tasmanites/Tytthodiscus spp.
Botryococcus braunii
Concentricystes sp.
Lecaniella sp.
Plaesiodictyon mosellanum
Foram lining indet
Total Sum of Squares
rarified genus richness
Pielou's Evenness
Dominance
Shannon Diversity
BB-D-19
BB-D-18
BB-D-17
BB-D-16
BB-D-15
BB-D-14
BB-D-13
BB-D-12
BB-D-11
BB-D-10
BB-D-09
BB-D-08
BB-D-07
BB-D-06
BB-D-05
BB-D-04
BB-D-03
BB-D-02
BB-D-01
1000 2000
20 40 60 80 100
20 40 60 80 100
20
20
20
20 40
20
20 40
20
20 40 60 80 100
20 40 60
20 40
20 40 60
20 40 60 80
20
20 40 60
20
0 2 4 6
12 22 32 42
0.6 0.7 0.8
0 0.1 0.2
2 2.2 2.4 2.6 2.8 3

Supplementary Figure 4. Terrestrial Palynology for the spore and pollen assemblage. All abundances from palynological analysis for the spore and pollen assemblage, i.e. pollen as well as spores amounting to 100% each. Grey or coloured abundances indicate sums of taxa that follow the coloured columns.

Bonenburg
100% spores/ 100% pollen



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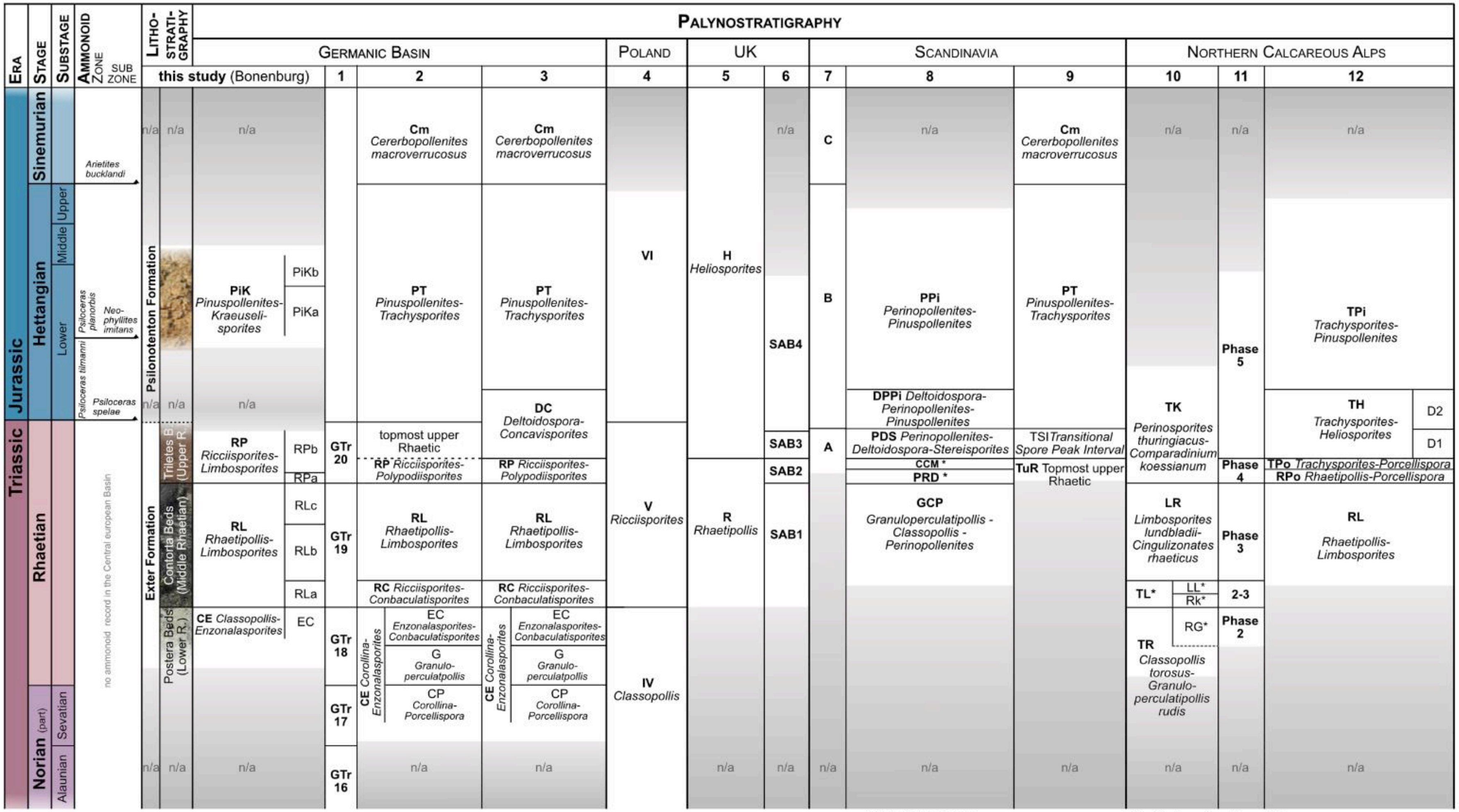
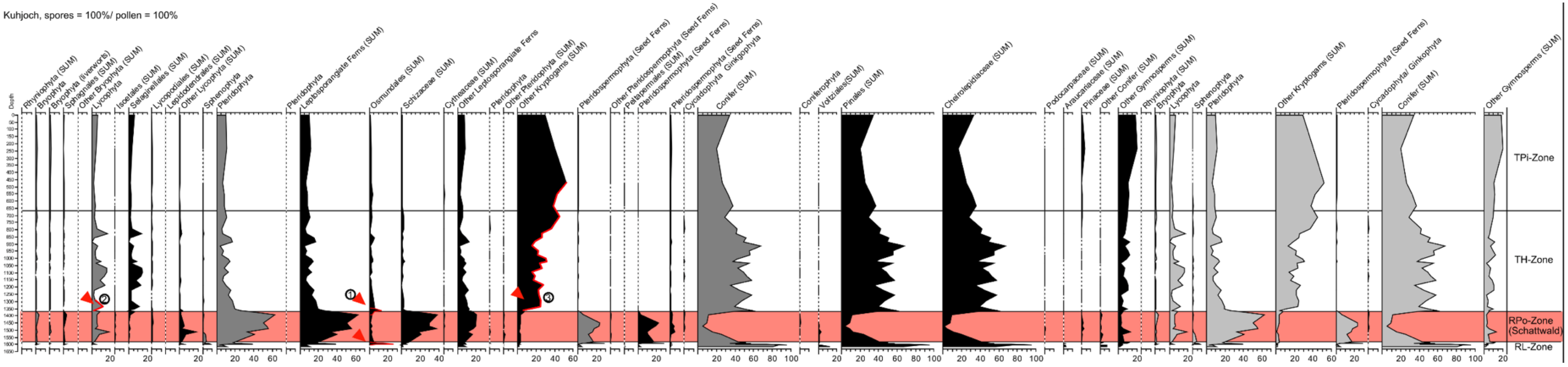
Supplementary Figure 5. Correlation of palynostratigraphy. Correlation of the informal palynostratigraphic zonations from the Bonenburg section with other preciously published palynostratigraphy, formal as well as informal zones alike. Bonenburg's palynostratigraphy is correlated based on palynostratigraphy with other sections from the Germanic Basin. Correlations beyond that is altered after Barth et al. (2018) with minor additions of four older zonation schemes (4, 5, 10 and 11). References are given for the numbered sections: **1.** Heunisch (1999), **2.** Lund (1977) **3.** Barth et al. (2018) **4.** Orłowska-Zwolińska (1983) **5.** Orbell (1973) **6.** Bonis et al. (2010) **7.** Dybkjær (1988) **8.** Lindström (2016) **9.** Larsson (2009) **10.** Morbey (1975) **11.** Schuurman (1979) **12.** Bonis et al. (2009); Hillebrandt et al. (2013); Kürschner et al. (2007).



***CCM** *Calamospora-Conbaculatisporites Monosulcites*
***PRD** *Polypodiisporites-Ricciisporites-Deltodiospora*

***TL** *Ricciisporites tuberculatus - Hystrichosphaeridium langi*
*RG *Rhaetogonyaulax rhaetica-Rhaetipollis germanicus*
*Rk *Rhombodella kendelbachia*
*LL *Carnisporites lecithus - Zebrasporites laevigatus*

Supplementary Figure 6. Kuhjoch's vegetation patterns inferred from botanical affinities for the spore and pollen assemblage. All abundances from palynological analysis for the spore and pollen assemblage, i.e. pollen as well as spores amounting to 100% each. Successional peak abundances of lycophytes (1), Osmundales (2) and other kryptogams (especially *Trachysporites* spp.) are given with numbers. The RPo-Zone/Schattwald Beds are indicated in red.


Kuhjoch, spores = 100%/ pollen = 100%
Depth
Rhyniophyta (SUM)
Bryophyta
Bryophyta (liverworts)
Sphagnales (SUM)
Other Bryophyta (SUM)
Lycophyta
Isoetales (SUM)
Selaginellales (SUM)
Lycopodiales (SUM)
Lepidodendrales (SUM)
Other Lycophyta (SUM)
Sphenophyta
Pteridophyta
Pteridophyta
Leptosporangiate Ferns (SUM)
Osmundales (SUM)
Schizaceae (SUM)
Cytheaceae (SUM)
Other Leptosporangiate Ferns
Pteridophyta
Other Pteridophyta (SUM)
Other Kryptogams (SUM)
Pteridospermophyta (Seed Ferns)
Other Pteridospermophyta (Seed Ferns)
Peltapermales (SUM)
Pteridospermophyta (Seed Ferns)
Pteridospermophyta (Seed Ferns)
Cycadophyta Ginkgophyta
Conifer (SUM)
Coniferophyta
Voltziales(SUM)
Pinales (SUM)
Cheirolepidiaceae (SUM)
Podocarpaceae (SUM)
Araucariaceae (SUM)
Pinaceae (SUM)
Other Conifer (SUM)
Other Gymnosperms (SUM)
Rhyniophyta (SUM)
Bryophyta
Lycophyta
Sphenophyta
Pteridophyta
Other Kryptogams (SUM)
Pteridospermophyta (Seed Ferns)
Cycadophyta/ Ginkophyta
Conifer (SUM)
Other Gymnosperms (SUM)
TPi-Zone
TH-Zone
RPo-Zone (Schattwald)
RL-Zone
①
②
③
20 40 60 80 100

I.ii. Supplementary Tables

Supplementary Table 1. Data table for correlations between diversity indices and relative pollen content. Spearman's rank correlation coefficient (rho) is given for non-normal distributed data and Pearson correlation coefficient (r) for normal distributed data.

	correlation	p-value
Genus richness ~ relative pollen content in palynofacies	**rho = - 0.4726925**	**0.0010**
Pielou’s evenness ~ relative pollen content in palynofacies	rho = - 0.1629225	0.2849
Shannon Diversity ~ relative pollen content in palynofacies	**r = - 0.4126954**	**0.0048**

Supplementary Table 2. Taxon names with author citation and botanical affinities. See next pages

Table 1. Taxa identified in Bonenburg in qualitative and quantitative analysis. For each taxon author citations, figure reference, and literature references for botanical affinities as used for vegetation reconstruction are given. Within each major group (e.g. spores, pollen, …) taxa are sorted alphabetically.

Taxon	Author	Fig.	General Affinity	(Sub)-Phylum	(Sub-)Class/ informal	Order	Family	References * known from *in situ* from the Triassic or Jurassic in NW Europe **known from *in situ* from the Upper Triassic/Jurassic in NW Europe
SPORES								
Acanthotriletes varius	(Nilsson 1958) Schuurmann 1971	6.9	Ferns	Pteridophyta	'leptosporangiate' ferns	Filicales	Botryopteraceae	Balme (1995), Taylor et al. (2009)
Annulispora folliculosa	(Rogalska 1954) de Jersey 1959	7.2	Moss	Bryophyta	Sphagnopsida	Sphagnales	/	Koppelhus (1991)
Annulispora sp. B	Manum 1977	7.8						
Aratrisporites sp.	(Leschik 1955) emend. Playford & Dettmann 1965		Clubmosses	Lycophyta	Lycopodiopsida	Isoetales	/	* *in situ* finds were reported in *Cyclostrobus* and *Lycostrobus* by Helby and Martin (1965), and in *Annalepis zeilleri* by Grauvogel-Stamm and Duringer (1983), which is now known as *Lepacyclotes* (Kustatscher et al., 2015); see also Taylor et al. (2009)
Aratrisporites crassitectatus	Reinhardt 1964							
Aratrisporites minimus	Schulz 1967	9.3						
Aratrisporites palettae	(Klaus 1960) Schulz 1967							
Aratrisporites scabratus	(Klaus 1960) Bharadwaj & Singh 1963	8.3						
Baculatisporites spp.	Thomson & Pflug 1953		Ferns	Pteridophyta	'leptosporangiate' ferns	Osmundales	Osmundaceae	this type of spores are found *in situ* in *Todites hartzii* and *Osmundopsis plectophora*, both of which belong to the Osmundaceae (Pedersen and Lund, 1980; van Konijnenburg-van Cittert, 2000)
Baculatisporites comaumensis	(Cookson 1953) Potonie 1956	6.4						
Osmundacidites (Baculatisporites) wellmanii	(Couper 1953) Krutzsch 1959							
Calamospora spp.	Schopf, Wilson & Bentall 1944		horsetails	Sphenophyta	Polypodiopsida	Equisetales	Equisetaceae	***in situ* in *Equisetites arenaceus* (Kelber and Van Konijnenburg-van Cittert, 1998)
Calamaspora tener	(Leschik 1955) Mädler 1964	6.1						
Camarozonosporites sp.	Pant 1954 ex Potonie 1965		Clubmosses	Lycophyta	Lycopodiopsida	Lycopodiales	Lycopodiaceae	Schulz (1967), similarity to extant species, not found *in situ* yet.
Camarazonosporites rudis	(Leschik 1955) Klaus 1960							
Camarozonosporites cf. *golzowensis*	Schulz 1967							

Camarazonosporites laevigatus	Schulz 1967	7.9						
Carnisporites spp.	Mädler 1964		Clubmosses	Lycophyta	Lycopodiopsida	/	/	*in situ* in the Carboniferous *Carinosstrobus* (USA), Balme (1995)
Carnisporites anteriscus	Morbey 1975	7.10						
Carnisporites spiniger	(Leschik 1955) Morbey 1975							
Cingulizonates spp.	(Dybova & Jachowicz 1957) Butterworth, Jansonius, Smith & Staplin 1964		Clubmosses	Lycophyta	Lycopodiopsida	Selaginellales	/	*In situ* in Carboniferous lycopsid cone *Sporangiostrobus* which contains triradiate, flanged megaspores and a range of microspores that includes dispersed taxa such as *Densosporites* and *Cingulizonates* (Taylor et al., 2009)
Cingulizonates rhaeticus	(Reinhardt 1961) Schulz 1967	7.33						
Clathroidites papulosus	Bai in Bai et al. 1983	6.8	NA	/	/	/	/	/
Conbaculatisporites sp.	Klaus 1960		Ferns	Pteridophyta	'leptosporangiate' ferns	Osmundales	? Osmundaceae	The strong similarity with *Baculatisporites* sp. suggests a similar affinity as some authors have assumed (Bonis, 2010). Even though Pederson and Lund (1980) report an *in situ* find of spores that comply with the circumscription of *Conbaculatisporites mesozoicus* in *Clathopteris mesicoides* this is based on Harris' (1931) publication with illustrations of rather poor quality which might confound a such small distinction. In view of intraspecific variety within a single sporangium in extant plants, the first suggestion is followed here.
Conbaculatisporites mesozoicus	Klaus 1960							
Convolutispora klukiforme	(Nilsson 1958) Schulz 1967	7.28	Ferns	Pteridophyta	‚eusporangiate' ferns	Marratiales	/	Balme (1995)
Cornutisporites spp.	Schulz 1962		Ferns	Pteridophyta	'leptosporangiate' ferns	Filicales	/	Schulz (1967), similarity to extant species, not found *in situ* yet.
Cornutisporites seebergensis	Schulz 1962	7.20						
Cornutisporites rugulatus	Schulz 1967							
Cosmosporites elegans	(Nilsson 1958) Achilles	7.14	NA	/	/	/	/	/
Deltoidospora spp.	Miner 1935	6.2	Ferns	Pteridophyta	'leptosporangiate' ferns	Filicales	Dipteridac., Matoniac. Gleicheniacea. Dicksoniac./ Cyatheac. Schizeac.	(**)This morphotaxon has been found *in situ* a number of different fossils assigned to different families: from Triassic/Jurassic *Dictyophyllum exile* (Braun) Nathorst 1978 (Triassic, Dipteraceae), *Gleicheniopsis suifunensis* Krassilov 1966 (Cretaceous, Gleicheniaceae), *Hausmannia forchammeri* Bartholin 1892 (Cretaceous, Gleicheniaceae) *Thaumatopteris brauniana* Popp 1863 (Triassic/Jurassic, Dipteraceae), and *Thaumatopteris schenkii* Nathorst 1878 (Triassic/Jurassic,

								Dipteraceae), *Delosorus heterophyllus* (Fontaine) Skog 1988 (Cretaceous, Matoniaceae), *Nathorstia alata* Halle 1913 (Cretaceous, Matoniaceae), and *Phlebopteris affinis* Schenk 1867 (Jurassic, Matoniaceae). Additionally, the spores were found most fossil tree ferns from the genera *Coniopteris*, *Dicksonia*, *Cycadocephalus*, *Onychiopsis*, *Gonatosorus*, Eboracia (Dicksoniaceae) and the *Alsophilites* and *Cyathea* (Cyatheaceae). see Balme (1995) and citations therein. Furthermore, this morphotaxon was found in *Paralygodium* (Schizeaceae) from the Upper Cretaceous and Eocene (Taylor et al., 2009) It is striking, that this taxon seem characteristic for tree ferns, but given its occurrence in other fern families as well makes a single assignment more difficult, wherefore this group is included in the group ‘ other leptosporangiate’ ferns groups in this paper.
Dictyophillidites mortonii	(De Jersey 1959) Playford & Dettmann 1965	6.3	Ferns	Pteridophyta	'lepto-sporangiate' ferns	Filicales ? Botry-opteridales	Dipteridac., Matoniac.	(**)Similar to *Deltoidospora* spp., spores assignable to the genus *Dictyophyllidites* were found *in situ* in a number of different fern families: *Clathropteris obovata* Turutanova-Ketova 1950 (Jurassic, Dipteraceae), *Dictyophyllum muensteri* (Göppert) Nathorst, 1878 (Triassic, Dipteraceae), *Dictyophyllum* nilssonii (Bronginiart) Göppert 1846 (Jurassic, Dipteraceae), *Dictyophyllum rugosum* Lindeley et Hutton 1834 (Jurassic, Dipteraceae). Matoniaceae in general are characterized by spores conforming by this morphotaxon occuring in *Matonia*, *Matonidium*, *Nathorstia*, *Phlebopteris*, *Piazopteris*, *Selenocarpus*. See Balme (1995) and references therein. Additionally, Balme (1995) reports some more scattered and more doubtful occurrences in Botryopteridales (*Donegia complura* Rothwell, 1978, Carboniferous; *Grambastia goldenbergii* (Andrae) Brousmiche 1978, Carboniferous; *Sermaya biseriata* Eggert et Delevoryas 1967, Carboniferous). As for Deltoidospora spp. the assignation is not so straight forward, wherefore these spores are also included in the ‘other leptosporangiate’ ferns group.
Concavisporites spp.	Pflug 1953		Ferns	Pteridophyta	'lepto-sporangiate' ferns	Filicales	/	Taxonomic and nomenclatorial distinction of *Concavisporites* spp. is not trivial. Some authors use *Deltoidospora* spp. for laevigate trilete spores without and *Concavisporites* spp. for those with thickenings, while other use *Matonisporites* vs. *Dictyophyllidites* (see discussion in van Konijnenburg-van Cittert (1993) and citations therein). All of them could have Matoniaceae as potential mother plants (see previous *in situ* occurrences for *Deltoidospora* and *Dictyophyllidites*). A taxonomic

								decision is not made here and thus spores are summarized as a *Deltoidospora*/*Concavisporites*/*Dictyophyllidites* complex and are assigned to 'other leptosporangiate' ferns as a whole, due to current lack of further unambiguous distinction.
Densosporites spp.	(Berry 1937) Potonie & Kremp 1954		Clubmosses	Lycophyta	Lycopodiopsida	Selaginellales	/	*In situ* in Carboniferous lycopsid cone *Sporangiostrobus* which contains triradiate, flanged megaspores and a range of microspores that includes dispersed taxa such as *Densosporites* and *Cingulizonates* (Taylor et al., 2009)
Densosporites fissus	(Reinhardt 1964) Schulz 1967	7.32	Clubmosses	Lycophyta	Lycopodiopsida	Selaginellales	/	see previous
Foraminisporis jurassicus	Schulz 1967	9.1	Hornworts	Anthocerophyta	/	/	/	Schulz (1967)
Gordonispora sp.	Van der Eem 1983		Moss	Bryophyta	Sphagnopsida	Sphagnales	/	Since *Gordonispora* is distinguishable only by minute differences with overall very similar characteristics to *Annulispora* (van der Eem, 1983), the same affinity is assumed as for the latter, see reference there
Kyrtomisporis sp.	Mädler 1964b emend. Van der Eem 1983		Ferns	Pteridophyta	/	/	/	Bonis (2010)
Kyrtomisporis gracilis	Bjaerke & Manum 1977	7.22						
Kyrtomisporites laevigatus	Mädler 1964b	7.21						
Kyrtomisporis speciosus	Mädler 1964b	7.23						
Kraeuselisporites sp.	(Leschik 1955) Scheuring 1974	7.34	Clubmosses	Lycophyta	Lycopodiopsida	Lycopodiales	/	Bonis (2010); Kustatscher et al., (2012)
Kraueselisporites reissingeri	(Harris 1957) emend. Morbey 1975	9.2	Clubmosses	Lycophyta	Lycopodiopsida	Selaginellales	/	Originally described as *Lycospora reissingeri* Harris 1957, the name already indicates its lycophytic association supported by *in situ* finds (Balme, 1995; Harris, 1957). The exact morphology of this specimen is very close to *Selaginella selaginoides* (Reissinger, 1950), which lead to its assignation to the Sellaginellales by previous authors (Bonis, 2010; Kustatscher et al., 2012a)
Leptolepidites spp.	(Couper 1953) Schulz 1967		Ferns	Pteridophyta		Polypodiales	/	Filatoff (1975)
Limbosporites sp.	Nilsson 1958	6.13					/	Bonis (2010)
Limbosporites lundbladii	Nilsson 1958	6.11-12	Clubmosses	Lycophyta	Lycopodiopsida	Selaginellales	/	See previous
Lycopodiacidites sp.	Couper 1953 emend. Potonie 1956		Clubmosses /	Lycophyta	Lycopodiopsida	Lycopodiales (/)	/	Most authors (Abbink, 1998; Bonis, 2010; Kustatscher et al., 2010, 2012a) follow the assignation to the Lycopodiales suggested by Filatoff

Lycopodiacidites rhaeticus	Schulz 1967	7.36	(Ferns)	(Pteridophyta)	(/)			(1975), while others follow Balme's assignation to ferns (Balme, 1995; Mander et al., 2010; Paterson et al., 2016). *In situ* finds are still lacking and morphological comparison does not render either possibility more or less likely. Due to only minor occurrences, we did not put too much emphasis on this decision and followed the majority for the sake of comparison, until further evidence is given.
Lycopodiacidites rugulatus	(Couper 1958) Schulz 1967	7.35						
Lycospora salebrosaceae	(Maljavkina 1949) Schulz 1967		Clubmosses	Lycophyta	Lycopodiopsida	Lycopodiales	/	Balme (1995)
Perinosporites thuringiacus	Schulz 1962	7.24	Ferns	Pteridophyta	/	/	/	Schulz (1967) assigns it to the Cyatheaceae based on morphological similarity. This is not supported by *in situ* finds yet. For now, as to the lack of data and other similar references, we do not assign this spore to any particular group.
Platyptera trilingua	(Horst 1943) Schulz 1967	7.16	NA	/	/	/	/	/
Polycingulatisporites sp.	(Simoncsics & Kedves 1961) Morbey 1975		Moss	Bryophyta	Sphagnopsida	Sphagnales	/	Koppelhus (1991)
Polycingulatisporites bicollateralis	(Rogalska 1965) Morbey 1975	7.8						
Polycingulatisporites mooniensis	De Jersey & Paten 1964	7.7						
Polypodiisporites sp.	(Potonié 1934) Potonié 1956		Ferns	Pteridophyta	'leptosporangiate' ferns	Filicales	/	Bonis (2010)
Polypodiisporites polymicroforatus	(Orlowska-Zwolinska 1966) Lund 1977	7.27						
Porcellispora longdonensis	(Clarke 1965) Scheuring 1970 emend. Morbey 1975	7.37	Liverworts	Marchantiophytina	/	/	/	Balme (1995)
Punctatisporites spp.	(Ibrahim 1933) Potonié & Kremp 1954		Ferns	Pteridophyta	'leptosporangiate' ferns	Marrattiales Osmundales	Osmundaceae Gleicheniaceae	*Found *in situ* in Marattiales in *Danaeopsis* (Middle- Upper Triassic in Australia, South America and Europe; Kustatscher et al., 2012b), Osmundaceae (various *Todites* species) and Gleicheniaceae (*Wingatea plumosa* (Daugherty) Litwin 1985 (Triassic)) Balme (1995). Due to a number of potential assignations, this taxon was plotted together with as 'other leptosporangiate' ferns without more detailed assignation.
Reticulatisporites sp.	Ibrahim 1933		Clubmosses	Lycophyta	Lycopodiopsida	/	/	Libertín et al., (2005) document spores of this type from *Kladnostrobus*, a presumably arborescent lycophyte.
Retitriletes spp.	(Pierce 1961) Döring et al. 1963		Liverworts (Clubmosses)	?Marchantiophyta (Lycophyta)	/	/	/	Spores of this type have been found *in situ* in the bryophytic *Trambauathallites sukhpurensis* (Bose et Banerji) Banerji 1989 from the Createaceous in India (Balme 1995) and extant *Fossombronia foveolata* and other marchantiophyta posess almost identical spores. Accordingly
Retitriletes austroclavatidites	(Cookson 1953) Döring et al. 1963	7.26						

								also Schulz (1967) has assumed a bryophytic association while some authors assign this taxon to the Lycopodiales (Abbink et al., 2004) based on (Potonié, 1967).
Retusotriletes sp.	Naumova 1953		Clubmosses	Lycophyta	Zostero-phyllopsida	/	/	Asides the affinity with Rhyniophyta, Balme (1995) describes the spores of Zosterophyllales generally as retusoid, and for seven of the ca. eleven genera (*Discalis*, *Nothia*, *Rebuchia*, *Sawdonia*, *Oricilla*, *Serrulacaulis*, *Zosterophyllum*) from the Devonian around the world are reported to show spores *in situ* that comply with the circumscription of *Retusotriletes*. (Balme 1995)
Retusotriletes mesozoicus	Klaus 1960	7.1						
Rogalskaisporites cicatricosus	(Rogalska 1954) Danzé-Corsin & Laveine 1963	7.4	Moss	Bryophyta	Sphagnopsida	Sphagnales	/	Koppelhus (1991), Schulz 1967, Filatoff (1975)
Semiretisporis sp.	Reinhardt 1962		NA	?Marchantio-phyta (?Lycophyta)	/	/	/	Schulz (1967) tentatively assigned this taxon to the Bryophytes and some authors assign similar spores from the Carboniferous (*Sagenotetradites*) to liverworts (Satterthwait and Playford, 1986), while others have tentatively assigned them to lycophytes, which can also show similar ornamentation (Paterson et al., 2016). Others have refrained from further assignation (Bonis, 2010), which is followed here, due to opposing possibilities of two major groups
Semiretisporis gothae	Reinhardt 1962	8.2						
Semiretisporis maljavkiniae	Schulz 1967	8.1						
Stereisporites spp.	Pflug 1953		Moss	Bryophyta	Sphagnopsida	Sphagnales	/	Koppelhus (1991), Schulz 1967, Filatoff (1975)
Stereisporites hauterivensis	Döring 1966	7.5						
Stereisporites radiatus	Schulz 1963	7.3						
Striatella sp.	Mädler 1964		Ferns	Pteridophyta	'lepto-sporangiate' ferns	Polypodiales	Polypodia-ceae	The given affinity is assumed based on morphology by Balme (1995), Filatoff (1975), Filatoff and Price (1988), Schulz (1967) and is followed here, especially in view of very similar spore morphology of extant *Pteris*.
Striatella parva	(Li & Shang) Filatoff and Price, 1988							
Striatella seebergensis	Mädler 1964	7.13						
Striatella jurassica	Mädler 1964							
Taurocusporites spp.	Stover 1962		NA	/	/	/	/	/
Thymospora sp.	Wilson & Venkatachala 1963		Ferns	Pteridophyta	Eu-sporangiate ferns	Marratiales	/	*In situ* finds were reported by Balme (1995) *from Pecopteris hemiteloides* Brongiart 1833 (Carboniferous, France), *Scoleopteris vallumii* Millay 1979 (Carboniferous, USA) both of which belong to the Marratiales.
Thymospora canaliculata	Schuurman 1977	7.29						
Thymospora ipsviciensis	(De Jersey 1962) Jain 1965	8.30						Spores complying with this taxon were found in *Asansolia phegopteroides* (Feistmantel) Pant et Misra 1976 (Marratiales, Permian in India) (Balme, 1995).
Tigrisporites spp.	Klaus 1960		Clubmosses	Lycophyta		Lycopodiales	/	Schulz (1967), Bonis (2010)
Trachysporites spp.	Nilsson 1958		Ferns	Pteridophyt		/	/	Bonis (2010)
Trachysporites asper	Nilsson 1958	6.6						

Trachysporites fuscus	Nilsson 1958	6.7			'lepto-sporangiate' ferns			
Triancoraesporites spp.	Schulz 1962		Clubmosses	Lycophyta	Lycopsida	Lycopodiales	/	Schulz (1967), Bonis (2010)
Triancoraesporites anchorae	(Reinhardt 1962) Schulz 1967	7.19						
Triancoraesporites reticulatus	Schulz 1962	7.18						
Tripartites cristatus	(Horst 1956) Dybová & Jachowicz 1957	7.17	NA-reworked					/
Triquitrites pulvinatus	Kosanke 1950	7.15	NA-reworked					/
Uvaesporites sp.	Döring 1965		Clubmosses	Lycophyta	Lycopsida	Selaginellales	/	**Spores very similar to the circumscription of this taxon were found in *Selaginellites hallei* Lundblad 1950 from the Triassic/Jurassic in Sweden (Balme 1995).
Uvaesporites argentaeformae	(Bolchovitina 1953) Schulz 1967	6.10						
Verrucosisporites sp.	(Ibrahim 1933) Smith 1971		NA	Lycophytes Ferns Gymno-sperms	Lycopsida Filicopsida Cycadopsida	Isoetales Botryopteri. Zygopterid. Marattiales Lagenoostom. Trigonocarp.	/	Balme (1995) reports *in situ* finds of spores AND pollen that comply with the rough circumscription of *Verrucosisporites*. Due to very unclear and many potential affinities the taxon is not further assigned here.
Zebrasporites sp.	Klaus 1960 emend. Schulz 1967		Ferns	Pteridophyta	'leptosporangiate' ferns	Filicales	/	Schulz (1967), Bonis (2010)
Zebrasporites interscriptus	(Thiergarth 1949) Klaus 1960	7.11						
Zebrasporites laevigatus	(Schulz 1962) Schulz 1967	7.9						
POLLEN								
Alisporites sp.	(Daugherty 1941) Jansonius 1971		Gymno-sperms	Pteridospermatophyta (Seed Ferns), Spermato-phyta	Coniferopsida	Corysto-spermales Coniferales	/	Found *in situ* in seed ferns and Voltziales (Balme, 1995; Taylor et al., 2009) and since many studies assign them to seed ferns (Abbink, 1998; Bonis, 2010; Mander et al., 2013) in their subsequent analyses, this assignation is followed here. Especially as this allows distinction of this taxon within the botanical affinities since it is the domineering one in the seed fern. This facilitates potential reinterpretation of the presented data, when considering both options.
Alisporites aequalis	Nilsson 1958							
Alisporites diaphanus	(Pautsch 1958) Lund 1977							
Alisporites radialis	(Leschik 1955) Lund 1977	9.17						
Alisporites robustus	Nilsson 1958	6.25						
Araucariacites australis	Cookson 1947	8.6	Gymno-sperms	Spermato-phyta	Coniferopsida	Araucariales	Araucaria-ceae	Pollen of this type were found *in situ* in a number of araucariaceous fossils: *Agathis yallournensis* Cookson et Duigan 1951, *Araucaria lignitica* Cookson et Duigan 1951 (Oligocene), in a number of

								Brachyphyllum species (Jurassic-Cretaceous), *Dammarites coriaceae* Barale 1992 (Cretaceous), and a number of *Masculostrobus* species (Jurassic) (Balme 1995 and citations therein). This is supported by ultrastructural similarities with extant pollen from the Araucariaceae (Batten and Dutta, 1997).
Brachysaccus sp.	Mädler 1964		Gymnosperms	Spermatophyta	Cycadopsida	?Cycadales	/	Paterson et al. (2016)
Callialasporites sp.	(Balme 1957) Dev 1959		Gymnosperms	Spermatophyta	Coniferopsida	Araucarialesc	Araucariaceae	Pollen of this taxon is found in male cones that show pollen that resemble both *Araucariacites* and *Callialasporites* (e.g. *Brachyphyllum*, *Masculostrobus* from the Jurassic – Cretaceous around the world) (Balme 1995 and references therein). The ultrastructural similarity with *Araucaricites* and extant araucariaceous pollen further supports this assignation (Batten and Dutta, 1997).
Callialasporites cf. *trilobatus*	(Balme 1957) Dev 1959	9.15						Pollen complying with this taxon were found *in situ* (together with pollen that comply with the description of *Araucariacites*) in *Brachiophyllum lorchii* Raab, Horowitz et Conway 1986 (Jurassic, Israel) and in *Apterocladus lanceolatus* Archangelski 1966 (Cretaceous, Argentina) together with *Callialasporites dampieri* (Balme 1995).
Callialasporites dampieri	(Balme 1957) Dev 1959							Apart of *Apterocladus lanceolatus* it is found *in situ* in *Brachyphyllum mamillare* Brongniart ex Lindley et Hutton 1836 (Jurassic, England) (Balme 1995).
Cerebropollenites sp.	Nilsson 1958		Gymnosperms	Spermatophyta	Coniferopsida	Coniferales	/	There is a long standing discussion as to affinity of this taxon, and morphological studies suggest an affinity with *Sciadopitys* and ultrastructural studies reveal strong similarity with *Tsuga* (Batten and Dutta, 1997). For the purpose of this study a mere affinity to Coniferales was assumed.
Cerebropollenites macroverrucosus	(Thiergarth 1949) Schulz 1967	9.14						
Cerebropollenites thiergartii	Schulz 1967	9.7 9.13						
Chasmatosporites spp.	(Nilsson 1958) Pocock & Jansonius 1961		Gymnosperms	Spermatophyta	Cycadopsida Ginkgopsida	Cycadales Ginkgoales Gnetales	/	(*)Pollen complying with this taxon were found *in situ* in *Androstrobus* (Cycadales), but an affinity with Ginkgoales and Gnetales is also put forward (Balme 1995) as a result of morphological similarity with extant Ginkgo pollen (especially *Chasmatosporites apertus*) which would also be possible in view of ultrastructural similarities (Batten and Dutta, 1997). For now, a more precise association remains unresolved. For the purpose of this study the three groups are plotted as one category Cycadales/Ginkgoales/Gnetales.
Chasmatosporites apertus	(Rogalska 1954) Nilsson 1958	9.9						
Chasmatosporites elegans	Nilsson 1958	9.11						
Chasmatosporites hians	Nilsson 1958	9.10						
Chasmatosporites major	(Nilsson 1958) Pocock & Jansonius 1961	9.12						
Cycadopites sp.	Wodehouse 1933	9.8	Gymnosperms	Spermatophyta	Cycadopsida Ginkgopsida	Cycadales Bennettitales Gnetales	/	This taxon was found *in situ* amongst many different plant

						Ginkgoales ?Peltasper.		groups (see a vast number of references and discussion in Balme (1995) and Taylor et al. (2009)). For the purpose of this study they were plotted as one category: Cycadales/Ginkgoales/Gnetales.
Monosulcites minimus	Cookson 1947		Gymnosperms	Pteridospermophyta Spermatophyta	Cycadopsida Ginkgopsida	Peltaspermal. Cycadales Bennettitales	/	**Pollen resembling this taxon were found *in situ* in the micropylar tube of the ovular structure *Vardekloeftia sulcata* Harris 1932 (Bennettitales) from the Upper Triassic from Greenland (see Balme 1995 and references therein). One should note however, that the distinction with *Cycadopitys* is not trivial, wherefore, for the purpose of this study they were plotted as one category: Cycadales/Ginkgoales/Gnetales.
Classopollis sp.	(Pflug 1953) Pocock & Jansonius 1961	9.6, 9.18, 9.19	Gymnosperms	Spermatophyta	Coniferopsida	Coniferales	Cheirolepidiaceae	**Being very distinct and well-studied, there is a well-established association with the Cheirolepidiaceae based on many *in situ* finds e.g. from *Brachyphyllum*, *Classostrobus*, *Frenelopsis*, *Hirmeriella* and others ranging from the TJ-boundary till the Cretaceous from around the world with many finds originating from England and Germany (see further discussion in e.g. Alvin, 1982; Balme, 1995; Taylor et al., 2009; Watson, 1988).
Classopollis meyeriana	(Klaus 1960) Venkatachala & Goczan 1964	6.17, 13.4, 13.8, 13.12, 13.16						
Classopollis torosus	(Reissinger) Klaus 1960, emend. Cornet & Traverse	6.18; 8.4; 9.4; 13.5, 13.9-10,13,17						
Enzonalasporites sp.	(Leschik 1955) Schulz 1967		Gymnosperms	Spermatophyta	Coniferopsida	Voltziales	/	Due to the morphological resemblance to *Patinasporites* (Balme, 1995; Lindström et al., 2016) assigned to the same plant group. Read further in *Patinasporites*.
Enzonalasporites vigens	Leschik 1955	6.14						
Geopollis zwolinskae	(Lund 1977) Brenner 1986	6.16	Gymnosperms	Spermatophyta	Coniferopsida	Coniferales	Cheirolepidiaceae	Mander et al. (2013)
Granuloperculatipollis rudis	(Venkatachala & Góczán 1964) Scheuring 1978	6.15	Gymnosperms	Spermatophyta	Coniferopsida	Coniferales	Cheirolepidiaceae	Schulz (1967) and see comment in *Classopollis* sp.
Lagenella sp.	(Maljavkina 1949) Klaus 1960		Gymnosperms	Spermatophyta	Gentopsida	Gnetales	/	Lindström et al. (2016)
Lagenella martinii	(Leschik 1955) Klaus 1960							
Lunatisporites sp.	Leschik 1955 emend. Scheuring 1970		Gymnosperms	Pteridospermatophyta (Seed Ferns) Coniferophyta	/	Peltasperm.	/	Looy et al. (2001)
Lunatisporites rhaeticus	(Schulz 1967) Warrington 1974	6.21						

Ovalipollis sp.	Krutzsch 1955	6.22	Gymno-sperms	Spermato-phyta	Coniferopsida	Voltziales	/	*Grauvogel-Stamm and Grauvogel (1975) found microspores in a male cone of *Voltzia* sp., which looks very similar to *Illinites*. Likewise, Balme (1995) found spores similar to *Illinites* in another conifer cone of *Aethophyllum stipulare* in the Upper Bunter (Triassic) of France. Due to the morphological similarity between *Ovalipollis* and *Illinites* Scheuring (1970) argues in favor of *Ovalipollis* being of coniferous origin.
Patinasporites sp.	(Leschik 1955) Klaus 1960		Gymno-sperms	Spermato-phyta	Coniferopsida	Voltziales	/	Patinasporites was found *in situ* in the voltzialean *Glyptolepis* sp. (Balme 1995 and citation therein). The family assignation is a bit problematic (see discussion in Taylor et al., 2009) and is thus not assigned here.
Perinopollenites elatoides	Couper 1958	8.16	Gymno-sperms	Spermato-phyta	Coniferopsida	Coniferales	Cupressa-ceae	*Pollen complying with this taxon were found *in situ* in a number of species of *Elatides*, *Masculostrobus*, *Stenomischus* (Jurassic -Createcous from around the world), all assigned to the Taxodiaceae, i.e. today the Cupressaceae that include that former family (Balme 1995 and citations therein).
Pinuspollenites minimus	(Couper 1958) Kemp 1970	9.16	Gymno-sperms	Coniferophyta		Pinales	Pinaceae	Balme (1995), Bonis (2010)
Platysaccus spp.	Naumova 1937		Gymno-sperms	Pteridosperm atophyta (Seed Ferns)	/	Corysto-spermales	/	Traverse (2007), Zavattieri et al. (2018)
Platysaccus papilionis	Potonié & Klaus 1954	8.9						
Podosporites sp.	Rao 1943	9.18	Gymno-sperms	Spermato-phyta	Coniferopsida	Coniferales	Podocarpa-ceae	Balme (1995), Olivera et al. (2015)
Podosporites amicus	Scheuring 1970							
Protodiploxpinus gracilis	Scheuring 1970	8.11	Gymno-sperms	Spermato-phyta	Coniferopsida	Coniferales	/	Balme (1955), Taylor et al (2009), Zavattieri et al. (2018)
Protohaploxypinus spp.	Samoilovich 1953 emend. Morbey 1975		Gymno-sperms	Pteridosperm-atophyta (Seed Ferns)	/	Peltasperm-ales	/	Balme (1955), Taylor et al (2009), Zavattieri et al. (2018)
Protohaploxypinus microcorpus	(Schaarschmidt 1963) Clarke 1965							
Protosacculina macrosacca	(Maljavkina 1953) Schulz 1967	8.10	Gymno-sperms	/	/	/	/	Overall morphology allows assignation to gymnosperms, but no further evidence for more precise assignation is known for the moment.
Quadraeculina annelaeformis	Maljavkina 1949	9.6	Gymno-sperms	Spermato-phyta	Coniferopsida	Pinales	?Podo-carpaceae	Boulter and Windle (1993)
Rhaetipollis germanicus	Schulz 1967	6.19; 9.5, 11,14-15,21	Gymno-sperms	/	/	/	/	Taxon with very dubious affinity. Schulz (1967) as speculated an affinity with Coniferales, but due to lack of other evidence, the taxon is only tentatively assigned to Gymnosperms, but not further.
Ricciisporites tuberculatus	Lundblad 1954	6.20; 13.1-3,7	Gymno-sperms	/	/	/	/	Kürschner et al. (2014), Mander et al. (2012)
Striatoabietites sp.	Sedova 1956				/		/	See comment in *Lunatisporites* sp.

Striatoabietites aytugii	(Visscher 1966) Scheuring 1970	8.7	Gymnosperms	Pteridospermatophyta (Seed Ferns)		Peltaspermales		
Triadispora spp.	Klaus 1964		Gymnosperms	Spermatophyta	Coniferopsida	Voltziales	/	*Found *in situ* in a number of Voltziales: *Darneya peltata* Schaarschmidt et Mauberge 1969 and *Sertostrobus laxus* Grauvogel-Stamm 1969 (Balme 1995 and references therein).
Tsugaepollenites spp.	(Potonie 1931) Potonie & Venitz 1934		Gymnosperms	Spermatophyta	Coniferopsida	Pinales	Pinaceae	Batten and Dutta (1997), Bonis (2010)
Tsugaepollenites pseudomassulae	(Maedler 1964) Morbey 1975	8.15						
Vesicaspora sp.	(Schemel 1951) Wilson & Venkatchala 1963		Gymnosperms	Spermatophyta	Coniferopsida	Cordaitales Callistophytales	/	Balme (1995), Taylor et al. (2009), Zavattieri et al. (2018)
Vesicaspora fuscus	(Pautsch 1958) Morbey 1975	6.28						
Vitreisporites sp.	Leschik 1955 emend. Jansonius 1962		Gymnosperms	Pteridospermatophyta (Seed Ferns)	/	Caytoniales	/	*Found *in situ* in *Caytonanthus and Salpingocarpus* from the Caytoniales from the Permian till the Cretaceous from around the world (Balme, 1995).
Vitreisporites bjuvensis	Nilsson 1958	6.24						
Vitreisporites pallidus	(Reissinger 1950) Nilsson 1958	6.23						
Botryococcus braunii	Kützing 1849	6.29	Chlorophyceae	Chlorophyta	Chlorophyceae	Tetrasporales	/	(Batten and Grenfell, 1996)
Plaesiodictyon mosellanum	Wille 1970	8.22				Chlorococcales	/	Taylor et al. (2009)
Cymatiosphaera spp.	(Wetzel 1932) Deflandre 1954		Prasinophyceae		Prasinophyceae	Pyramimonadales	/	Guy-Ohlson (1996)
Cymatiosphaera polypartitia	Morbey 1975	6.31 6.32					/	
Cymatiosphaera polypartitia forma 1	Morbey 1975	6.32					/	
Cymatiosphaera polypartitia forma 2	Morbey 1975	6.31					/	
Leiosphaeridia spp.	Eisenack 1958	6.34					/	/
Tasmanites sp.	Newton 1875	9.3					/	Guy-Ohlson (1996)
Tytthodiscus sp.	Norem 1955	9.4					/	Guy-Ohlson (1996)
Concentrycystes sp.	Rossignol 1962	8.14	freshwater algae	Charophyta	Zygnematophyceae	Zygnematales	/	Grenfell (1995), Head (1992)
Lecaniella sp.	Cookson & Eisenack 1962	8.13					/	Grenfell (1995), Head (1992)
Tetraporina compressa	Kondratyev 1963	8.20					/	Grenfell (1995), Head (1992)
ACRITARCHS								

Micrhystridium sp.	(Deflandre 1937) Sarjeant 1967	6.26, 9.23		/	/	/	/	/
Veryhachium sp.	(Deunff 1954) Downie & Sarjeant 1963	8.19		/	/	/	/	/
Multiplicisphaeridium spp.	(Staplin 1961) restrict. Staplin, Jansonius & Pocock 1965	8.18	Acritarch	/	/	/	/	/
Multiplicisphaeridium dendroidium	Morbey 1975	8.17		/	/	/	/	/
DINOFLAGELLATES									
Dapcodinium priscum	(Evitt 1961) emend. Below 1987	6.35	Dino-flagellate	Dinokaryota	Dinophyceae	Gonyau-lacales	Rhaetogony-aulacacea	/
Rhaetogonyaulax rhaetica	(Sarjeant 1963) Loeblich & Loeblich 1968 emend. Hardland et al 1975, emend. Below 1987	6.33						/
Beaumontella sp.	Below 1987a	/				Suessiales	Suessiaceae	/
Beaumontella cf. *caminuspina*	(Wall 1965a) Below 1987a	6.27						
Suessia swabiana	(Morbey 1975) emend. Below 1987	6.30						/
FORAMINIFERAS									
Foraminifera Type 1	/	9.25	Fora-minifera	/	/	/	/	/
Foraminifera Type 2	/	9.26		/	/	/	/	/
Foraminifera Type 3	/	9.24		/	/	/	/	/
OTHER									
Fungal spore indet	/	Fungi		/	/	/	/	/
Palaeopericonia sp.	Ibañez 1996	9.19	Fungi	/	/	/	/	/
Halosphaeropsis sp.	Mädler 1963	8.12	NA	/	/	/	/	/

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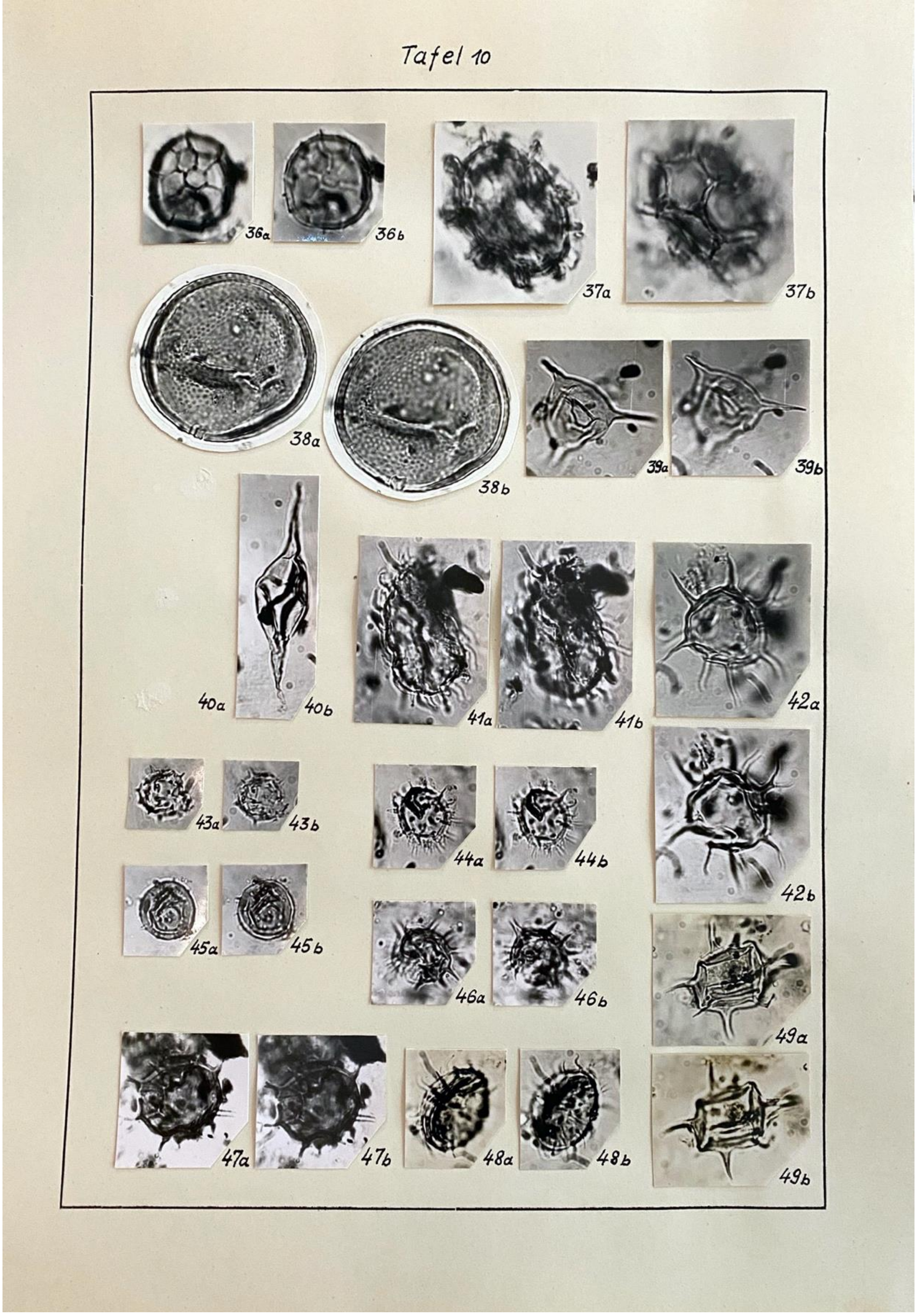
II. Supplements for Chapter 4 – Taxonomy and Nomenclature

II.i. Supplementary Figure



Supplementary Fig. 1. Template for Plates with analogue images from Schulz inheritance.

III. Supplements for Chapter 6 – Name Usage Statistics II

III.i. Supplementary File

Species names and authorities in case study 1:

Semiretisporis achimensis MÄDLER 1964

Semiretisporis antiquus DE JERSEY 1964

Semiretisporis denmeadii DE JERSEY 1964

Semiretisporis flaccida SHANG & LI 1991

Semiretisporis gothae REINHARD 1961,

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Semiretisporis lycopodioides BAI ET AL. 1983

Semiretisporis maljavkinae SCHULZ 1967,

Semiretisporis ornatus ORLOVSKA-ZWOLINSKA 1966

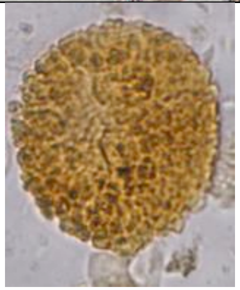
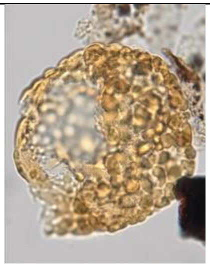
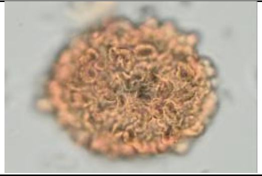
Semiretisporis reticulatus MÄDLER 1964

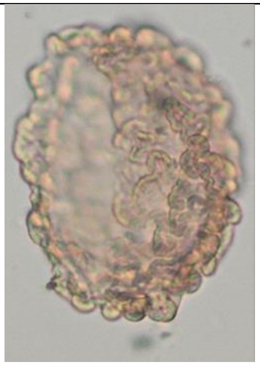
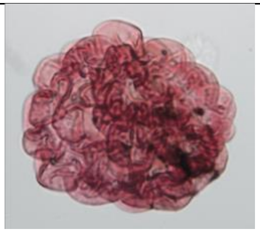
Semiretisporis taiwanensis HUANG et al. 1984

Semiretisporis wielichoviensis ORLOVSKA-ZWOLINSKA 1966

IV. Supplements for Chapter 8 – Re-evaluation of *Cerebropollenites*

IV.i. Supplementary Table: Misapplication list of names

Type		Basionym	Name	
A		*Cerebropollenites thiergartii* Thiergart 1949	*Sciadopityspollenites thiergartii* f. *schulzii*	cf. *Pollenites serratus* f. *helmstedtensis* pl. 11 fig. 14 (Rogalska 1954); ***Cerebropollenites thiergartii***, pl. 9 fig. 7 (Dybkjær 1988); *Cerebropollenites* ***thiergartii***, pl. 9 fig. 3+5 (Heunisch et al. 2010); *Cerebropollenites* ***thiergartii***, pl. 6 fig. 7-8 (Lindström et al. 2017)
B		*Pollenites macroserratus* fm. *Doggerensis* Thiergart 1949	*Sciadopityspollenites thiergartii f. multiverrucosus*	cf. *Pollenites serratus* f. *helmstedtensis* pl. 11 fig. 13 (Rogalska 1954); cf. *Pollenites serratus* f. *helmstedtensis* pl. 16 fig. 1-2 ; (Rogalska 1956)*; Tsugaepollenites macroserratus* f. ***doggerensis**,* pl. 8 fig. 7 (Bóna 1969); *Cerebropollenites* ***thiergartii***, pl. 5 fig. 2 (Lund and Pedersen 1984); *Sciadopityspollenites multiverrucosus***,** pl. 9 fig. 1+2 (Iljina 1985); *Cerebropollenites* ***thiergartii***, pl. 13 fig. 2-6 (Dybkjær 1991),
C			*Sciadopityspollenites megaorbicularius*	*Tsugaepollenites macroverrucosus*, pl. 8 fig. 8-9 (Bóna 1969); *Sciadopityspollenites mesozoicus* pl. 24, fig. 6 (Waksmundzka 1981); *Cerebropollenites macroverrucosus*, pl. 9 fig. 4 (Dybkjær 1988); (?) *Cerebropollenites thiergartii,* pl. 6 fig. 3 (Lindström et al. 2017)
D			*Sciadopityspollenites carlylensis* comb. nov.	*Tsugaepollenites mesozoicus*, pl. 20, fig. 2, 4-5 (Tralau 1968) *Cerebropollenites thiergartii* pl. 12, fig. 5-9 (Srivastava 1987)*;* *Cerebropollenites carlylensis* pl. 21, fig. 14 (Pocock 1970)

E		*Pollenites macroverrucosus* Thiergart 1949	*Sciadopityspollenites macroverrucosus*	*Cerebropollenites findlaterensis* pl. 21, fig. 7 (Pocock 1970); *Cerebropollenites thiergartii*, pl. 7, fig. 15 (Lund 1977), *Sciadopityspollenites mesozoicus* pl. 24, fig. 3 (Waksmundzka 1981) *Cerebropollenites* ***macroverrucosus***, pl. 5 fig. 1 (Lund and Pedersen 1984); *Cerebropollenites* sp., pl.3, fig, F (Guy-Ohlson and Malmquist 1985) *Cerebropollenites mesozoicus*, pl. 14, fig. 1-2 (Guy-Ohlson 1986), *Cerebropollenites thiergartii*, pl. 9 fig. 4 (Heunisch et al. 2010); *Cerebropollenites* ***macroverrucosus***, pl. 9 fig. 6 (Heunisch et al. 2010); *Cerebropollenites* ***macroverrucosus***, pl. 6 fig. 13 (Lindström et al. 2017)
F		*Tsugaepollenites mesozoicus* Couper 1958	*Sciadopityspollenites mesozoicus*	*Cerebropollenites* ***mesozoicus*** pl. 27, fig4 and 28 fig. 1-2 (Burger 1966)*;* *Cerebropollenites mesozoicus* pl. 21, fig. 3, 9,10, 12, 16, 17 (Pocock 1970); *Tsugaepollenites* ***mesozoicus***, pl. 15, fig. 6 (Ashraf 1977); *Cerebropollenites macroverrucosus*, pl. 7, fig. 14 (Lund 1977); *Sciadopityspollenites macroverrucosus* pl. 7, fig. 3-4 (Iljina 1985); *Cerebropollenites macroverrucosus* pl. 11, fig. 4-5 (Srivastava 1987)*;* *Cerebropollenites macroverrucosus*, pl. 9 fig. 5 (Dybkjær 1988); *Cerebropollenites macroverrucosus*, pl. 13 fig. 1 (Dybkjær 1991); *Cerebropollenites* ***mesozoicus***, pl. 4, fig. 34 (Guy-Ohlson 1989); *Sciadopityspollenites* ***mesozoicus***, pl. 10, fig. 10 (Selkova et al. 2011)
G		*Camerosporites pseudomassulae* Mädler 1964	*Pseudomassulites pseudomassulae* comb. nov.	*Tsugaepollenites* ? ***pseudomassulae***, pl. 10 fig. 9-12 (Morbey 1975); *Cerebropollenites mesozoicus, pl. 2, fig. 5+7* (Orbell 1973), *Cerebropollenites macroverrucosus,* pl. 14, fig. 2+3 (Achilles 1981); *Cerebropollenites macroverrucosus,* fig. 8.1 (Brenner 1986); *Tsugaepollenites* ***pseudomassulae,*** pl. 2 fig. 8 (Lachkar et al. 2000); *Cerebropollenites mesozoicus*, pl. 5, fig. 11 (Holstein 2004); *Tsugaepollenites* ***pseudomassulae***, pl. 9 fig. 7-10 (Heunisch et al. 2010)

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Appendix III

Inventory of consulted collections and studied type material

I. Thiergart collection (1949)

In total 67 microscope slides could be uncovered that could be associated with the 1949 publication “Der stratigraphische Wert mesozoischer Pollen und Sporen”. For four locations mentioned in that study no slides could be retraced. Therefore, the holo- or syntypes for *Sporites saturni* (=*Aratrisporites saturni*), *Pollenites pseudoalatus* (= *Ovalipollis pseudoalatus*), *Pollenites deformatus, Pollenites lucifer, Pollenites trialatus, Pollenites lucifer, Sporites trichopunctatus, Pollenites triangulates, Pollenites macroserratus f. doggerensis*; *Sporites appendicifer* are hereby documented as ‘lost’. Slides with holotypes highlighted with dark grey. Lost slides are highlighted in light grey.

Table. 1: Overview of curated material of Thiergart 1949. For each slide the name of the section the type of material that was sampled is given as well. Further sample identification (ID), e.g. letters or depths are given where such information was written on the respective slide. Location information and age determinations were taken from the labelling on the slide and complemented by the information in Thiergart 1949. Missing slides are depicted in grey shading. Slides that contain holotypes relevant for this thesis are marked with an asterisk (*) and slides that should contain holotypes are shaded in dark grey. In the comment section potential types are mentioned mainly for new species; for new forms only when it is to some extant relevant to this thesis.

Section/ material	nr. of slides & ID/depth	Location	Age	Preservation	Comment/ types that should be contained, if they could be retraced, EF references are given
Blatt Magdala/ core	a	Thüringen/ Hannoversche Gegend	Lower Keuper		*Sporites wicheri;* 2 syntypes for **Pollenites macroserratus Keuperianus; Pollenites rostratus,*
	b				
	c				
	d				
Blatt Hohenwestedt/ core	*570m	Thüringen/ Hannoversche Gegend	Lower Keuper	missing	*2 syntypes for ***Sporites saturni*** (=*Aratrisporites saturni*) **Holotype for* **Pollenites pseudoalatus** **(=*Ovalipollis pseudoalatus*)** 4 syntypes for *Pollenites deformatus* 3 syntypes for *Pollenites lucifer*
Helmstedt/ outcrop	ID added: *S1	Helmstedt near Berlin	Upper Rhaetian	Some pockets of glycerin jelly left with good preservation	Confirmation of Upper Rhaetian (contains *Rhaetipollis germanicus, Ricciisporites tuberculatus, Lycopodiacidites rhaeticus* and other typical taxa. Should contain the Holotype for ***Sporites interscriptus*** **(=*Zebrasporites interscriptus*)**, two specimens (S45/1; W51.4) could be the holotype, both ambiguous and partially covered by organic material that was moved, probably as a result of the drying process. This or the other slide should also contain 3 syntypes for **Pollenites serratus fa. helmstedtensis*; after inspection of the slide it is concluded

					that the depicted taxon is compliant with the circumscription of *Riccisporites.*
	ID added: S2		Upper Rhaetian		This or the other slide should contain holotype for *Sporites rhaeticus*
Alsenstrasse/ core	416-17m	Berlin	Upper Rhaetian	Was remounted and framed with red nail varnish before this study	
	416-17m			Was remounted and framed with red nail varnish before this study	
	416-17m				
	416-17m				
	393-394 m		Limnic Liassic		One of these 4 slides should contain 3 syntypes for * ***Pollenites reclusus*** **(=*Classopollis reclusus*)** (the fourth of the 4 syntypes is in the missing Langenhangen slide)
	393-394 m				
	393-394 m				
	393-394 m				
Degow I/ core	*253-55 m a	Hannoversche Gegend	Dogger	some small pockets of gelatine left with better preservation	Contains holotype for * ***Pollenites macroverrucosus*** (P44/0) 1 syntype for *Sporites trichopunctatus*
	*253-55 m b			some small pockets of gelatine left with better preservation	Contains last remaining syntype of *****Pollenites macroserratus*** **f.** ***dogerensis***. And *Pollenites granulatus* Holotype for *Sporites mariformis*
	253-55 m				
Blatt Langenhagen/ core	520m		Dogger	missing	*Pollenites trialatus* 1 syntype for *Pollenites lucifer* 1 syntype for *Sporites trichopunctatus* 2 syntypes for *Pollenites triangulates* *2 syntypes for *Pollenites macroserratus f. doggerensis*;
Kurland	Kur 3	Baltikum Alsi	Jurassic		All slides say additionally ‘1938’; One of these slides should contain the holotype for *Sporites interruptus* 3 syntypes for *Sporites spinifer*
	Kur 3				
	Kur 3				
	Kur 4x				
	Kur 4				
	Kur 4				
	Kur 8				
	Kur 8				
	Kur 8				
Eldagsen	114.25				

	114.25	Deister, Hannoversche Gegend			
Blatt Gamsen/ core	385 m	Braunschweig	Cypridae layers	missing	
Blatt Gamsen/ core	373.5-379 m	Braunschweig	Cypridae layers	missing	
Blatt Gamsen/ core	300.5 m	Braunschweig	Cypridae layers	missing	
Blatt Ahlfeld/outcrop	22/38		Wealden		
	22/39				
	22/40				
	22/41				
	22/42				
Blatt Thoeren	718 m; WA1	Kr. Celle, Hannover	Upper Wealden		One of these slides should contain the holotype for *Sporites trichopapillosus*
	718 m; WA1				
	718 m; WA1				
Blatt Thoeren	727 m; WA2	Kr. Celle, Hannover	Upper Wealden		
	727 m; WA2				
	727 m; WA2				
	727 m; WA2				
Wesergebirge/ outcrop			Wealden		
Wenig-Rackwitz/outcrop			Upper Cretaceous	missing	Holotype for *Sporites appendicifer*
Ullersdorf			Upper Cretaceous	missing	
Grünbach	2. VII	Tirol	Upper Cretaceous		
	2. VII				
	2. VII				
Nettgau	2. VII	Hannover	Transitions Upper Cretaceous - Paleocene		
	2. VII				
	2. VII				
	2. VII				
	2. VII				
	2. VII				
Ehra 4		Hannover	Transitions Upper Cretaceous - Paleocene		
	275 m				
	275 m				

II. Couper collection (1958)

The Couper collection is well curated and accessible through the Sedgewick Museum for Earth Sciences in Cambridge. Since the original publication the material is stored at the same institution and was at the time of request already included in the collections database. Using the database information together with information on slides from the publication itself the following summarizing table was made indicating holo- and previously not indicated paratypes. Slides with holotypes highlighted with dark grey. Lost slides/types are highlighted in light grey.

Table. 1: Overview of Couper (1958) available from the Sedgwick Museum for Earth Sciences in Cambridge. Inventory numbers are given for each specimen. Holotypes are given in bold and the type of type is indicated where applicable. Those specimens that were borrowed are marked with an x. That material that was borrowed simply because attached on the same slide is marked with an (x)

Inventory number	slide	Taxon name	Sort of type	Figure reference from publication	Material borrowed for study for this thesis marked with an x	Comment
K 5001		*Monolites* sp.		p.149 Pl.25 Fig.18		
K 5002		*Osmundacidites wellmanii,* Couper		p.134 Pl.16 Fig.5		
K 5003	C 34/2	***Matonisporites phlebopteroides***, Couper 1958	H	p.140 Pl.20 Fig.15		
K 5004	C 44/1	***Marattisporites scabratus***, Couper 1958	H	p.133 Pl.15 Fig.20		
K 5005		*Cyathidites minor*, Couper		p.139 Pl.20 Fig.9		
K 5006		*Monosulcites minimus*, Cookson		p.157 Pl.26 Fig.25		
K 5007	C 47/1	***Klukisporites variegatus,*** Couper 1958	H	p.137 Pl.19 Fig.7		
K 5008	C 47/1	***Trilites bossus***, Couper 1958	H	p.148 Pl.25 Fig.11		
K 5009		*Monosulcites carpentieri*, Delcourt & Sprumont		p.158 Pl.26 Fig.26		
K 5010	C 47/1	*Trilites bossus*, Couper 1958	paratype	p.148 Pl.25 Fig.12		
K 5011	C 48/8	*Dictyophyllidites harrisii*, Couper 1958	paratype	p.140 Pl.21 Fig.5		
K 5012	C 50/5	***Cingulatisporites pseudoalveolatus,*** Couper 1958	H	p.147 Pl.25 Fig.5		
K 5013	C 52/1	***Perotrillites rugulatus*,** Couper 1958	H	p.147 Pl.25 Fig.7		
K 5014	C 52/1	*Cingulatisporites pseudoalveolatus*, Couper 1958	paratype	p.147 Pl.25 Fig.6		
K 5015	C 52/1	*Lycopodiumsporites clavatoides,* Couper 1958	paratype	p.132 Pl.15 Figs.12-13		
K 5016	C 56/1	*Cingulatisporites problematicus*, Couper 1958	paratype	p.146 Pl.24 Fig.12	x	
K 5017	C 57/1	***Foveotriletes microreticulatus,*** Couper 1958	H	p.143 Pl.22 Fig.7		
K 5018	C 57/2	*Foveotriletes microreticulatus,* Couper 1958	paratype	p.143 Pl.22 Fig.8		

K 5019		*Matonisporites phlebopteroides*, Couper		p.140		
K 5020	C 73/1	***Cingulatisporites dubius***, Couper 1958	H	p.146 Pl.24 figs 3-4		
K 5021	C 73/1	***Parvisaccites enigmatus***, Couper 1958	H	p.154 Pl.30 Figs. 3-4		
K 5022		****Tsugaepollenites mesozoicus,*** Couper 1958	H	p.155 Pl.30 Fig.8	x	Good condition
K 5023	C 73/2	*Cingulatisporites dubius,* Couper 1958	paratype	p.146 Pl.24 Fig.5		
K 5024	C 73/2	*Lycopodiumsporites gristhorpensis,* Couper 1958	paratype	p.133 Pl.15 Fig.16		
K 5025	C 73/2	*Tsugaepollenites mesozoicus*, Couper 1958	paratype	p.155 Pl.30 Fig.9	x	
K 5026	C 73/2	*Tsugaepollenites mesozoicus,* Couper 1958	paratype	p.155 Pl.30 Fig.10	x	
K 5027	C 87/1	***Pilosisporites brevipapillosus,*** Couper 1958	H	p.144 Pl.22 Figs.11-12		
K 5028	C 87/1	*Lygodioisporites perverrucatus*, Couper	paratype	p.144 Pl.23 Fig.5		
K 5029	C 87/3	***Lygodioisporites perverrucatus,*** Couper 1958	H	p.144 Pl.23 Fig.4		
K 5030		*Gleicheniidites senonicus,* Ross		p.138 Pl.19 Fig.15		
K 5031		*Cyathidites minor*, Couper		p.139 Pl.20 Fig.10		
K 5032	C 90/2	***Pteruchipollenites microsaccus*,** Couper 1958	H	p.151 Pl.26 Fig.13	x	
K 5033	C 90/2	*Parvisaccites enigmatus,* Couper	paratype	p.154 Pl.30 Fig.5		
K 5034	C104/2	***Pteruchipollenites thomasii***, Couper 1958	H	p.150 Pl.26 Fig.10		
K 5035		*Eucommiidites troedssonii,* Erdtman		p.160 Pl.31 Fig.26		
K 5036	C 104/2	*Marattisporites scabratus*, Couper 1958	paratype	p.133 Pl.15 Fig.23		
K 5037	C 104/2	*Pteruchipollenites microsaccus*, Couper 1958	paratype	p.151 Pl.26 Fig.14		
K 5038	C106/1	***Cicatricosisporites dunrobinensis*,** Couper 1958	H	p.137 Pl.17 figs 13-14		
K 5039	C106/1	*Cingulatisporites rigidus,* Couper 1958	paratype	p.147 Pl.25 Fig.2		
K 5040	C106/1	*Monosulcites subgranulosus,* Couper 1958	paratype	p.158 Pl.26 Fig.29		
K 5041		*Sphagnumsporites psilatus,* (Ross) Couper		p.131 Pl.15 Fig.1		
K 5042	C106/3	***Cingulatisporites rigidus***, Couper 1958	H	p.147 Pl.25 Fig.1		
K 5043		*Lycopodiumsporites cerniidites,* (Ross) Delcourt & Sprumont		p.132 Pl.15 Figs.6,7		
K 5044	C106/5	*Cingulatisporites scabratus,* Couper 1958	paratype	p.147 Pl.25 Fig.4		
K 5045	C107/5	*Abietineaepollenites dunrobinensis,* Couper 1958	paratype	p.153 Pl.29 Fig.2		
K 5046	C107/6	***Abietineaepollenites dunrobinensis*,** Couper 1958	holotype	p.153 Pl.29 Fig.1		
K 5047	C109/2	***Foveotriletes irregulatus***, Couper 1958	holotype	p.143 Pl.22 Fig.9		
K 5048	C109/2	*Foveotriletes irregulatus,* Couper 1958	paratype	p.143 Pl.22 Fig.10		

K 5049		*Lycopodiumsporites cerniidites,* (Ross) Delcourt & Sprumont		p.132 Pl.15 Figs.8-9		
K 5050		*Matonisporites equiexinus,* Couper		p.140 Pl.20 Fig.14		
K 5051		*Trilobosporites bernissartensis,* (Delcourt & Sprumont) Potonié		p.141 Pl.21 Fig.9		
K 5052	C127/5	*Classopollis torosus,* (Reissinger) Couper		p.156 Pl.28 Fig.6	x	
K 5053	C134/2	*Perinopollenites elatoides*, Couper 1958	paratype	p.152 Pl.27 Fig.10	x	
K 5054	C134/3	***Klukisporites pseudoreticulatus*,** Couper 1958	holotype	p.138 Pl.19 Figs.8-9		
K 5055		*Pilosisporites trichopapillosus*, (Thiergart) Delcourt & Sprumont		p.144 Pl.23 Fig.3		
K 5056		*Trilobosporites bernissartensis,* (Delcourt & Sprumont) Potonié		p.141 Pl.21 Fig.10		
K 5057		*Eucommiidites troedssonii*, Erdtman		p.160 Pl.31 Fig.23		
K 5058		*Eucommiidites troedssonii,* Erdtman		p.160 Pl.31 Fig.24		
K 5059		*Monosulcites subgranulosus*, Couper		p.158 Pl.26 Fig.30		
K 5060		*Cicatricosisporites dorogensis,* Potonié R. & Gelletich		p.136 Pl.17 Fig.12		
K 5061	C 18/1	*Cingulatisporites valdensis,* Couper 1958	paratype	p.146 Pl.24 Fig.7		
K 5062	C 18/1	*Peromonolites asplenioides,* Couper 1958	paratype	p.148 Pl.25 Fig.10		
K 5063		*Pilosisporites trichopapillosus*, (Thiergart) Delcourt & Sprumont		p.144 Pl.23 Fig.1		
K 5064		*Appendicisporites tricornitatus*, Weyland & Greifeld		p.135 Pl.17 Fig.7		
K 5065		*Cicatricosisporites dorogensis*, Potonié R. & Gelletich		p.136 Pl.17 Fig.10		
K 5068	C124/2	***Concavisporites variverrucatus,*** Couper 1958	holotype	p.142 Pl.22 Fig.4		
K 5069	C124/2	***Cingulatisporites complexus*,** Couper 1958	holotype	p.145 Pl.24 Fig.1		
K 5070		*Araucariacites australis,* Cookson		p.151 Pl.27 Fig.5		
K 5071		*Cicatricosisporites dorogensis,* Potonié R. & Gelletich		p.136 Pl.17 Fig.11		
K 5072	C124/2	*Cingulatisporites complexus,* Couper 1958	paratype	p.145 Pl.24 Fig.2		
K 5073	C124/2	*Clavatipollenites hughesii,* Couper 1958	paratype	p.159 Pl.31 Fig.19		
K 5074	C124/2	*Clavatipollenites hughesii,* Couper 1958	paratype	p.159 Pl.31 Fig.20		
K 5075		*Concavisporites punctatus,* Delcourt & Sprumont		p.142 Pl.22 Fig.1		
K 5076		*Concavisporites punctatus,* Delcourt & Sprumont		p.142 Pl.22 Fig.2		
K 5077		*Concavisporites punctatus,* Delcourt & Sprumont		p.142 Pl.22 Fig.3		
K 5078	C124/2	*Klukisporites pseudoreticulatus*, Couper 1958	paratype	p.138 Pl.19 Fig.10		
K 5080	C124/3	*Trilobosporites apiverrucatus*, Couper 1958	paratype	p.142 Pl.21 Fig.13		
K 5081		*Cyathidites australis,* Couper		p.138		

K 5082	C125/3	***Peromonolites asplenioides,*** Couper 1958	holotype	p.148 Pl.25 Fig.9		
K 5083		*Pilosisporites trichopapillosus*, (Thiergart) Delcourt & Sprumont		p.144 Pl.23 Fig.2		
K 5084		*Cicatricosisporites dorogensis*, Potonié R. & Gelletich				
K 5085	C128/9	***Cicatricosisporites brevilaesuratus*****,** Couper 1958	holotype	p.136 Pl.18 Fig.1		
K 5086	C128/9	***Trilobosporites apiverrucatus,*** Couper 1958	holotype	p.142 Pl.21 Fig.11		
K 5087		***Clavatipollenites hughesii,*** Couper 1958	holotype	p.159 Pl.31 Figs.21, 22		
K 5088	C128/9	*Cicatricosisporites brevilaesuratus,* Couper 1958	paratype	p.136 Pl.18 Fig.2		
K 5089	C128/9	*Cicatricosisporites brevilaesuratus*, Couper1958	paratype	p.136 Pl.18 Fig.3		
K 5090	C128/9	*Parvisaccites radiatus*, Couper 1958	paratype	p.154 Pl.29 Fig.7		
K 5091	C128/9	*Parvisaccites radiatus,* Couper 1958	paratype	p.154 Pl.29 Fig.8		
K 5092	C128/9	*Parvisaccites radiatus*, Couper 1958	paratype	p.154 Pl.30 Fig.1		
K 5093	C128/9	*Parvisaccites radiatus*, Couper 1958	paratype	p.154 Pl.30 Fig.2		
K 5094		*Trilobosporites apiverrucatus*, Couper		p.142 Pl.21 Fig.12		
K 5095	C128/9	***Spheripollenites subgranulatus*****,** Couper 1958	holotype	p.158 Pl.31 Fig.9		
K 5096	C128/9	***Parvisaccites radiatus*****,** Couper 1958	holotype	p.154 Pl.29 Figs.5-6		
K 5097	C128/10	***Abietineaepollenites minimus,*** Couper 1958	holotype	p.153 Pl.28 Figs.14-15	x	lost?
K 5098	C128/10	*Abietineaepollenites microalatus,* Potonié R.		p.152 Pl.28 Figs.11-12	x	
K 5099	C128/10	*Abietineaepollenites microalatus*, Potonié R.		p.152 Pl.28 Figs.13	x	
K 5102	C131/6	***Cingulatisporites valdensis*****,** Couper 1958	holotype	p.146 Pl.24 Fig.6		
K 5103		*Cyathidites australis, Couper*		p.138 Pl.20 Fig.8		
K 5105		*Appendicisporites tricornitatus*, Weyland & Greifeld		p.135 Pl.17 Figs.8-9		
K 5106		*Gleicheniidites senonicus,* Ross		p.138		
K 5107	C138/6	***Cingulatisporites foveolatus*****,** Couper 1958	holotype	p.146 Pl.24 Figs.8-9		
K 5108	C 16/1	*Caytonipollenites pallidus*, (Reissinger 1950) Couper 1958		p.150 Pl.26 Fig.8		
K 5109	C138/6	***Cingulatisporites foveolatus*****,** Couper 1958	paratype	p.146 Pl.24 Fig.10		
K 5111	C155/3	***Trilites distalgranulatus*****,** Couper 1958	holotype	p.149 Pl.25 Figs.15-16		
K 5112	C155/3	***Spheripollenites psilatus,*** Couper 1958	holotype	p.159 Pl.31 Fig.4		
K 5113	C155/3	*Spheripollenites psilatus,* Couper 1958	paratype	p.159 Pl.31 Fig.5		
K 5114	C155/3	*Spheripollenites psilatus,* Couper 1958	paratype	p.159 Pl.31 Fig.6		
K 5115	C155/4	*Spheripollenites psilatus,* Couper 1958	paratype	p.159 Pl.31 Fig.7		

K 5116	C155/4	*Spheripollenites psilatus*, Couper 1958	paratype	p.159 Pl.31 Fig.8		
K 5117		*Todites williamsoni,* (Brongniart) Seward		p.107 Pl.16 Fig.1 (k.5117b) Fig.2 (k.5117a)		
K 5118		*Marattiopsis anglica,* Thomas		p.105 Pl.15 Fig.19		
K 5119		*Klukia exilis*, (Phillips) Raciborski		p.109 Pl.19 Figs.2-3 (k.5119a)		
K 5120		*Stachypteris hallei,* Thomas		p.109 Pl.19 Figs.4-5		
K 5121		*Coniopteris hymenophylloides,* (Brongniart)		p.114 Pl.20 Fig.5 (k.5121a) Fig.6 (k.5121b)		
K 5122		*Williamsoniella coronata*, Thomas		p.127 Pl.26 Fig.22		
K 5123		*Anemia colwellensis,* Chandler		p.110 Pl.17 Fig.1 (k.5123a) Fig.2 (k.5123b) Fig.3 (k.5123c)		
K 5124	C 2/2	*Trilites equatibossus*, Couper		p.148 Pl.25 Fig.14		
K 5129	C106/2	***Lycopodiumsporites clavatoides,*** Couper 1958	holotype	p.132 Pl.15 Figs.10-11		
K 5130		*Cingulatisporites scabratus,* Couper	holotype	p.147 Pl.25 Fig.3		
K 5131	C106/2	***Monosulcites subgranulosus,*** Couper 1958	holotype	p.158 Pl.26 Fig.28		
K 5132	C106/2	*Cicatricosisporites dunrobinensis,* Couper 1958	paratype	p.137 Pl.17 Fig.15		
K 5133	C106/2	*Pteruchipollenites thomasii,* Couper	paratype	p.150 Pl.26 Fig.11		
K 5134	C127/4	*Concavisporites variverrucatus*, Couper		p.142 Pl.22 Fig.5		
K 5139		*Gleicheniidites senonicus*, Ross		p.138 Pl.19 Fig.14		
K 5140	C 8/2	*Matonisporites phlebopteroides,* Couper 1958	paratype	p.140 Pl.20 Fig.17		
K 5141	C 2/1	*Perotrilites rugulatus,* Couper 1958	paratype	p.147 Pl.25 Fig.8		
K 5142	C 106/2	*Pteruchipollenites thomasii*, Couper	paratype	p.150 Pl.26 Fig.12		
K 5143	C 122/4	*Spheripollenites scabratus,* Couper		p.158 Pl.31 Fig.14		
K 857		*Dictyophyllum rugosum*, Lindley & Hutton		p.471 Pl.xx Fig.6 (k.8857b), Fig.7 (k.857c)		
K 948	C 1/4	*Spheripollenites scabratus*, Couper 1958	holotype	p.158 Pl.31 Fig.12		
K 949	C 1/4	*Spheripollenites scabratus*, Couper 1958	paratype	p.158 Pl.31 Fig.13		
K 950	C 1/4	*Spheripollenites subgranulatus,* Couper 1958	holotype	p.158 Pl.31 Fig.10		
K 951	25/5	*Klukisporites variegatus,* Couper 1958	paratype	p.137, Pl.19, Fig. 7		
K 953	C 1/6	***Lycopodiumsporites gristhorpensis,*** Couper 1958	holotype	p.133 Pl.15 Figs.14,15		
K 954	C 2/6	***Calamospora mesozoica***, Couper 1958	holotype	p.132 Pl.15 Fig.3	(x)	

K 955	C 2/6	***Trilites equatibossus*,** Couper 1958	holotype	p.148 Pl.25 Fig.13	(x)	
K 956	C 2/6	***Perinopollenites elatoides***, Couper 1958	holotype	p.152 Pl.27 Fig.9	x	
K 957	C 2/7	*Perinopollenites elatoides,* Couper 1958	paratype	p.152 Pl.27 Fig.11	x	
K 958	C 3/1	*Marattisporites scabratus,* Couper	paratype	p.133 Pl.15 Fig.22		
K 959	C 4/2	***Concavisporites subgranulosus*,** Couper 1958	holotype	p.143 Pl.22 Fig.6		
K 960	C 5/5	***Matonisporites equiexinus***, Couper 1958	holotype	p.140 Pl.20 Fig.13		
K 961		*Leptolepidites major,* Couper		p.141 Pl.21 Fig.8		
K 962		*Monolites* sp.		p.149		
K 963		*Monolites* sp.		p.149 Pl.25 Fig.17		
K 964		*Abietineaepollenites microalatus*, Potonié R.		p.152		
K 965	C 7/6	*Classopolis torosus*, (Reissinger 1950) Couper 1958		p.156 Pl.28 Fig.7	x	
K 966	C 8/6	*Cingulatisporites problematicus*, Couper		p.146 Pl.24 Fig.13	x	
K 967		*Araucariacites australis*, Cookson		p.151 Pl.27 Fig.3		
K 968	C 9/2	*Spheripollenites subgranulatus*, Couper		p.158 Pl.31 Fig.11		
K 969	C 10/3	*Densoisporites perinatus*, Couper	paratype	p.145 Pl.23 Fig.9		
K 970	C 16/1	*Caytonipollenites pallidus,* (Reissinger 1950) Couper 1958		p.150 Pl.26 Fig.7		
K 971		*Sphagnumsporites psilatus*, (Ross) Couper		p.131 Pl.15 Fig.2		
K 972	C 20/3	***Todisporites major*,** Couper 1958	holotype	p.134 Pl.16 Fig.6	x	
K 973	C 20/3	***Dictyophyllidites harrisii***, Couper 1958	holotype	p.140 Pl.21 Fig.6	(x)	
K 974	C 20/5	***Todisporites minor***, Couper 1958	holotype	p.135 Pl.16 Fig.9	x	
K 975	C 20/5	*Todisporites major*, Couper 1958	paratype	p.134 Pl.16 Fig.7	x	
K 976	C 20/5	*Todisporites major*, Couper 1958	paratype	p.134 Pl.16 Fig.8	x	
K 977	C 29/5	*Todisporites minor*, Couper 1958	paratype	p.135 Pl.16 Fig.10	x	
K 978		*Eucommiidites troedssonii,* Erdtman		p.160 Pl.31 Fig.25		
K 979	25/5	*Klukisporites variegatus,* Couper 1958	paratype	p.137 Pl.19 Fig.6		
K 980		*Osmundacidites wellmanii,* Couper		p.134 Pl.16 Fig.4		
K 981	C27/7	***Cingulatisporites problematicus*,** Couper 1958	holotype	p.146 Pl.24 Fig.11	x	
K 982	C27/7	*Classopolis torosus*, (Reissinger 1950) Couper 1958		p.156 Pl.28 Fig.2	x	
K 983	C27/7	*Classopolis torosus*, (Reissinger 1950) Couper 1958		p.156 Pl.28 Fig.3	x	
K 984	C27/7	*Classopolis torosus*, (Reissinger 1950) Couper 1958		p.156 Pl.28 Fig.4	x	

K 985	C27/7	*Classopolis torosus,* (Reissinger 1950) Couper 1958		p.156 Pl.28 Fig.5	x	
K 986		*Eucommiidites troedssonii,* Erdtman		p.160 Pl.31 Fig.27		
K 987		*Monosulcites minimus,* Cookson		p.157 Pl.26 Fig.23		
K 988		*Monosulcites minimus*, Cookson		p.157 Pl.26 Fig.24		
K 989	C 27/9	***Densoisporites perinatus,*** Couper 1958	holotype	p.145 Pl.23 Figs.6-7		
K 990	C 27/9	*Densoisporites perinatus*, Couper 1958	paratype	p.145 Pl.23 Fig.8		
K 991		*Gleicheniidites senonicus*, Ross		p.138 Pl.19 Fig.13		
K 992	C 27/9	*Matonisporites phlebopteroides*, Couper 1958	paratype	p.140 Pl.20 Fig.16		
K 993	C 28/5	***Leptolepidites major*, **Couper 1958	holotype	p.141 Pl.21 Fig.7	x	
K 994		*Monosulcites carpentieri*, Delcourt & Sprumont		p.158 Pl.26 Fig.27		
K 995		*Monolites* sp.		p.149		
K 997		*Araucariacites australis*, Cookson		p.151 Pl.27 Fig.4		
K 998		*Calamospora mesozoica*, Couper		p.132 Pl.15 Fig.4		
K 999		*Marattisporites scabratus*, Couper		p.133 Pl.15 Fig.21		
L 832		*Cyathea pubescens*, Mett. ex Kuhn		p.471 Pl. xx Fig.1 (l.832 a) Fig.2 (l.832 b) Fig.3 (l.832 c) Fig.4 (l.832 d)		
L 834		*Ginkgo biloba*, Linné		p.123 Pl.26 Figs.19-20		
L 836		*Thuja orientalis*, Linné		p.159 Pl.31 Figs.1-3		
L 837		*Matonia pectinata*, Robert Brown		p.117 Pl.20 Figs.11-12		
L 838		*Anemia phyllitidis*, (Linné) Swartz		p.111 Pl.16 Figs.11-13		
L 839		*Cheiropleuria bicuspis*, (Blume) Presl		p.119 Pl.21 Figs.1, 2		
L 841		*Pinus cembra*, Linne		p.152 Pl.28 Figs.8, 9 (l.841 a)		
L 842		*Cunninghamia lanceolata*, (Lambert) Hook		p.129 Pl.27 Fig.6		
L 836		*Voltzia heterophylla* ?, Brongniart		pp.249-331		
L 837		*Monolites* sp.		p.149 Pl.25 Fig.18		

III. Klaus collection (1960)

The Klaus collection is still curated and stored at its original place mentioned by Klaus (1960) at the GB in Vienna. Except for a few slides (see below) it is in an overall good condition to work with, although it was only permitted to study it on site with limited photographic equipment. Slides with holotypes highlighted with dark grey. Lost slides/types are highlighted in light grey.

Inventory number	EK-Nr.	Sample	Taxon name	Sort of type	Figure reference from publication	Foto	Comment
1960/5/1	346	Pr.198	*Calamaspora nathorstii* (Halle 1908) Klaus 1960		p. 116, Pl. 28, Fig. 1	x	
1960/5/2	347	AT 31	*Aulisporites astigmosus* (Leschik 1955) Klaus 1960		p. 118, Pl. 28, Fig. 2	x	The crucial and distinctive characteristics are hardly visible
1960/5/3	349	/	***Retusotriletes mesozoicus*** Klaus 1960	H	p. 120, Pl. 28, Fig. 6	x	The crucial and distinctive characteristics are hardly visible, due to the dried out gelatin
1960/5/4	351	/	***Paraconcavisporites lunzensis*** Klaus 1960	G+H	p. 123, Pl. 28, Fig. 7, 9		Spore at the very edge of the cover slip, documentation not successful
1960/5/5	384	198	*Paraconcavisporites sp.* Klaus 1960		p. 123, Pl. 28, Fig. 5	x	Glycerin jelly is dried out, but characteristics are still well visible
1960/5/6	352	AT 31	*Anapiculatisporites telephorus* (Pautsch 1958) Klaus 1960		p. 124, Pl. 29, Fig. 17	x	Broken in 2 pieces, but spore could still be documented.
1960/5/7	354	AT 31	*Baculatisporites comaumensis* (Cookson 1953) R. Potonié 1956		p. 125, Pl. 29, Fig. 13	x	Glycerin jelly is dried out, but characteristics are still well visible
1960/5/8	355	AT 31	***Conbaculatisporites mesozoicus*** Klaus 1960	G+H	p. 125, Pl. 29, Fig. 15	x	The spore is well preserved in a pocket of glycerin jelly. Due to the camera equipment the baculae are not as nicely visible as in the original photomicrograph
1960/5/9	353	/	***Osmundacidites alpinus*** Klaus 1960	H	p. 127, Pl. 31, Fig. 17	x	The glycerin jelly is dried out, but the ornamentation is still well visible, in fact better than on the original photomicrograph
1960/5/10	348	AT 31	***Conosmundasporites othmari*** Klaus 1960	G+H	p. 128, Pl. 28, Fig. 4	x	Glycerin jelly dried out, granulate ornamentation therefore not as nicely visible as on the original photomicrograph
1960/5/11	357	/	*Trilites tuberculiformis* Cookson 1947		p. 129, Pl. 30, Fig. 21, 23, 25	x	No ink marking to indicate place of palynomorph, but the spore can be retraced and is well preserved despite the dried-out glycerin jelly
1960/5/12	356	/	***Verrucosisporites morulae*** Klaus 1960	H	p. 130, Pl. 29, Fig. 11	x	No ink marking to indicate place of palynomorph, but the spore can be retraced and is well preserved despite the dried-out glycerin jelly
1960/5/13	350	/	***Distalanulisporites punctatus*** Klaus 1960	G+H	p. 133, Pl. 28, Fig. 8		
1960/5/14		/	*Microreticulatisporites opacus* Klaus 1960		p. 133, Pl. 29, Fig. 10	x	Glass slide with remount, but original lino-slide preserved, despite the dried-out glycerin jelly, characteristics are still well visible

1960/5/15	358	AT 31	***Lycopodiacidites kuepperi*** Klaus 1960	H	p. 135, Pl. 31 Fig. 27	x	the spore is well preserved despite the dried glycerin jelly; the crucial characteristics are even better visible than from the original micrograph
1960/5/16	359	56/1b	*Camarozonosporites rudis* (Leschik 1955) Klaus 1960	H	p. 135, Pl. 29 Fig. 12	x	the spore is well preserved despite the dried glycerin jelly; the crucial characteristics are even better visible than from the original micrograph
?	360	/	***Zebrasporites kahleri*** Klaus 1960	G+H	p. 138, Pl. 30, Fig. 18-20	x	Spore is well preserved despite the dried-out glycerin, but ornamentation not visible in as much details as when the mounting medium would be preserved.
1960/5/18	361	/	***Zebrasporites fimbriatus*** Klaus 1960	H	p. 138, Pl. 30, Fig. 22	x	The spore is in itself very fragile and partially damaged, but well preserved in a remaining pocket of glycerin jelly.
1960/5/19		/	*Zebrasporites corneolus* (Leschik 1955) Klaus 1960			x	The spore is preserved but remnants of the mounting medium are obstructing the view on the subtle differences of the spore chracteristics.
1960/5/20	362	AT 31	***Tigrisporites hallensis*** Klaus 1960	G+H	p. 140, Pl. 31, Fig. 28, 30	x	No ink marking to indicate place of palynomorph, but it can be retraced and is well preserved despite the dried-out glycerin
1960/5/21	363	/	***Styxisporites cooksonae*** Klaus 1960	H	p. 141, Pl. 31, Fig. 29, 31	x	Spore is well preserved despite the dried-out glycerin
1960/5/22	364	/	***Saturnisporites fimbriatus*** Klaus 1960 ***(=Aratrisporites fimbriatus***)	G+H	p. 142, Pl. 32, Fig. 32-33	x	Spore is well preserved despite the dried-out glycerin, but ornamentation not visible in as much details as when the mounting medium would be preserved.
1960/5/23	365	/	***Saturnisporites granulatus*** Klaus 1960 ***(=Aratrisporites granulatus***)	H	p. 143, Pl. 32, Fig. 34	x	Spore is well preserved despite the dried-out glycerin, but ornamentation not visible in as much details as when the mounting medium would be preserved.
1960/5/24	366	AT 31	***Saturnisporites palettae*** Klaus 1960 ***(=Aratrisporites palettae***)	H	p. 144, Pl. 32, Fig. 36	x	Glass slide; glycerine jelly dried out. Makes the ornamentation less visible.
missing	367	AT 31	***Saturnisporites fischeri*** Klaus 1960 ***(=Aratrisporites fischeri***)	H	p. 144, Pl. 32, Fig. 35		missing
1960/5/25	368	198	***Aratrisporites scabratus*** Klaus 1960	H	p. 147, Pl. 32, Fig. 37, 38		Glass slide with remount, but original lino-slide preserved, slide in such a state, that it was impossible to photograph the specimen.
1960/5/26	369	198	***Aratrisporites coryliseminis*** Klaus 1960	H	p. 147, Pl. 33, Fig. 39, 40	x	Spore is well preserved despite the dried-out glycerin, but ornamentation not visible in as much details as when the mounting medium would be preserved.

1960/5/29	381	/	***Aratrisporites coryliseminis*** Klaus 1960	P	p. 147, Pl. 33, Fig. 41		broken
1960/5/28	371	167	***Aratrisporites paraspinosus*** Klaus 1960	H	p. 148, Pl. 33, Fig. 43	x	Spore is well preserved despite the dried-out glycerin, but ornamentation not visible in as much details as when the mounting medium would be preserved.
1960/5/?	372	/	***Ovalipollis lunzensis*** Klaus 1960	H	p. 152, Pl. 34, Fig. 46-49	x	Glass slide with remount, but original lino-slide preserved; Pollen is well preserved despite the dried-out glycerin
1960/5/30	373	/	***Ovalipollis grebae*** Klaus 1960	H	p. 154, Pl. 35, Fig. 52, 55	x	Pollen is well preserved despite the dried-out glycerin
1960/5/31	374	169	***Ovalipollis rarus*** Klaus 1960	H	p. 154, Pl. 35, Fig. 50	x	Pollen is preserved, but as a result of the drying process of the glycerin jelly organic material seems to have moved and is now partially covering the pollen which is not visible in the original photomicrograph.
1960/5/32	/	/	*Lueckisporites kraeusil* (Leschik 1955) R. Potonié 1958		p. 156		
1960/5/33	375	AT 31	***Lueckisporites junior*** Klaus 1960	H	p. 156, Pl. 33, Fig. 42		
1960/5/34	376	/	***Chordasporites singulichorda*** Klaus 1960	G+H	p. 158, Pl. 33, Fig. 45	x	the pollen is in itself not an optimally preserved specimen, but due to a pocket of glycerin gelatine around it, it is from a preparation point of view as well preserved as possible
1960/5/35	/	AT 31	*Duplicisporite granulatus* (Leschik 1955) Klaus 1960		p. 161, Pl. 35, Fig. 53	x	Glass slide; pollen is preserved, but without the mounting medium, there is no clear view on the already enigmatic characteristics.
1960/5/36	380	AT 31	*Duplicisporites mancus* (Leschik 1955) Klaus 1960		p. 161, Pl. 35, Fig. 51	x	Glass slide; pollen is preserved, but without the mounting medium, there is no clear view on the already enigmatic characteristics.
1960/5/37	381	AT 31	*Praecirculina granifer* (Leschik 1955) Klaus 1960		p. 162, Pl. 36, Fig. 61	x	Glass slide
1960/5/38	/	AT 31/1	***Praecirculina maljavkina*** Klaus 1960	G+H	p. 163, Pl. 36, Fig. 62-63		Glass slide, we could not find the palynomorph, it was probably lost in the remounting process.
1960/5/39	383	AT 28	***Circulina meyeriana*** Klaus 1960	H	p. 165, Pl. 36, Fig. 58	x	Glass slide, pollen well preserved despite the missing glycerin jelly.
1960/5/40	382	AT 28	***Circulina meyeriana*** Klaus 1960	P	p. 165, Pl. 36, Fig. 57	x	Tetrad, glycerin jelly is dried out in such a way that it is partially obstructing the view, but overall the crucial characteristics are visible.
1960/5/?		/	***Circulina meyeriana*** Klaus 1960	P	p. 165, Pl. 36, Fig. 5?	x	Tetrad, label badly damages and partially illegible; pollen tetrad well preserved, but with the missing mounting medium degraded, the iridizing effect takes part of the clarity of the view.
1960/5/?		AT 28	***Circulina meyeriana*** Klaus 1960	P	p. 165, Pl. 36, Fig. ?		label badly damages and partially illegible

		AT 28	***Circulina meyeriana*** Klaus 1960		/		Tetrad Nr.
		AT 28	***Circulina meyeriana*** Klaus 1960		/		
		AT 28	***Circulina meyeriana*** Klaus 1960		/		
		/	*Enzonalasporites tenuis* (Leschik 1955) Klaus 1960		p. 168, Pl. 37, Fig. 66	x	pollen is preserved, but without the mounting medium, there is no clear view on the already ver fine differences of the ornamentation.
		/	*Enzonalasporites*				
missing	377	AT 31	***Patinasporites iustus*** Klaus 1960	H	p. 169, Pl. 37, Fig. 68, 69		Although the slide that would hold the cover slip is preserved, the cover slip itself with the pollen is missing and has to be accounted for as 'lost'
missing	378	AT 31	***Elipsovelatisporites plicatus*** Klaus 1960	G+H	p. 171, Pl. 36, Fig. 65		Although the slide that would hold the cover slip is preserved, the cover slip itself with the pollen is missing and has to be accounted for as 'lost'
	379	/	*Pityosporites neomundanus* (Leschik 1955) Klaus 1960		p. 172, Pl. 37, Fig. 70		
		144/ Lunz	***Pityosporites ruttneri*** Klaus 1960	H	p. 172, Pl. 38, Fig. 76		
		/	*Lagenella martinii* (Leschik 1955) Klaus 1960		p. 174, Pl. 38, Fig. 71-74	x	Glass slide with remount, but original lino-slide preserved, nicely preserved palynomorph in a remaining pocket of glycerin jelly.
		/	cf. *Hystrichosphaeridium*		p. 176, Pl. 38, Fig. 75		
		/	Aratrisporites, Duplo		/		
		/	???? with *Ovalipollis*		/		

IV. Mädler collection (1964)

The Couper collection is well curated and accessible through the LBEG in Hannover. Since the original publication the material is stored at the same institution and was at the time of request already included in the collections database. Using the database information together with information on slides from the publication itself the following summarizing table was made. Slides with holotypes highlighted with dark grey. Lost slides/types are highlighted in light grey.

Inventory number	slide	Taxon name	Holotypes marked with an x	Figure reference from publication	Material borrowed for study for this thesis marked with an x	Comment
3125	M 703	***Anulatizonites drawehni***	x	Pl.2, fig, 1	x	Netz 1 J8
3126	M 703	*Anulatizonites drawehni*		Pl.2, fig, 2	x	Netz 2, C3
3127	M 703	***Anulatizonites rotundus***	x	Pl.2, fig, 3	x	Netz 2, A1
3128	M 703	*Anulatizonites* sp.		Pl.2, fig, 4	x	Netz 2, C5
3129	M 703/III	***Semiretisporis reticulatus***	x	Pl.2, fig, 5	x	EF C17/3
3130	M 703/III	***Ballosporites hians***	x	Pl.2, fig, 6	x	
3131	M 703	*Ballosporites hians*		Pl.2, fig, 7	x	Netz 1 F5
3132	M 703	*Ballosporites hians*		Pl.2, fig, 8	x	Netz 1 K3
3133	M 703	*Ballosporites hians*		Pl.2, fig, 9	x	Netz 2 K7
3134	M 703	*Ballosporites hians*		Pl.2, fig, 10	x	Netz 1 E3
3138	M115	***Dentellisporites achimensis***	x	Pl.2, fig, 13	x	Netz 1 E6
3139	M116	*Semiretisporis cf. gothae*		Pl.2, fig, 14	x	Netz 1 B1
3140	M116	***Semiretisporis achimensis***	x	Pl.2, fig, 16	x	EK1
3141	M116	***Camerosporites pseudomassulae***	x	Pl.2, fig, 17	x	Netz 1 E10
3142	M116	*Cingulatizonites rhaeticus*		Pl.2, fig, 18	x	Netz 1 K1
3143	M116	***Cingulatizonites rhaeticus***	x	Pl.2, fig, 19	x	EK3
3144	M116	***Trizonites cerebralis***	x	Pl.3, fig, 1	x	EK2; L24/3
3145	M116	***Monosulcites rhaetoliassicus***	x	Pl.3, fig, 2	x	Netz 1 B5
3146	M317	***Lycopodiacidites infragranulatus***	x	Pl.3, fig, 3	x	EK21
3147	M317	***Kyrtomisporis laevigatus***	x	Pl.3, fig, 4	x	EK11
3148	M317	***Kyrtomisporis speciosus***	x	Pl.3, fig, 5, 6	x	EK8
3149	M317	*Kyrtomisporis speciosus*		Pl.3, fig, 7	x	EK9
3150	M318	***Striatella seebergensis***	x	Pl.3, fig, 8	x	EK7
3151	M317	***Trizonites rugulatus***	x	Pl.3, fig, 9	x	EK12
3152	M317	***Cingulatizonites marginatus***	x	Pl.3, fig, 10	x	EK1
3153	M317	***Aequitriradites inequalis***	x	Pl.3, fig, 11	x	EK14
3154	M300/I,21	***Striatella jurassica***	x	Pl.3, fig, 12	x	

3155	M300/II	***Paraklukisporites foraminis***	x	Pl.3, fig, 13	x	
3156	M295/II	***Kyrtomisporis laevigatus***	x	Pl.3, fig, 14	x	
3158	M300/I	*Camarozonosporites rudis*		Pl.3, fig, 16	x	‘lost’
3159	M300/I	*Ephedripites tortuosus*		Pl.3, fig, 17	x	‘lost’

V. Schulz collection (selection)

The Schulz collection is accessible through the BGR in Spandau. Since the original publication the material has been stored in different locations and currently under very poor conditions (strong temperature changes). Consequently the material is generally poorly preserved. Here only a selection of some of most important holotypes from Schulz' publications are listed.

Inventory number	slide	Taxon name	Holotypes marked with an x	Reference from publication	Material borrowed for study for this thesis marked with an x	Comment/ EF references when relocated
X 11182		*Cornutisporites rugulatus*	x	Schulz (1962)		
X 11184	Möckern 1E – 10184/1	*Triancoraesporites reticulatus*	x	Schulz (1962), p. 311, Pl. 2, Figs. 12-13	x	Triassic R46/3
X11271	Gorlosen 4 – 3/5	*Leptolepidites macroverrucosus*	x	Schulz (1967), p. 559, Taf. 2, Fig. 7-9, Taf. 23, Fig. 1 a-b	x	Jurassic
X 11272	Möckern 1E – 10184/13	*Lophotrilites verrucosus*	x	Schulz (1967), p. 561, Pl. 2, Figs. 12-14	x	Triassic
X 11273	Lübben 2 – 81/1	*Converrucosisporites luebbenensis*	x	Schulz (1967), p. 561, Pl. 2, Figs. 15-17, Pl. 25, Fig. 1	x	Jurassic
X 11274	Golzow 3 – 133/2	*Uvaesporites microverrucatus*	x	Schulz (1967), p. 560, Pl. 3, Figs. 1-4	x	Jurassic O29/0
X 11280	Camin 4 – 26/2	*Ceratosporites spinosus*	x	Schulz (1967), p. 563, Pl. 3, Figs. 14-15		Jurassic
X 11281	Seeberg 1/1	*Foraminispores jurassicus*	x	Schulz (1967), p. 564, Pl. 4, Fig. 1-3, Pl. 23, Fig. 3	x	Jurassic
X 11283	Groß-Muckrow 1–8/2	*Anaplanisporites echinatus*	x	Schulz (1967), p. 565, Pl.. 4, Figs. 6-8		Triassic
X 11286	Wilsnack 4– 3/1	*Taurocusporites verrucatus*	x	Schulz (1967), p. 566, Pl. 4, Fig. 14-16, Pl. 23, Fig. 7	x	Jurassic
X 11287	Lychen 2–204a/1	*Carnisporites granulatus*	x	Schulz (1967), p. 567, Pl. 4, Figs. 17-19		Triassic
X 11288	Golzow 3–111/1	*Mesozoicisporites punctatirugulatus*	x	Schulz (1967), p. 567, Pl. 5, Fig. 1, Pl. 25, Fig. 5		Jurassic
X 11289	Möckern 1E – 10184/1	*Selagosporis mesozoicus*	x	Schulz (1967), p. 568, Pl. 5, Figs. 2-4		Triassic
X 11296	Möckern 1E – 10184/1	*Convolutispora microrugulata*	x	Schulz (1967), p. 570, Pl. 6, Fig. 7-9		Triassic
X 11297	Waddekath 7–112/2	*Convolutispora microfoveolata*	x	Schulz (1967), p. 571, Pl.. 6, Figs. 10-11		Triassic

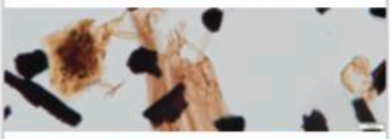
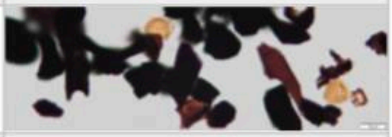
X 11298	Möckern 1E – 10184/3	*Tigrisporites microrugulatus*	x	Schulz (1967), p. 572, Pl. 7, Figs. 1-3		Triassic
X11300	Möckern 1E – 10184/3	*Camarozonosporites laevigatus*	x	Schulz (1967), p. 572, Pl. 7, Figs. 7-9, Pl.. 25, Fig. 3	x	Triassic
X 11301	Golzow 3– 394/1	*Camarozonosporites golzowensis*	x	Schulz (1967), p. 572, Pl. 7, Figs. 10-11	x	Jurassic K41/4
X 11302	Aulosen 1 – 128/1	*Camarozonosporites aulosensis*	x	Schulz (1967), p. 573, Pl. 7, Figs. 12-14	x	Jurassic
X 11304	Möckern 1E – 10184/21	*Lycopodiacidites rhaeticus*	x	Schulz (1967), p. 571, Pl. 8, Figs. 1-2	x	Triassic G48/1
X 11317	Möckern 1E – 10184/21	*Semiretisporis maljavkinae*	x	Schulz (1967), p. 578, Pl. 10, Fig. 6, Pl. 11, Fig. 3	x	Triassic L39/1
X 11320	Möckern 1E – 10184/3	*Cornutisporites rugulatus*	x	Schulz (1967), p. 580, Pl. 11, Figs. 8-9, Pl. 12, Fig. 1	x	Triassic
X 11322	Möckern 1E – 10184/17	*Densoisporites spongiosus*	x	Schulz (1967), p. 581, Pl. 12, Figs. 3-4, Pl.. 26, Figs. 1		Triassic
X 11324	Möckern 1E – 10184/1	*Densosporites foveocingulatus*	x	Schulz (1967), p. 582, Pl. 12, Figs. 7-8		Triassic
X 11326	Möckern 1E – 10184/1	*Densosporites cingulatus*	x	Schulz (1967), p. 583, Pl. 13, Fig. 1-2, Pl. 25, Fig. 4		Triassic
X 11334	Golzow 3– 171/1	*Polycingulatisporites liassicus*	x	Schulz (1967), p. 587, Pl. 14, Figs. 7-9, Pl. 23, Figs. 5 a-b		Jurassic
X 11340	Golzow 3– 59/1	*Laevigatosporites mesozoicus*	x	Schulz (1967), p. 590, Pl. 16, Figs. 1-2		Jurassic
X 11343	Wellmitz 1	*Aratrisporites minimus*	x	Schulz (1967), p. 592, Pl. 16, Figs. 7-9	x	Jurassic “lost”?
X11353	Möckern 1E – 10184/1	*Taeniaesporites rhaeticus*	x	Schulz (1967), p. 597, Pl. 18, Figs. 3-4	x	Triassic
X 11360	Golzow 3– 406/1	*Eucommiidites granulosus*	x	Schulz (1967), p. 601, Taf. 19, Fig. 8-9		Jurassic
X 11361	Lychen 2– 201/1	*Eucommiidites major*	x	Schulz (1967), p. 601, Pl. 19, Fig. 10		Jurassic
X11369	Marnitz 3 – 59/2	*Cerebropollenites thiergartii*	x	Schulz (1967), p. 603, Pl. 21, Figs. 7-8	x	Jurassic V38/2
X11373	Möckern 1E – 10184/1	*Rhaetipollis germanicus*	x	Schulz (1967), p. 605, Pl. 22, Figs. 10-12	x	Triassic X28/0
X 11422	Calau 1-54	*Echinitosporites iliacoides*	x	Schulz & Krutzsch 1961, p. 122, Pl.. 18, Fig. 1-4,	x	Triassic, N39/4

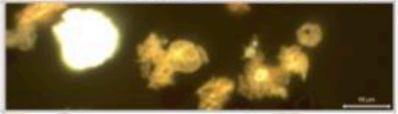
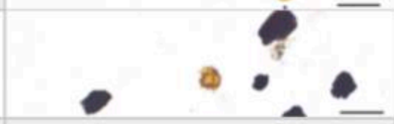
Appendix IV

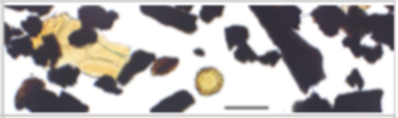
Facies Overview & Sampling Details of the Bonenburg Section

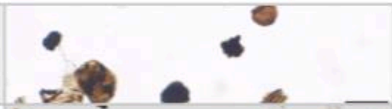
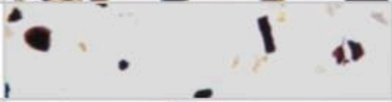
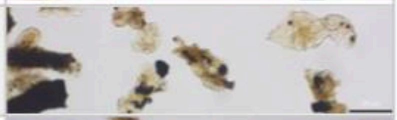
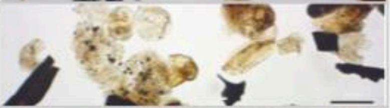
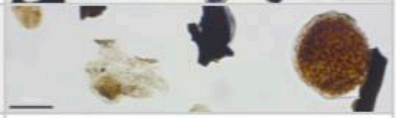
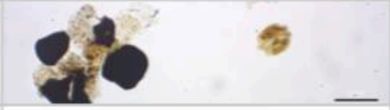
In the following table all samples that were taken from the Bonenburg section are listed. Where isotopes were measure the delta $^{13}C_{TOC}$ values are given. Those that were analysed for palynology indicate the amount of rock material processed together with a brief description, which represents neither a quantitative nor qualitative analysis, but merely a first impression that was noted when the samples were looked at for the first time, to facilitate orientation. Similarly, visual facies impressions are given on the right (studied with an 10x objective).

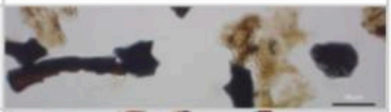
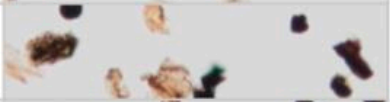
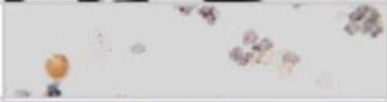
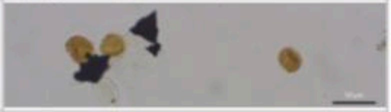
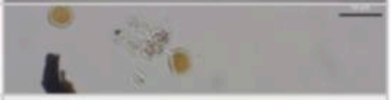
I. Facies Overview & Sampling Details

ID: BB	del13Ctoc Sometimes multiple measurements	height	g rock processed	Brief Description, very obvious taxa, etc.	Facies impression if palynology was analysed
(+)730		3730	7,404	*Riccisporites* (tetrades), *Tasmanites*	
(+)600		3600	6,991	*Tasmanites* *Suessia* (many) *Thittodiscus*	
(+)520		3520	7,143	*Tasmanites*, *Botryococcus* NO *Classopollis*, some *Riccisporites*	
3550	-27,546	3490	12,038	*Rhaetipollis*, *Tasmanites* *Botryococcus*	
3475	NA	3475			
3530	-25,388	3475			
3450	-25,982	3450			
3500	-25,831	3450			
3425	NA	3430			
3400	-25,359	3405	8,868	very few; strong pyrites impressions	
3375	-26,228	3380			
3350	-25,951	3355			
3315	-26,078	3315			
3300	-26,31	3300	11,064	Many dinoflagellates	

3270	NA	3270			
3250	-27,377	3250			
3220	-29,985	3220			
3200	-26,924	3200	11,359	*Thittodiscus* *Cymatiosphaera*	
3170	-26,871	3170			
3140	-28,593	3140			
3125	-29,235	3125	8,0697	Many acritarchs, *Cymatiosphaera*, *Classopollis*	
3100	-27,977	3100	12,083	Many acritarch and *Heliosporites* in Tetrads	
3060	-26,558	3060	12,712	Less AOM than in 3060, many acritarchs in AOM	
3040	-28,759	3040	7,803	*Classopollis* dominant	
3020	-27,651	3020			
3000	-27,526	3010	14,824	Classopollis, Riccisporites, *Cymatiosphaera*, *Thittodiscus*, *Acritarchs*	
2970	-22,642/ -22,105	2980	10,872	Very little organic material, *Classopollis* (no tetrads), *Rhaetipollis*	
2950	-22,853	2960	12,268	Few palynomorphs, mainly spores (*Limbosporites*)	
2920	-24,165	2930			
2890	-22,831	2910			
2850	-23,2/ -22,327	2870	8,234	Few palynomorphs, *Deltoidospora*, *Semiretisporis* (fragments)	
2820	-22,951	2840			
2800	-23,068	2820			
2770	-23,46	2805			
2750	-23,176/ -22,661	2790			
2700	-23,432	2760			
2650	-23,415/ -22,593	2710			
2600	-23,322/ -22,662	2660			

2550	-23,164/ -22,47	2620	16,171	Spores dominate	
2500	-23,482	2580			
2450	-23,345	2530	16,081	Spores dominate	
2400	-23,612	2500			
2350	-23,342	2460			
2300	-23,346	2405			
2250	-23,415	2370			
2200	-22,792/ NA / NA	2325			
2150	-23,256/ -22,237	2280			
2095	-23,52	2230	9,207	*Limbosporites, Cosmosporites*	
2045	-23,598	2195			
2000	-24,838	2155			
1950	-23,802	2115			
1900	-23,974	2080			
1850	-23,424	2030			
1800	-23,979/ NA	1995	8,853	*Cingulizonates, Porcellispora*	
1755	-23,221	1960			
1700	-23,046/ NA	1910			
1650	-22,967	1870	8,97	Almost barren	
1600	-23,291	1820			
1550	-23,472	1780			
1500	-23,237	1730			
1450	-23,496	1700	13,441	Very high maturity of spores *Limbosporites,*	
1400	-23,332	1660			
1350	-23,193	1610			
1300	-23,604	1580			
1250	-23,723	1530			
1200	-23,371	1490			

1150	-23,856	1440	9,473		
1100	-24,008	1400	10,193	*Kyrtomisporis*, *Botryococcus*, Dinoflagelates	
1075	-22,998	1380	15,031	High maturity (*Classopollis* in spore colour)	
1051	-25,145	1350	6,025	*Limbosporites*	
1042	-28,113	1340	11,752	*Rhaetipollis*, *Classopollis*, *Rhaetogonyaulax*, *Ovalipollis*	
1036	-27,693	1330	8,677	*Rhaetipollis*, *Classopollis* *Rhaetogonyaulax*, *Cleistosphaeridium*	
1018	-27,069	1320	9,024	*Rhaetipollis*, *Classopollis*, *Rhaetogonyaulax*,	
1012	-27,553	1310	10,153	*Rhaetipollis*, *Classopollis* (many), few *Riccisporites*	
1000	-26,498	1300	10,398	Different *Classopollis* types, Dinoflagelates	
980	-27,174	1280	9,018	Small acritarchs, *Classopollis*, *Rhaetipollis*	
952	-27,031	1252	10,873	*Geopollis*, *Rhaetipollis*, *Botryococcus*, Acritarchs	
920	-27,119	1220	9,705	Many (!) *Rhaetipollis*, Dinoflagelates	
900	-26,696	1200	10,923	Many (!) *Rhaetipollis*, *Riccisporites*, *Ovalipollis*	
850	-25,071	1150			
800	-24,789	1100			
750	-25,096	1050	9,612	Very long wood remains	
700	-28,388	1000			
650	-26,984	950			
610	-27,042	910	11,950	*Rhaetipollis*, *Suessia*	
550	-29,215	850			

500	-27,647	800			
450	-25,417	750	10,551	*Ricciisporites* (strongly dominates)	
400	-27,025	700			
350	-27,49	650			
300	NA /-27,054	600		*Classopollis* (Tetrads) (!!!)	
250	-27,626	550			
200	-27,832	500			
150	-26,983	450	11,651	*Classopollis* (Tetrads) (!!!)	
100	-27,312	400			
60	-25,455	360			
0	-27,458	310	8,465	*Classopollis* (Tetrads), AOM +Acritarchs, *Enzonalaspor.*	
-25		295	6,883	*Leiosphaeridia* (dominates), *Rhaetipollis*	
-50		270	7,998	*Leiosphaeridia* (dominates), *Ricciisporites*, *Rhaetipollis*	
-75		255	7,104	*Ricciisporites* + *Ovalipollis* dominant, *Botryococcus*, *Leiosphaeridia*	
-100		225	7,655	*Heliosporites*, few and broken up palynomorphs	
-125		200	6,251	Poor preservation, pyrite	
-150		175	8,761	Few *Classopollis*, almost nothing else	
-175		150	7,502	Not even organics only *Lycopodium*	Barren
-200		125	7,245	Only one slide with hardly anything but *Lycopodium*, not organics	
-225		50	6,642	Not more than 76 items countable, residue empty	
-250		25	7,007	Not even organics only *Lycopodium*	Barren
-275	-27,021	0			

II. Facies Overview of Detailed Sampling