



## Research article

# 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

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## ABSTRACT

The end-Triassic mass extinction is often linked to environmental and climate change triggered by the activity of the Central Atlantic Magmatic Province ca. 201 Mya. In the German Triassic Basin, the transition from pre-extinction to the so-called extinction interval is documented from the fossil-rich Contorta Beds to the mostly barren Triletes Beds. However, despite the lack of macrofossils, plant microfossils are present and studying palynomorph diversity and assemblages still give us a detailed insight into the impact of environmental changes on the flora.

Here, we present data from 64 samples taken from the new Triassic-Jurassic section 'Bonenburg', which originates from a brick quarry in North Rhine-Westphalia (Germany), and encompasses the Triassic-Jurassic transition in the Germanic Basin. Using palynofacies analysis, we document changes in the depositional environment. Based on terrestrial and marine palynological analysis, we also document quantitative changes in four assemblage zones for correlation with other European sections. Further, we discuss the vegetation history with special focus on the transition from the pre-extinction to extinction interval (Contorta to Triletes Beds). Additionally, we investigate palynofloral diversity patterns especially prior to the Triassic-Jurassic transition, to evaluate the ecological impact of environmental upheaval on the flora. Furthermore, we document intraspecific palynomorph variability, indicating a variety of aberrant spore, pollen, and tetrad formation, in the middle Rhaetian, the lowermost upper Rhaetian, and the lowest Hettangian.

Our study supports existing paleogeographical reconstructions for the region and reveals, that vegetation underwent gradual changes with intermediate successional stages rather than dramatic extinction or drastic turnover as documented for animals. Diversity patterns coinciding with aberrant palynomorph occurrences, potentially associated with episodes of increased environmental stress, suggest three disturbances pulses of probably increasing severity. Although environmental stress in the context of diversity patterns seems a likely explanation for the occurrence of aberrant palynomorphs, further investigations are needed to better understand the underlying mechanisms and their evolutionary significance and temporal connection with biotic crises.

## 1. Introduction

The end-Triassic mass extinction (ca. 201.5 Ma) is one of the 'Big Five' mass extinctions regularly discussed as a reference point to evaluate the potential sixth mass extinction of the present day (Bambach, 2006; Barnosky et al., 2011; Wotzlaw et al., 2014), which is a topic of increasing significance for society as movements like the 'extinction rebellion' illustrate (Farand, 2018; Iqbal, 2019). The end-Triassic mass extinction is often linked to the activity of the Central Atlantic

Magmatic Province as the trigger of environmental and climate change (e.g. Blackburn et al., 2013; Deenen et al., 2010; Landwehrs et al., 2020; Percival et al., 2017; Ruhl et al., 2020; Tanner, 2018). Its severity for marine organisms is estimated as a 63% generic diversity loss of marine invertebrates and severe ecological devastation, but its impact on the floral realm is still disputed (Alroy et al., 2008; Bambach, 2006; Dunhill et al., 2018; Hönisch et al., 2012; Kiessling and Aberhan, 2007; Kiessling and Simpson, 2011; Sepkoski, 1981). Firstly, because of conflicting results from palynology, i.e. plant microfossils as opposed to

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their macrofossils, due to differences in taphonomy and taxonomical resolution (Mander et al., 2010). And secondly, because some studies document high taxonomic plant loss and biodiversity disturbance (Lindström, 2016; McElwain and Punyasena, 2007; Olsen et al., 1990), whereas others do not document such severe changes in the flora (Götz et al., 2011; Pedersen and Lund, 1980; Ruckwied and Götz, 2009) and/or interpret changes in composition as gradual ecosystem change (Barbacka et al., 2017; Bonis and Kürschner, 2012; Li et al., 2018). Yet, a better understanding of the impact on plants is crucial, because they represent the primary producers, and any effect on them can cascade throughout the entire ecosystem (McElwain et al., 2007; Vermeij, 2004).

To study the impact on the flora, many paleobotanical studies focus on diversity. The most commonly used response variable for diversity in ecological studies is species richness (Svensson et al., 2012). Accordingly, the impact of disturbance on the floral realm and the severity of the biotic crisis is usually measured in terms of variation in species richness and taxonomic diversity in paleopalynological studies (Barbacka et al., 2017; Bonis et al., 2009; Bonis and Kürschner, 2012; Lindström et al., 2016). Despite elaborate discussions about which indices depict diversity most adequately, there is a general consensus amongst modern ecologists, that diversity cannot be described by richness, i.e. the number of species, alone, but has to be complemented by evenness, i.e. how equal abundances are distributed amongst these species (Jost, 2010; Lloyd and Ghelardi, 1964; Pielou, 1966; Tuomisto, 2012). While standardly investigated in younger time intervals and faunal studies, especially molluscs, throughout earth history (e.g. Alroy et al., 2008; Giesecke et al., 2014; Holland, 2016; Martinelli et al., 2017), richness is more rarely examined together with evenness in floral, especially in Mesozoic paleopalynological studies (but see Barreda et al. (2012) for plant microfossils and McElwain et al. (2007) for plant macrofossils). As a result, some modern ecologists have criticised paleobotanical studies, especially those leading up to mass extinctions, to underutilize evenness and thus provide insufficient data to compare with community changes of the present (Lyons and Wagner, 2017). Studies comparing fossil and extant assemblages suggest that preservation biases generally elevate evenness values in the past, but also show, that evenness is discernible in the fossil record (Lyons and Wagner, 2017; Olszewski and Kidwell, 2007).

Similarly, studies on mass extinctions from a variety of disciplines, also stress the necessity to study ecological severity beyond taxonomic loss, as a severe impact on the ecosystem, i.e. a disturbance might also manifest itself in form of ecological restructuring (Droser et al., 2000; McElwain et al., 2007; McElwain and Punyasena, 2007; McGhee et al., 2004; Twitchett, 2006). In classical ecology, the relationship between disturbance, i.e. environmental change and biodiversity, can be described by the intermediate disturbance hypothesis (IDH), which predicts that diversity peaks at an intermediate level of disturbance (Connell, 1978; Grime, 1973; Osman, 1977). Although rather simplistic (Huxham et al., 2000; Shea et al., 2004), the IDH is still the most commonly used tool in ecology and conservation management, e.g. in Yellowstone National Park (US), to evaluate the impact of a changing environment on an ecosystem (Svensson et al., 2012). It is based on the classical ecological assumption, that few species dominate the assemblage when disturbance is absent. Reversely, it assumes, that, if the community is stressed, this causes ecological restructuring and changes the abundance distribution amongst the present taxa. This is supported and can be exemplified by the different forest successional stages. For the impact on the ecosystem disturbances (e.g. a wildfire) have two important aspects, their magnitude (e.g. the severity of the fire) and temporal distribution (e.g. how frequent the fires reoccur and how much time has passed since the last wildfire). After a disruptive disturbance (e.g. a severe fire), propagules (e.g. seeds or spores) quickly colonize the cleared space and dominate immediately after the disturbance leading to high dominance of pioneers, but low richness/evenness in the first stage of succession. In the second successional stage, when either lower levels of disturbance occur or the time-interval in between disturbances increases, species with lower dispersal power and

slower growth can reach maturity, wherefore richness and evenness increase. During the third successional stage, when a long-lasting disturbance further decreases in strength or time interval to the initial disturbances further increases, richness and evenness will decrease again as those species that are most competitive (e.g. exploit resources most effectively) start to outcompete others, wherefore some species become more dominant. Given that disturbances regularly interrupt the competitive process, most communities never reach an equilibrium, but move between stages depending on the magnitude of and frequency in between disturbances, with the highest richness and evenness occurring in times of intermediate disturbance, i.e. intermediate strength or an intermediate time interval to the initial or in between disturbances (Connell, 1978).

Following this, dominance could be used as an immediate disturbance indicator, but is potentially difficult to discern in the palynological record. Even today pioneering plant assemblages are quickly, often within a few years, replaced by later successional stages. In the microfossil record, unless sampling allows very high-resolution, temporal compression and taphonomically biased dominance peaks can make it hard to trace the pioneering successional stage. While dominance can inform about disturbance in temporarily highly resolved samples, evenness, studied together with richness in view of dominance for one ecosystem, can over longer periods of time, inform not only about the magnitude of disturbances but also about their frequency.

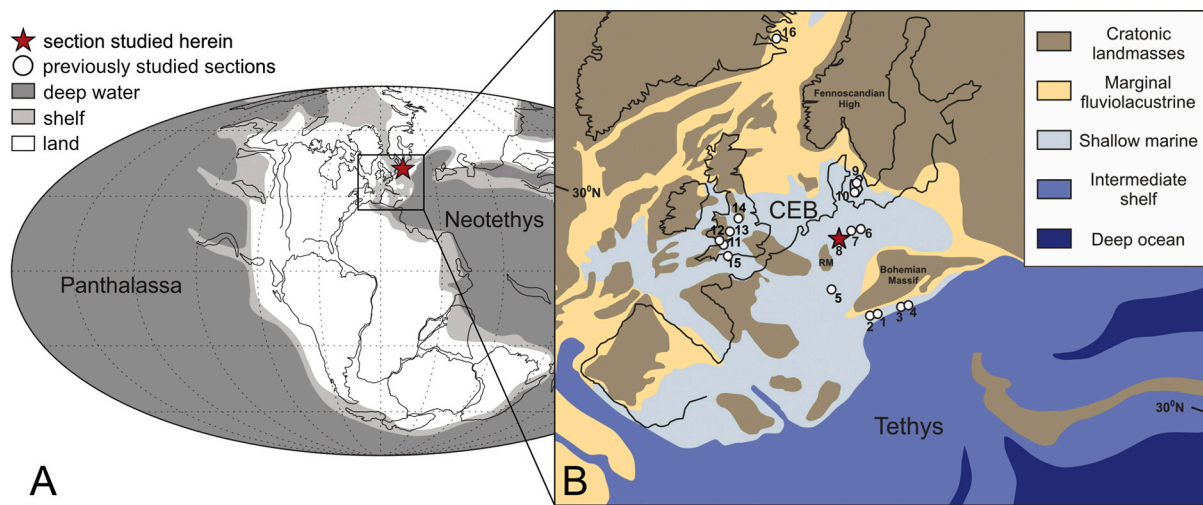
Using diversity to assess floral ecosystem change leading up to the end-Triassic extinction event, this study focuses on the onset of the biotic crisis, i.e. the transition from the pre-extinction to the extinction interval. While most studies focus on the Triassic-Jurassic (TJ) transition itself, this new focus can help to understand the events that led up to the biotic crisis and when the tipping point was reached. This is not only relevant for a better understanding of the end-Triassic transition as such, but also to provide more data for ecological systems in crisis, and adds to our understanding and identification of warning signs of ecological transitions in the past, as well as in the present day (Dakos et al., 2008; Kéfi et al., 2014; Scheffer et al., 2009).

In the Germanic Basin, the transition from the pre-extinction to the extinction interval is documented from the fossil-rich Contorta Beds to the palynomorph-rich, but otherwise barren, Triletes Beds. The new TJ-section from Bonenburg, from which the first Rhaetian plesiosaurus was recovered (Sander et al., 2016; Wintrich et al., 2017), is a particularly extended succession of Rhaetian to Hettangian strata and therefore ideal to open a broad window into the onset of environmental upheaval as well as the biotic crisis itself. So far, it has been mainly studied for vertebrates, chemo- and biostratigraphy only (Sander et al., 2016; Schobben et al., 2019; Wintrich et al., 2017).

Here we investigate this new section (1) for its depositional environment in order to contextualize subsequent data into a changing environment and to consider potential biases introduced by the latter, and (2) to provide the first detailed palynostratigraphic framework of this new section to allow comparison of our findings with other contemporaneous European sections. Based on palynomorphs, the only fossil group continuously occurring from the pre-extinction and throughout the extinction interval, we (3) reconstruct the vegetation history as recorded in the palynoflora, and employ standard diversity indices (richness, evenness, dominance and the Shannon index) over time to (4) study the plant ecosystem-response and impact of environmental change on the (palyno-) floral realm. We focus especially on the transition from the pre-extinction to extinction interval from an ecological perspective, and evaluate extinction patterns and ecosystem changes at the onset of the end-Triassic biotic crisis.

## 2. Regional setting

In the Late Triassic, Northern Europe was situated at temperate latitudes (between 30° N and 50° N) in a shallow epicontinental sea with emerged cratonic landmasses, such as the Bohemian and Rhenish Massif and the Fennoscandian High. A number of well-studied TJ-sections are known from the shallow marine Central European Basin



**Fig. 1.** Paleogeographical reconstruction for the Late Triassic (Rhaetian). A. worldwide reconstruction, star indicating Bonenburg section location studied herein (modified after Golonka et al., 2018; Martindale et al., 2015). B. Central European Basin and western Tethys shelf seas with previously palynologically studied sections: 1. Kuhjoch (Austria)-Bonis et al. (2009); Hillebrandt et al. (2013), 2. Hochalplgraben (Austria)-Bonis et al. (2009); Bonis and Kürschner (2012), 3. Kendlbachgraben (Austria)-Morbey (1975), 4. Tiefengraben (Austria)-Kürschner et al. (2007), 5. Mingolsheim (Germany)-Lindström et al. (2017b), 6. Mariental (Germany)-Heunisch et al. (2010), 7. Schandelah (Germany)-Lindström et al. (2017b); van de Schootbrugge et al. (2019), 8. Bonenburg (Germany)-this study, 9. Stenlille (Denmark)-Lindström et al. (2012), 10. Rødby (Denmark)-Lund (1977), 11. St. Audrey's Bay (UK)-Bonis et al. (2010a); Bonis and Kürschner (2012), 12. Lavernock Point (UK)-Orbell (1973), 13. Upton (UK)-Orbell (1973), 14. Owthorpe (UK)-Orbell (1973), 15. Charton Bay (UK)-Orbell (1973), 16. Astartekløft (Greenland)-Mander et al. (2013). Modified after Schobben et al. (2019); van de Schootbrugge et al. (2009).

(CEB) and the western Tethyan intermediate shelf seas (see Fig. 1 and references for localities therein) (Schobben et al., 2019).

The Bonenburg section (Fig. 1) is situated in the middle of British sections to the west (St. Audrey's Bay-Bonis et al., 2010; Lavernock Point, Upton Borehole, Owthorpe, Charton Bay-Orbell, 1973), Scandinavian and Greenland sections to the north (Rødby-Lund, 1977; Stenlille-Lindström et al., 2012; Astartekløft-Mander et al., 2013), and southern sections from Germany (Mingolsheim-Lindström et al., 2017b) and Austria, i.e. sections from the Eiberg Basin, including the Global Stratotype Section and Point (GSSP) Kuhjoch-Bonis et al., 2009; Hillebrandt et al., 2013; van de Schootbrugge et al., 2009. Together with the other German sections Mariental (Heunisch et al., 2010) and Schandelah (Lindström et al., 2017b; Van de Schootbrugge et al., 2019), Bonenburg has the potential to improve correlations and increase our understanding of vegetational gradients from the Tethys to the north of the CEB. Compared to all the other Central European Basin sections, Bonenburg is the one situated closest to the Rhenisch Massif.

In the Germanic Basin in the center of the CEB, the Upper Keuper is divided into three distinct lithological units, which are distinguished by their respective fossil assemblages (Will, 1969). The pale green dolomitic marlstones of the Postera-Beds depict a species-poor bivalve fauna (especially *Unionites postera*). The Postera Beds have been typified as a transitional marine-terrestrial setting, ranging from brackish to fresh-water, based on the occurrence of conchostracans and ostracods (De Graciansky et al., 1998; Hallam, 1981), and following the transition from the non-marine deposits to progressive deepening of the CEB in the Late Triassic (Bachmann et al., 2008; Fischer et al., 2012). The siliciclastic Contorta Beds developed under ongoing rising sea-levels and represent a change to fully marine depositional settings across the CEB and are named after the abundantly occurring bivalve *Rhaetavicula contorta* (Bachmann et al., 2008; Fischer et al., 2012; Seegis, 2005). The contemporaneous change in facies to high quantities of clastic and terrestrial plant remains, and the infrequent development of bonebeds, has, furthermore, led to the suggestion that these deposits were part of vast deltaic plains with materials sourced from the nearby Fennoscandian and Bohemian highs (Bachmann et al., 2008; Barth et al., 2018; Fischer et al., 2012; Nielsen, 2003; Trueman and Benton, 1997). The black shale unit is indicative of a marine to coastal depositional setting following a deepening of the CEB during the early Rhaetian, which appears to have been forced by a global transgression (Hallam and Wignall,

1999). Peak occurrences of marine palynomorphs are interpreted to indicate a Late Triassic sea-level high-stand during this interval (Barth et al., 2018; Lindström and Erlström, 2006).

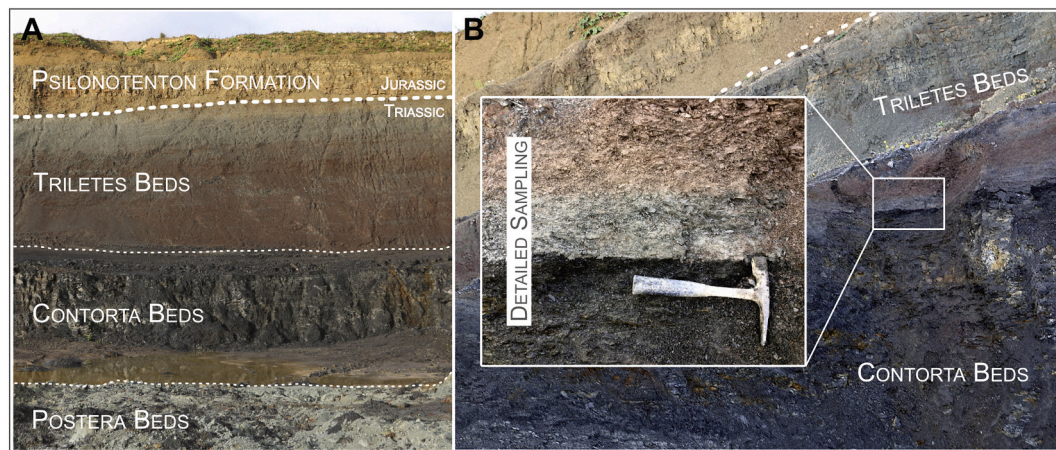
The Contorta Beds are succeeded by an organic matter-poor silt and deltaic sandstone with sporadic small-scaled wave ripples and faint cross-stratification in the Triletes Beds, that are depleted of marine fauna and characterized by plant microfossils and the eponymous megaspore *Triletes* (Schobben et al., 2019; Schulz and Heunisch, 2005). Similar units are known from Scandinavia (Lindström et al., 2017b, 2015, 2012; Vajda et al., 2013) and from the Eiberg Basin with a unit, similarly reddish as the Triletes Beds, known as the 'Schattwald Beds' (Krystyn et al., 2005; McRoberts et al., 2012, 1997). Their similarities in lithology and palynological assemblages, especially the *Polypodiisporites polymicroforatus* abundance interval, has facilitated their correlation and given their faunal depletion, representing the end-Triassic extinction interval, they have been addressed under the shared name 'Event Beds' (Lindström et al., 2017b; Schobben et al., 2019). This progradational unit marks successive shallowing of the CEB, and other basins in Europe, triggered by either sea-level drop or a change to increased terrigenous input to the basin (Hallam and Wignall, 1999; Lindström et al., 2017b; Pálffy and Zajzon, 2012; van de Schootbrugge et al., 2009).

The base of the Jurassic is defined by the first occurrence of *Psiloceras spelaetirolicus*, the oldest known psiloceratid ammonite (Hillebrandt et al., 2013; von Hillebrandt and Krystyn, 2009), in the GSSP section Kuhjoch of the western Tethys shelf. In the CEB, the earliest Jurassic sediments contain ammonites from the younger *Planorbis* biozone (Pylonotenton Formation) and therefore lack a part of the TJ-transition or are highly condensed (e.g. Barth et al., 2018; Lindström et al., 2017b; Schobben et al., 2019; van de Schootbrugge et al., 2008). Superimposed marl- and mudstones with occasional well-bedded to nodular, ammonite-bearing limestone beds of the Pylonotenton Formation signify a return to more open marine conditions relative to the underlying unit (Blind, 1963; Bloos, 1999; Wetzel, 1929).

### 3. Material and methods

#### 3.1. Materials

The Bonenburg section (Fig. 2) derives from an outcrop in an active



**Fig. 2.** Overview of the Bonenburg section. A. Outcrop in an active brick quarry near the village of Bonenburg (51.5631°N; 9.0401°E), showing the Rhaetian Postera, Contorta and Triletes beds and the Lower Jurassic Ppsilonotenton Formation. The studied section is 40 m in height. B. Close-up of the lithological shift from the Contorta Beds to the Triletes Beds (i.e. from the pre-extinction to the extinction interval).

clay pit operated by a brick-factory, August Lücking GmbH & Co.KG, situated 1 km NW of the village of Bonenburg (City of Warburg, Germany; 51.5631°N; 9.0401°E). Over a 40 m interval, 69 samples were collected with denser sampling across lithological changes. Six samples were taken from the Postera Beds, 19 from the Contorta Beds, 13 from the Triletes Beds, and 12 from the Ppsilonotenton Formation (Fm.). 19 high-resolution samples (detailed sampling) (Fig. 2B) were taken from the transition from the black shaly Contorta Beds, through a conspicuous grey clayey layer at the very bottom of the Triletes Beds until the typically reddish mudstone to fine-grained sandstone of the Triletes Beds, which is very pronounced in Bonenburg and somewhat reminiscent of the Schattwald Beds of the Austrian localities.

### 3.2. Palynological processing

All samples were processed in the palynological lab of the University of Oslo (UiO, Norway). Between 5 and 15 g of dry sediment was crushed, supplemented with a *Lycopodium* tablet (containing 12,542 spores on average). Samples were then processed to standard palynological protocol (Traverse, 2007) using cold 10% hydrochloric acid (HCl) and 38% hydrofluoric acid (HF), heated in warm water bath for 2 days to 60 °C and finally heavy liquid separation with Zinc chloride (ZnCl<sub>2</sub>) to remove carbonate, silicate minerals and the remaining inorganic residue (e.g. pyrite), respectively. After each step, the residue was neutralized. Samples were sieved with a 15 µm mesh and the organic residue was mounted with Entellan®Neu on four slides. They are stored at the Geoscience Department of the University in Oslo (UiO), Norway.

### 3.3. Counting

All slides were studied using an Olympus CX31 mounted with an Olympus SC50 camera. Palynofacies analysis was conducted by counting ca. 300 particles per sample and classifying them according to the palynofacies classification by Tyson (1995). Quantitative palynological analysis was conducted by counting all palynomorphs until a minimum of 300 terrestrial palynomorphs was reached. Each specimen was counted as one, while those occurring in clusters such as tetrads, triads, dyads were counted as four, three, and two, respectively. However, the amount of each cluster type was recorded, to allow calculations of lumped occurrences as one item, i.e. to avoid overrepresentation due to this clustering effect and to facilitate comparison to other profiles, where different counting/calculation schemes were used. For qualitative analysis, the rest of the counted slide, plus one additional slide, were scanned for rare taxa outside the count.

Palynomorph classification was based on Klaus (1960), Morbey (1975), Nilsson (1958), Pedersen and Lund (1980), Schulz (1967), Schuurman (1976, 1977).

### 3.4. Statistics and visualization

Palynofacies and palynology counts were transformed into concentrations and percentages and visualized in Tilia (Grimm, 2011). According to standard practice, palynological data is represented with the terrestrial and aquatic components set as 100%, respectively (Figs. 4, 5, 10 and Supplementary Fig. 3). Due to strong pollen dominance in many samples, we additionally figured the spore and pollen assemblages separately (i.e. each treated as 100% percent; in Fig. 10 and Supplementary Fig. 4) to also allow visualization of changes within the spore assemblage. For comparison of our data of the transition from the pre-extinction to the extinction interval, the same procedure was conducted for corresponding datasets from previously published sections with sufficient data points: Kuhjoch and Hochalplgraben (Bonis et al., 2009).

Assemblage zones and subzones were calculated by constrained clustering analysis using the CONISS-function in Tilia with a threshold of 3.5 total sum of squares (TSS) for palynofacies zones, 9 TSS for palynomorph zones of first-order (assemblage zones), and 6 TSS for palynomorph zones of second-order (sub-zones). AOM-Palynomorph-Phytoclast Ternary diagrams after (Tyson, 1995, 1993) and diversity indices (genus richness, rarified richness ( $n = 100$ ), and Pielou's Evenness (J), Shannon index (H), and Dominance (D)) were analyzed in Past (Hammer et al., 2001, 2018). Genus richness was preferred over species richness to reduce the classification bias introduced by varying states of preservation within a section. This also allows easier comparison with other published records across the TJ-boundary with classifications to varying taxon levels. In order to verify the independence of the diversity indices from the depositional environment, e.g. through the 'Neves Effect' (Chaloner, 1958), we tested the correlation with the relative pollen content from palynofacies analysis. This is to avoid the overrepresentation of pollen-producing upland plants with increasing distance to the shore, which can confound assemblage composition.

For normal and non-normal distributed data we used R to perform Pearson and Spearman correlation, respectively (R Core Team, 2019). Botanical affinities are inferred from in situ finds. Where no in situ data is available, broader associations to groups (e.g. Lycophytes, Gymnosperms) are assumed based on morphological traits and literature discussion (e.g. Balme, 1995; Bonis, 2010; Lindström, 2016). Diversity and isotope curves were plotted using C2 (Juggins, 2016).

### 4. Results

#### 4.1. Palynofacies

Seven palynofacies zones (F1-F7) derived from CONISS-cluster analysis (supplementary Fig. 1) could be identified and generally correspond well with clustering of samples in palynofacies fields (I-IX) in the Tyson ternary plot (A-C) (Fig. 3). Minor differences between palynofacies zones and clustering in the ternary plot are indicated through colour-coding in the palynofacies zone column. This is caused by samples with a transitional character, i.e. those with quickly fluctuating changes from one sample to another that subsequently plot in very different palynofacies fields in the ternary plot (compare arrows in Fig. 3A-C).

F1 (0–2.25 m): The first palynofacies zone is dominated by translucent phytoclasts and contains 10–20% opaque phytoclasts, 10–20% AOM, pollen and prasinophytes. In the Tyson plot (T-Plot), samples cluster together in field II (marginal basin), while the last two samples depict a shift towards the shelf to basin transition (field IV) (Fig. 3A, rhombus symbol).

F2 (2.55–2.7 m) is similar to F1, but with distinctly higher abundance of terrestrial palynomorphs (15–35%), especially pollen. Samples from this zone connect those from the previous and ensuing zone in the T-Plot (Fig. 3A, star symbols and arrow). An acritarch acme (40%) occurs at 2.7 m (BB-50) and the sample plots in field V ('distal shelf').

F3 (2.95–12.8 m) is characterized by the highest terrestrial

palynomorph content, as well as high numbers of aquatic palynomorphs, while other palynofacies components are similar to F1, but AOM is less abundant (up to 10%). In the T-Plot, the first samples of this zone plot in the shelf to basin transition (field IV) and all subsequent samples in the proximal shelf field (III) (Fig. 3A, triangle symbol).

F4 (13–13.4 m) is distinguished by a peak abundance of AOM and dinoflagellates and the T-plot depicts the transitional character of the zone (Fig. 3B, star symbol and arrow). The first samples plot in the shelf to basin transition (field IV) succeeded by a sample from a dysoxic episode in field VII, returning to more oxic conditions in field V (oxic 'distal shelf') with the last sample of the zone. The same pattern can be observed in more detail, when plotting the detailed samples (BB-D) in the ternary diagram (supplementary Fig. 2).

F5 (13.5–29.6 m) depicts a strong dominance of spores amongst the palynomorph component of kerogen. AOM is almost absent and translucent phytoclasts dominate with the highest amounts of cuticles along the profile, often preserved in macroscopic pieces. In the T-Plot all of the samples plot in the highly proximal shelf or basin field (I) (Fig. 3B, circle symbol).

F6 (29.8–31.25 m) is characterized by the highest abundance of AOM within the profile and increased abundance of acritarchs. In the T-Plot, this zone again depicts a transitional character, (fields VII and VI, distal 'shelf' and proximal shelf, respectively), i.e. bridging over to the following samples in the next zone (Fig. 3C, star symbol and arrow).

F7 (32–37.30 m) samples resemble the description of F1 and,

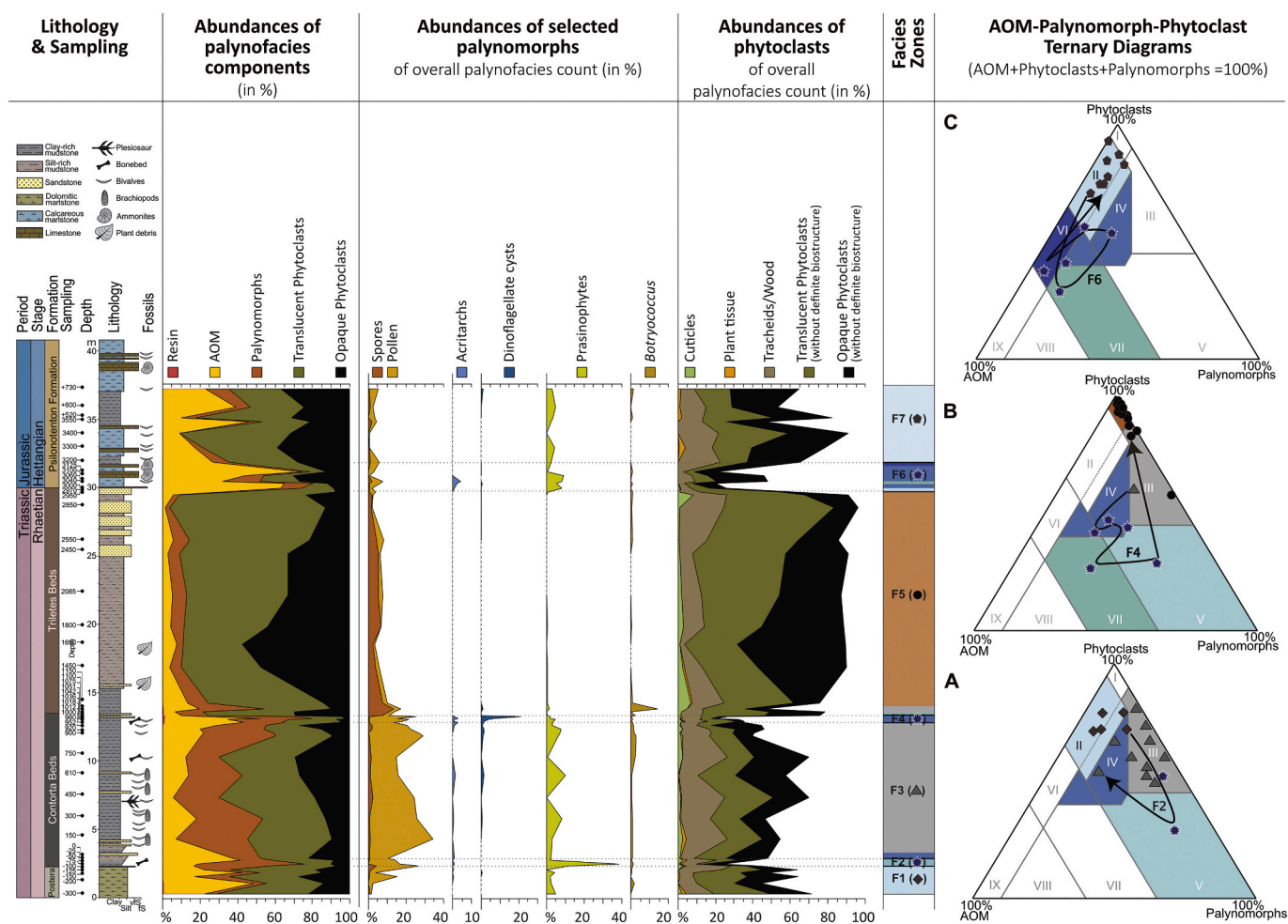
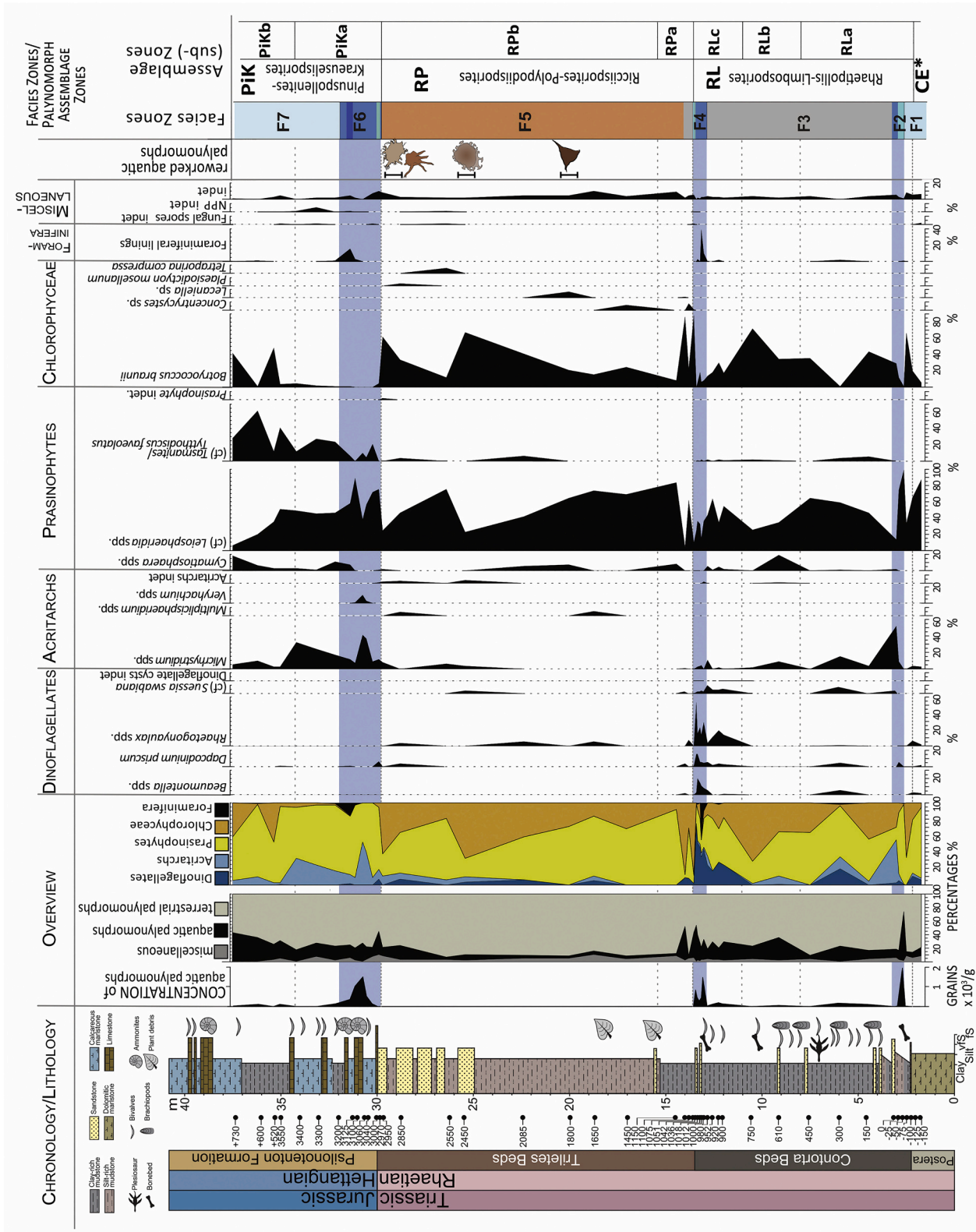


Fig. 3. Palynofacies analysis and abundances of their components along the Bonenburg section. Palynofacies zones derived from CONISS-analysis (dendrogram given in supplementary Fig. 2), and colour-coded to match the respective samples as plotted in the AOM-Palynomorph-Phytoclast Ternary Plots (A-C) after Tyson (1995). 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.



**Fig. 4.** Overview of aquatic palynology and non-pollen palynomorphs (NPPs). Miscellaneous groups refer to fungal spores, NPPs, and undetermined items that cannot with certainty be included in aquatic nor terrestrial group. Concentration of aquatic palynomorphs is given per g of analyzed rock sample. For each of the stacked groups of aquatic palynomorphs, the respective individual constituents are depicted on the right. Palynomorph assemblage zones from terrestrial palynomorph analysis and palynofacies zones from palynofacies analysis are given on the right for comparison; marine incursions are indicated in blue. CE\* = Classopolis – Enzonelasporites zone. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

accordingly, plot in the same palynofacies field (II-marginal basin) (Fig. 3.C, pentagon symbol).

In general, major palynofacies zones (F1, 3, 5, 7) more or less correspond with main lithological changes (see Schobben et al., 2019 for more details), but within one and the same lithology often a number of different palynofacies are recognized (compare F4), while at other times one palynofacies encompasses different lithologies (compare top of F5).

## 4.2. Palynology

### 4.2.1. Aquatic palynology and non-pollen palynomorphs

Aquatic elements are constantly present and generally make up 20–40% of the overall palynoflora throughout the Bonenburg section. However, they exhibit distinct changes with peak abundances (40–80%) at the base and top of the Contorta Beds, as well as two relatively smaller peaks at the base of the Pylonotenton Fm., with a steady increase afterwards (Fig. 4). Except for the first peak in the Pylonotenton Fm., these abundance peaks coincide with peaks in aquatic palynomorph concentrations.

Most samples from the base of the section, i.e. the Postera Beds, were barren, but two samples (1.5, 2.25 m) were productive and dominated by *Leiosphaeridia*. The base of the Contorta Beds depicted the first peak abundance of aquatic palynomorphs in relation to terrestrial palynomorphs, driven by successive peaks of *Botryococcus*, *Leiosphaeridia* and *Micrhystridium*. The middle of the Contorta Beds depicts a clear *Cyatiosphaera* acme. Towards the end of the Contorta Beds, *Botryococcus* spp. is decreasing, while other marine elements are increasing in abundance, especially the dinoflagellate cyst *Rhaetogonyaulax rhaetica*. The base of the Triletes Beds is characterized by a short peak abundance of *Botryococcus*.

The high-resolution sampling depicts the same trends across the transition from the Contorta Beds to the Triletes Beds (supplementary Fig. 3). The high abundance of *Rhaetogonyaulax rhaetica* is replaced by an abundance of *Micrhystridium* at the top of the Contorta Beds, which in turn is succeeded by increased abundances of *Botryococcus* at the base of the Triletes Beds. Thereafter, *Leiosphaeridia* and *Botryococcus* alternate in high abundance.

Noteworthy is the occurrence of *Concentricystes* with the first sample of the conspicuous grey layer at the base of the Triletes Beds and its continued, but reduced occurrence until its complete disappearance after the first third of the Triletes Beds (i.e. after 18.7 m). After 26.3 m, i.e. the beginning of last third of the Triletes Beds, we noted a short influx of Chlorophyceae (*Plaesiodyctyon mosellanum*) and Zygnemataceae (*Tetraporina crassa*, *Lecaniella* sp.), coinciding with decreased numbers of *Botryococcus*; the latter increases again towards the very top of the Triletes Beds. At the same time, reworked, probably Paleozoic palynomorphs, however rare and mostly apparent through qualitative analysis, occur continuously after the noted influx of Chlorophyceae, coinciding with a continued appearance of fungal spores and other non-pollen-palynomorphs (NPPs). They are not present any more above the top of the Triletes Beds.

From the Pylonotenton Fm., *Micrhystridium* becomes a more dominant feature of the assemblage and Prasinophytes strongly increase in abundance, especially *Tasmanites*. Fungal remains and non-pollen-palynomorphs continue to appear throughout the Pylonotenton Fm. and a small but distinct acme of cf. *Paleopericonia* sp. in BB3300 (Fig. 9S) is noticed at 33 m.

### 4.2.2. Terrestrial palynology

The succession is generally dominated by pollen and terrestrial components constituting ca. 60–75% of the palynological assemblage (Fig. 5). The Triletes Beds is an exception as it contains very low amounts of aquatic palynomorphs (< 10%) and high number of excellently preserved spores (compare Figs. 6 and 7). Terrestrial palynomorph concentrations are rather low throughout the section, except at the base and top of the Contorta Beds, and at the base of the

Pylonotenton Fm. Terrestrial palynomorph concentration peaks mainly consist of pollen and coincide with marine incursions and relatively poor preservation (compare Fig. 9.15–17) at the top and base of the Contorta Beds and Pylonotenton Fm., respectively. The base of the latter also depicts the only spore peak within the section, which is more than three-times bigger than the average concentrations during the spore dominated Triletes Beds (Fig. 5). Based on the changes of palynomorph abundances throughout the profile, the four informal assemblage zones and seven subzones, could be distinguished based on CONISS-Cluster analysis (Fig. 5), complementing the semi-quantitative results published in Schobben et al. (2019). The zones mostly correspond with and are therefore named after Lund's (1977) zonation, except for the PiK zone.

The Classopollis-Enzonasporites zone (CE-zone; up to 1.5 m) is represented by only one sufficiently productive sample, originating in the Postera Beds, that contains around 20 taxa with a strong dominance of *Classopollis* and *Geopollis*, with very few spores (mainly *Deltoidospora/Concavisporites* spp.). Three other samples from the top of the Postera Beds did not yield enough palynomorphs for qualitative analysis (i.e. less than 300 terrestrial palynomorphs), but qualitative analysis of these samples documents the presence of the nominate taxon *Enzonasporites* (also compare Schobben et al., 2019) and supports tentative designation of this zone.

The Rhaetipollis-Limbosporites zone (RL-zone, 1.75–13.40 m) is distinguished by the appearance of the eponymous taxon *Limbosporites lundbladiae* [originally published as '*lundbladii*' Nilsson, 1958]. It should be noted that this writing is not a typographical error. The taxon was named after Brita Lundblad and the gender of the epithet is in its current form incorrect and is here corrected in conformity with Art. 60.8 (International Code of Botanical Nomenclature) to appropriately reflect the gender of the person it commemorates. It should be henceforth used in this corrected form.

The RL-zone is further characterized by a sharp increase in *Ricciisporites tuberculatus* and the highest percentage of *Rhaetipollis germanicus* and *Ovalipollis* within the section. *Classopollis* is still abundant, but less prominent than in the previous zone. The zone can be further subdivided in three sub-zones (a-c) mainly driven by abundance changes in the three just mentioned taxa. RLa (1.75–7.5 m) is characterized by decreasing *Classopollis* abundance and a small peak (5%) of *Geopollis* and *Granuloperculatipollis rudis* in the middle of the sub-zone. At the top of this sub-zone *R. tuberculatus* reaches its highest abundance within the section. RLb (9.1–10.5 m) is distinguished by very lowest abundance of *R. tuberculatus* in favor of a peak abundance in *Ovalipollis*. Spores like *Densosporites*, *Lycopodiacidites* and *Triancoraesporites* have their first appearances at the base of this sub-zone. RLc (12–13.4 m) shows decreasing *Ovalipollis* amounts, and although *R. tuberculatus* depicts a renewed dominance at the base of the sub-zone, it continuously decreases throughout the sub-zone in favor of *Classopollis* and *Geopollis*.

The transition from the RL-zone to the Ricciisporites-Polypodiisporites zone (RP-zone), i.e. from the Contorta Beds to the Triletes Beds, which is also covered by the detailed sampling (Fig. 2B) is shown in greater detail in the summarizing supplementary Fig. 3 and depicts the same trends as before, but with higher resolution compared to Fig. 5. The assemblages from the black shale samples (BBD1 to 5) yielded a palynoflora typical of the previously described RL-zone and accordingly cluster together in CONISS analysis. Together with a first occurrence of *Uvaesporites argenteiformis* in the section and an increased number of spores (especially *Perinosporites thuringiacus*, *Densosporites fissus*) appear in the last detailed samples (BBD3 to 5) of the RL-zone. In accordance to what was said for sub-zone RLc, *Geopollis zwolinskae* has a short peak occurrence at the top of the Contorta Beds before the base of the grey layer (Fig. 2B, supplementary Fig. 3). In the first sample of the grey layer (BBD6) several spores typical of the new Ricciisporites-Polypodiisporites zone (RP-zone) appear (*Kyrtomispuris* spp., *Lycopodiacidites rugulatus*, *Cingulizonates rhaeticus*, *Punctatisporites* spp., *Stereisporites* spp., compare Fig. 7), but pollen occur still in unchanged

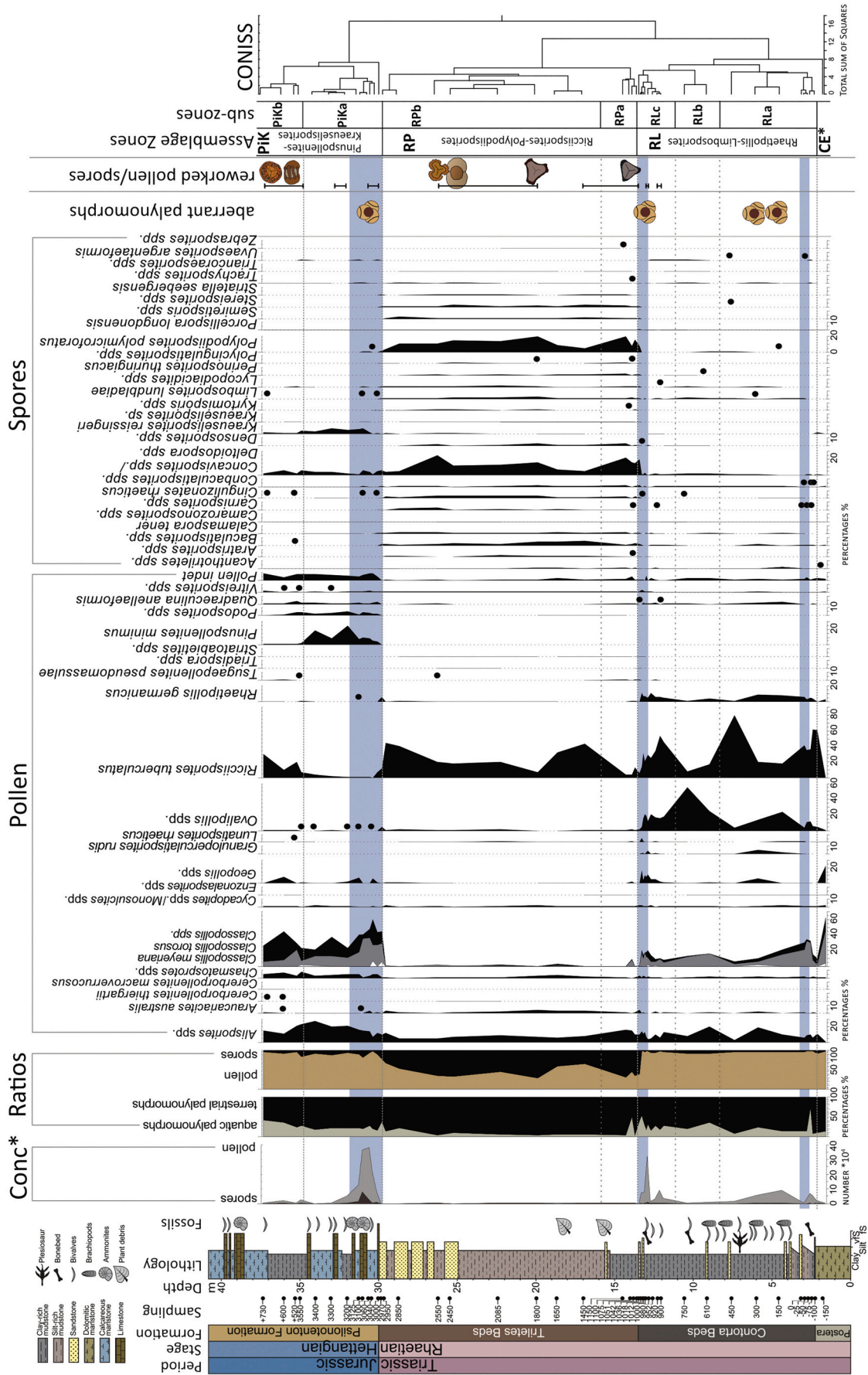
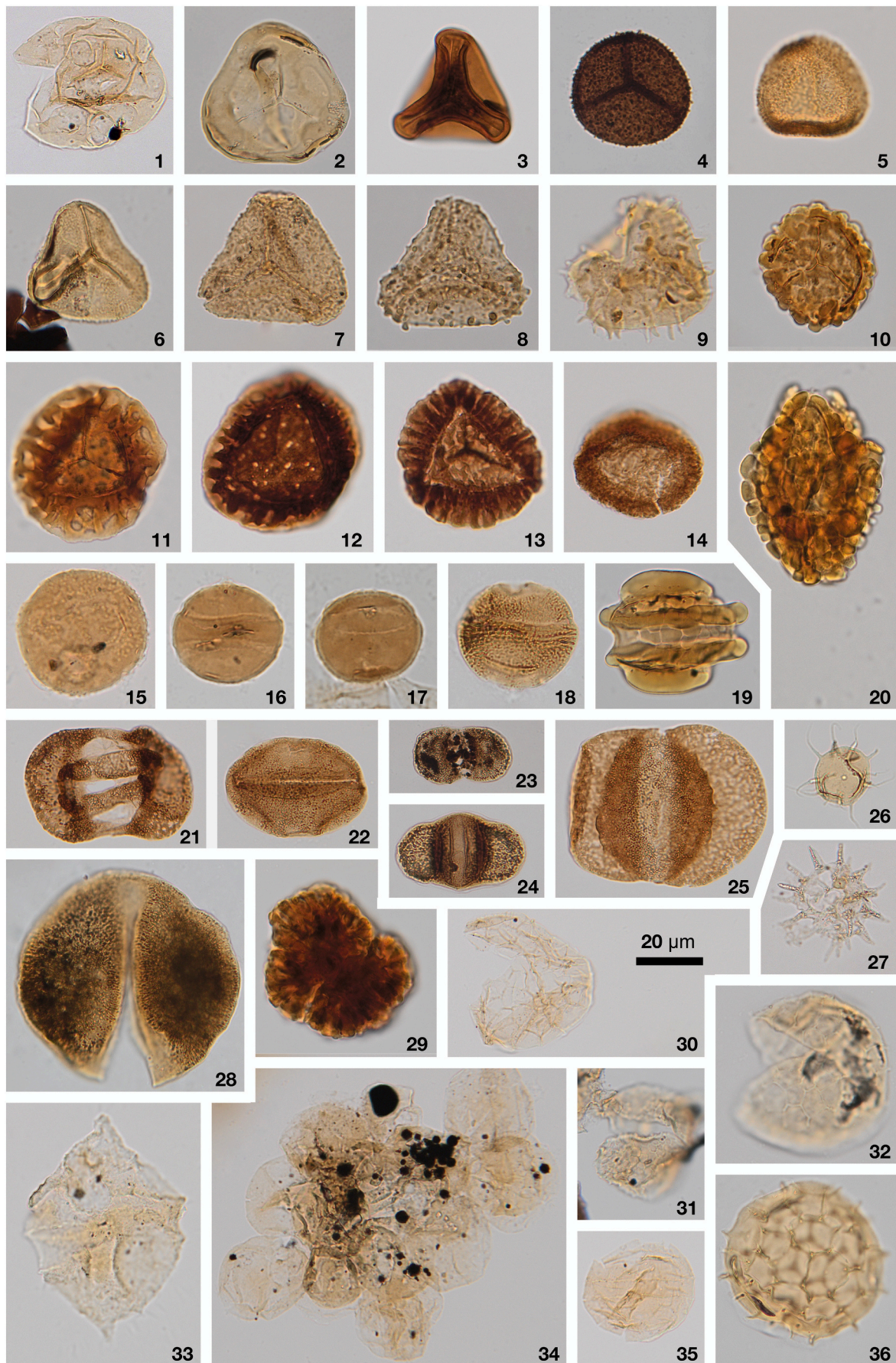


Fig. 5. Palynomorph abundances in the terrestrial assemblage. CONISS-cluster dendrogram and derived informal assemblage zones: CE\*-Classopollis-Enzanasporites; RL-Rhaetipollis-Limbosporites; RP-Ricciisporites-Polypodiisporites, PIK-Pinuspollenites-Kraeuselisporites. Subzones are labeled alphabetically. Occurrences of aberrant and reworked palynomorphs are indicated with icons. Marine ingressions identified through palynofacies analysis are given in blue. Conc\* = Concentration. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)





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**Fig. 6.** Assemblage Impression of the Contorta Beds. 1. *Calamaspora tener*, 2. *Deltoidospora* sp., 3. *Dictyophyllidites mortonii*, 4. *Baculatisporites comaumensis*, 5. *Osmundacidites wellmanii*, 6. *Trachysporites asper*, 7. *Trachysporites cf. asper*, 8. *Clathroidites papulosus*, 9. *Acanthotriletes varius*, 10. *Uvaesporites argenteaformae*, 11–12. *Limboisporites lundbladiae*, 13. *Limboisporites* sp., 14. *Enzonalasporites vigens*, 15. *Granuloperculatipollis rudis*, 16. *Geopollis zwolinskae*, 17. *Classopollis meyeriana*, 18. *Classopollis torosus*, 19. *Rhaetipollis germanicus*, 20. *Cycadospites* sp., 21. *Lunatisporites rhaeticus*, 22. *Ovalipollis* sp., 23. *Vitreisporites pallidus*, 24. *Vitreisporites bjuvensis*, 25. *Alisporites robustus*, 26. *Micrhystridium* sp., 27. *Beaumontella cf. caminuspinia*, 28. *Vesicaspora fuscus*, 29. *Botryococcus braunii*, 30. *Suessia swabiana*, 31. *Cymatiosphaera polypartita* forma 2, 32. *Cymatiosphaera polypartita* forma 1, 33. *Rhaetogonyaulax rhaetica*, 34. Aggregation of *Leiosphaeridia* spp. 35. *Dapcodinium priscum*, 36. *Cymatiosphaera* sp. (Names with full author citation and botanical affinities are given in supplementary Table 1).

abundances. In the second sample of the grey layer (BBD7) more spores typical of the Triletes Beds (Figs. 7–8) have their first appearance (*Lycopodiacidites rhaeticus*, *Triancoraesporites anchorae* and *Zeborasporites interscriptus*). *Polypodiisporites polymicroforatus*, which had appeared already at the top of RLa, now appears abundant (15%–20% of the terrestrial as well as the spore assemblage).

The Ricciisporites-Polypodiisporites zone (RP-zone, 13.5–29.6 m), which spans the Triletes Beds, is distinguished by the dominance and great variety of spores (Figs. 7–8). Especially *Polypodiisporites polymicroforatus* and *Deltoidospora/Concavisporites* spp. together totaling ca. 50%, dominate the terrestrial assemblage. Other spores that appeared in the grey layer of the detailed sampling continue to occur, now in higher though moderate abundance of 5–10%. Pollen are scarce and sometimes reworked (Figs. 8.5, 7, 8) or preserved in much darker colour (compare *Classopollis torosus* in Figs. 6.18, 8.4 and 9.4). *Alisporites* spp. and *R. tuberculatus* are still frequent, but other pollen taxa occur only in sporadic percentages. *R. tuberculatus*, however, occurs more often as single grains than in tetrads, compared to other parts of the succession. Mainly driven by abundance changes in *Ricciisporites tuberculatus*, the zone can be further divided into two sub-zones. Sub-zone RPa (13.5–14.4 m) is distinguished by the very low percentages of *R. tuberculatus*, the continuous occurrence of *Tsugaepollenites pseudomassulae* and *Quadraeculina anellaeformis*, both of which temporarily disappear thereafter. Sub-zone RPb (17–29.6 m) is characterized by the reoccurring dominance of *R. tuberculatus*. At the base of the RP-zone, reworked elements like Carboniferous spores (e.g. *Tripartites* and *Triquitrites* (Fig. 7.15–17)), are rare and often outside the count, but still a characteristic feature. Similarly, reworked elements appear as a typical feature in the middle to the top of the RP-zone, mainly constituted by older Triassic pollen (e.g. *Triadispora* spp., *Striatoabietites ayugii*), more Carboniferous spores, and coincide with reworked aquatic, probably Paleozoic, material (compare Fig. 4) at the top of the RP-zone.

With the base of the Pinuspollenites-Kraeuselisporites zone (PiK-zone, 29.8–37.3 m), palynomorph preservation becomes relatively poor and pollen regain dominance in the terrestrial assemblage. This abrupt change is related to the unconformity between the Triletes Beds and the Psilonotenton Fm. A singular, and rather poorly preserved *Cerebropollenites thiergartii*, together with *Pinuspollenites minimus* distinguishes the first sample from PiK-zone stratigraphically (Figs. 5 and 9). Aside the autonymous *P. minimus*, *Classopollis* spp. are the most abundant pollen in this zone, with a small peak of *C. meyeriana* at the very base of the PiK-zone. Spore variety is low, yet *Deltoidospora/Concavisporites* spp. and *Kraeuselisporites reissingeri* together still amount to 15–20% of the terrestrial assemblage throughout the PiK-zone. Sub-zone PiKa (29.8–34.05 m) is generally distinguished by the almost entire absence of *Ricciisporites* pollen, but with abundant *P. minimus* pollen and *K. reissingeri* spores. This relationship is reversed in sub-zone PiKb (34.9–37.3 m) and accompanied by singular occurrences of typical, but badly preserved (compare Fig. 9.5) Rhaetian elements (*Rhaetipollis germanicus*, *Lunatisporites rhaeticus*, and *Limboisporites lundbladiae*).

It is noteworthy that very few species actually disappear with the TJ-transition. *Granuloperculatipollis rudis* disappears with the transition from the RL to RP-zone. Similarly, *Zeborasporites* is restricted to the lower half of the RP-zone and does not survive the TJ-transition, apparently not even reach the last of the Triassic beds at Bonenburg. Other species that supposedly go extinct (*Lunatisporites rhaeticus*, *Rhaetipollis*

*germanicus*, *Perinosporites thuringiacus*, *Limboisporites lundbladiae*), however, still occur at the bottom and top of the PiK-zone, yet often as singular and sometimes badly preserved occurrences. Nevertheless, many singular occurrences, like that of *R. germanicus* still appear continuously in many samples. *Geopollis zwolinskae* although greatly diminished during the RP-zone does not go extinct with the TJ-transition, and, compared to the Triassic, occurs in unchanged abundances in the PiK-zone in Bonenburg.

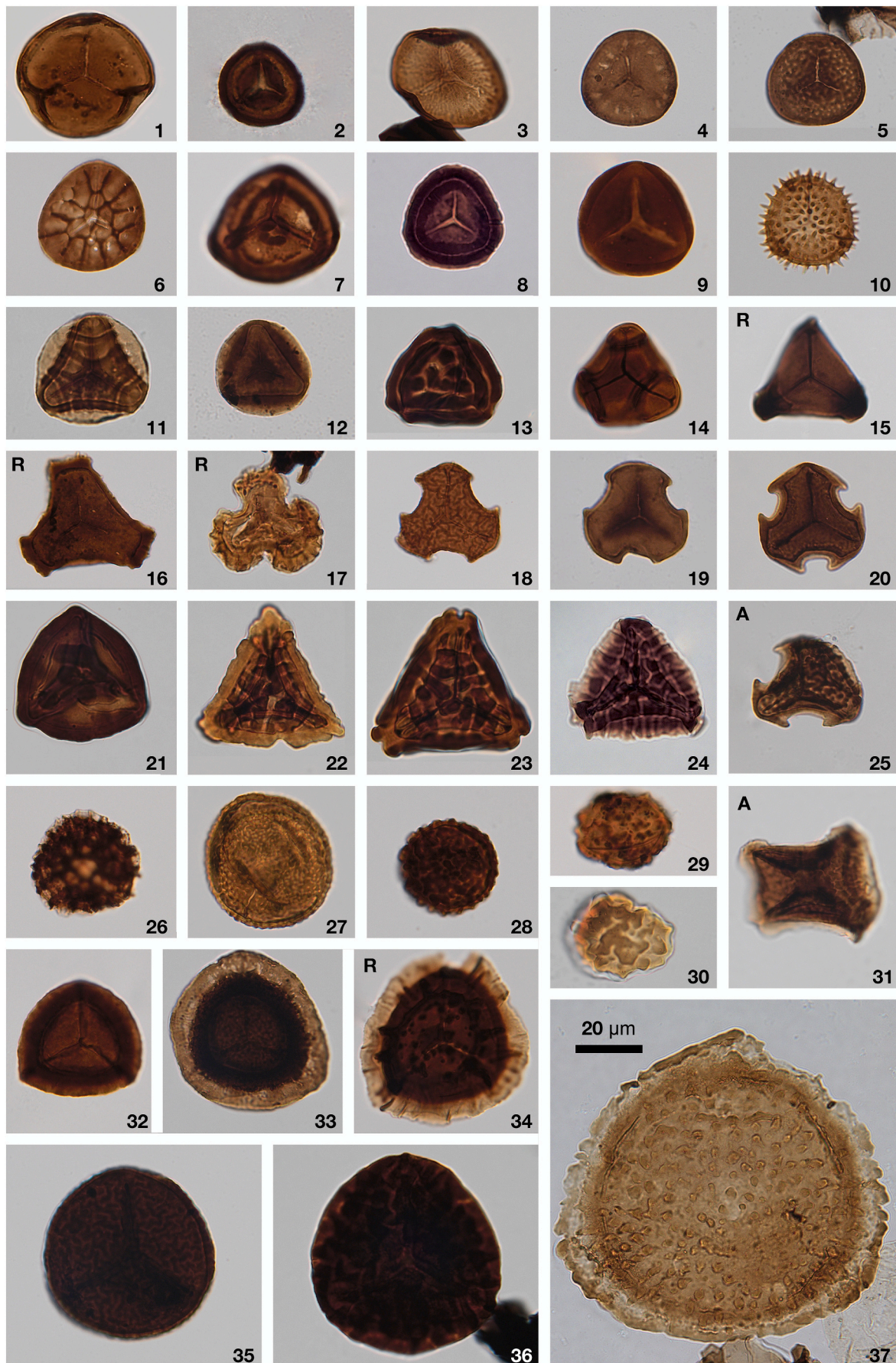
#### 4.3. Vegetation patterns

Based on *in situ* finds of palynomorphs in spore- and pollen-producing organs and certain morphological features (botanical affinities and references are given in supplementary Table 1), the previously discussed assemblages from Fig. 5 were translated into varying abundances of major plant lineages in Fig. 10. Due to the strong dominance of pollen and potential overrepresentation due to the Neves Effect, standard representation of terrestrial palynomorphs as 100% can obscure minor changes in the spore assemblage. Therefore, we additionally depict percentages of botanical affinities for spore-producing and pollen-producing plants separately, i.e., with spores and pollen each amounting to 100% (grey abundance curves), as well as for the terrestrial assemblage as a whole (black abundance curves) (Fig. 10).

The CE-zone represents a Cheirolepidiaceae dominated community which, after the marine ingressions, shifts towards a mixed gymnosperm forest community in the RL-zone, dominated by Cheirolepidiaceae, Voltziales, and the unassignable gymnosperm *R. tuberculatus*. *Corystospermales* are also common with a groundcover of lycophytes and Osmundales and leptosporangiate ferns underneath. During the onset of the marine ingressions at the top of the Contorta Beds liverworts, lycophytes, and horsetails increase in abundance, while gymnosperms, except for Cheirolepidiaceae, decrease. After a preliminary dominance of horsetails at the beginning of the marine ingressions, ferns (especially ‘other leptosporangiate ferns’ and Osmundales) dominate together with Cheirolepidiaceae. As opposed to the former mixed gymnosperm forest, the Triletes Beds consist of a more shrubby and herbaceous community, dominated by mixed seed ferns, cycads and tree-ferns with a ground-layer of clubmosses and bryophytes, and ferns. During the marine ingressions at the bottom of the Psilonotenton Fm. we note the opposite trends as for the marine ingressions of the Contorta Beds: after a temporary abundance of ferns (especially ‘other leptosporangiate ferns’ and Osmundales) and Cheirolepidiaceae, both decrease after the ingressions in favor of a new type of mixed gymnosperm forest with pines, podocarps, and much more dominated by Cheirolepidiaceae. Besides, Voltziales and the group to which *R. tuberculatus* should be assigned have lost their dominating role, whereas *Corystospermales* have gained significance compared to their previous abundance.

#### 4.4. Diversity patterns

Diversity indices for terrestrial palynomorph genera are plotted for the Bonenburg section together with the carbon isotope curve from Schobben et al. (2019) in Fig. 11. Evenness, Dominance, and Shannon Diversity indices, are depicted for two counting strategies: counting palynomorph tetrads/triads/dyads as four/three/two grains (grey outline) versus counting every tetrad as an item, i.e. as one grain (dotted



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**Fig. 7.** Assemblage Impression of the Triletes Beds I. 1. *Retusotriletes mesozoicus*, 2. *Annulispora folliculosa*, 3. *Stereisporites radiatus*, 4. *Rogalskiasporites cicatricosus*, 5. *Stereisporites hauterivensis*, 6. reticulate spore indet., 7. *Polycingulatisporites mooniensis*, 8. cf. *Annulispora* sp. B, 9. *Camarazonosporites laevigatus*, 10. *Carnisporites anteriscus*, 11. *Zebrasporites interscriptus*, 12. *Zebrasporites laevigatus*, 13. *Striatella seebergensis*, 14. *Cosmosporites elegans*, 15. *Triquitrites pulvinatus*, 16. cf. *Platyptera trilingua*, 17. *Tripartites cristatus*, 18. *Triancoraesporites reticulatus*, 19. *Triancoraesporites anchorae*, 20. *Cornutisporites seebergensis*, 21. *Kyrtomisporis laevigatus*, 22. *Kyrtomisporis gracilis*, 23. *Kyrtomisporis speciosus*, 24. *Perinosporites thuringiacus*, 25. *Perinosporites thuringiacus/aberrant*, 26. *Retitriletes austroclavaticites*, 27. *Polypodiisporites polymicroforatus*, 28. *Convolutispora klukiforme*, 29. *Thymospora canaliculata*, 30. *Thymospora ipsviciensis*, 31. *Perinosporites thuringiacus/aberrant*, 32. *Densosporites fissus*, 33. *Cingulizonates rhaeticus*, 34. *Kraeuselisporites*, 35. *Lycopodiacidites rugulatus*, 36. *Lycopodiacidites rhaeticus*. 37. *Porcellispora longdonensis*. Aberrant and reworked palynomorphs are indicated with 'A' and 'R' respectively in upper left corner. Names with full author citation and botanical affinities are given in supplementary Table 1.

line).

The rarified richness (dotted line) and richness curves (grey histogram) depict similar trends, with rarified values slightly higher in the Rhaetian and slightly lower in the Jurassic. Therefore, varying sample size only delimits slightly different amplitudes and does not seem to change the overall implications of this index. Below rarefied genus richness is compared with the other indices and simply referred to as richness for easier reference. The counting scheme, on the other hand, seems to have a major impact on varying diversity values. Diversity values, especially in the Triletes Beds, are much more stable, i.e. with fewer outliers when palynomorphs that occur in clusters (especially tetrads) are counted as one item (i.e. as the sedimenting unit they represent) (compare section 3.3). This is illustrated by the Dominance and Shannon Index in particular. This becomes very clear through an evenness outlier in the middle of the Contorta Beds, caused by a peak dominance of *Ricciisporites tuberculatus* (compare Fig. 5). Dominance peaks owed to *Classopollis* spp. dominance are still visible, but slightly less pronounced. A peak dominance at the top of the RLb-zone, caused by *Ovalipollis* which more rarely occurs in clusters, remains unchanged.

Overall, (rarified) richness, evenness and Shannon Diversity values are highest in the Triletes Beds, whilst dominance, showing usually the antagonistic trend to the other indices, is lowest. As a general trend, richness and evenness increase together, coinciding with decreases in dominance throughout the profile. Marine ingressions, as identified through palynofacies analysis (compare Fig. 3), coincide with richness loss and lowest Shannon Diversity values. Correlation analysis, using relative pollen abundance from palynofacies count as an indicator for potential transport effects as a result of palynofacies changes, confirms that this coincidence is in fact a negative correlation (richness:  $\rho = -0.472$ ;  $p = 0.001$ ; Shannon:  $r = -0.412$ ;  $p = 0.004$ ; see also supplementary Table 2). Accordingly, richness and Shannon Diversity are significantly confounded by palynofacies changes, i.e. influenced by the changing depositional environment. Evenness, on the other hand, was not significantly confounded ( $p = 0.285$ ).

Approximately six evenness peaks (E1–6) can be discerned throughout the section. Preceding the marine ingression evenness peaks in E1 and decreases again during the ingression. Towards the top of sub-zone RLa richness recovers to rather stable values close to the median, while evenness values continue to increase after temporary low values, climbing above the median to a second evenness peak (E2) to steadily decrease thereafter until the top of the RLb sub-zone, as a result of Voltziales dominance (compare Fig. 10). Towards the top of the RLc sub-zone, richness as well as evenness increase, independently of any detectable palynofacies change (also compare Fig. 3), and reach values above the median in the third evenness peak (E3), preceding the next marine ingression (F4).

Contradictory to the previously observed pattern of joined evenness and richness change, evenness increases to a renewed peak values (E4) at the end of the marine ingression, and is now paired with decreasing dominance and richness values. This is also evident in high resolution (supplementary Fig. 3).

After E4 in Bonenburg, we note a temporarily decreased evenness, with increased dominance, but rather stable, although high, richness values, in the middle of the grey layer at the very base of the Triletes Beds. After these low evenness values, richness and evenness increase and dominance decreases, to values typical of the rest of the Triletes

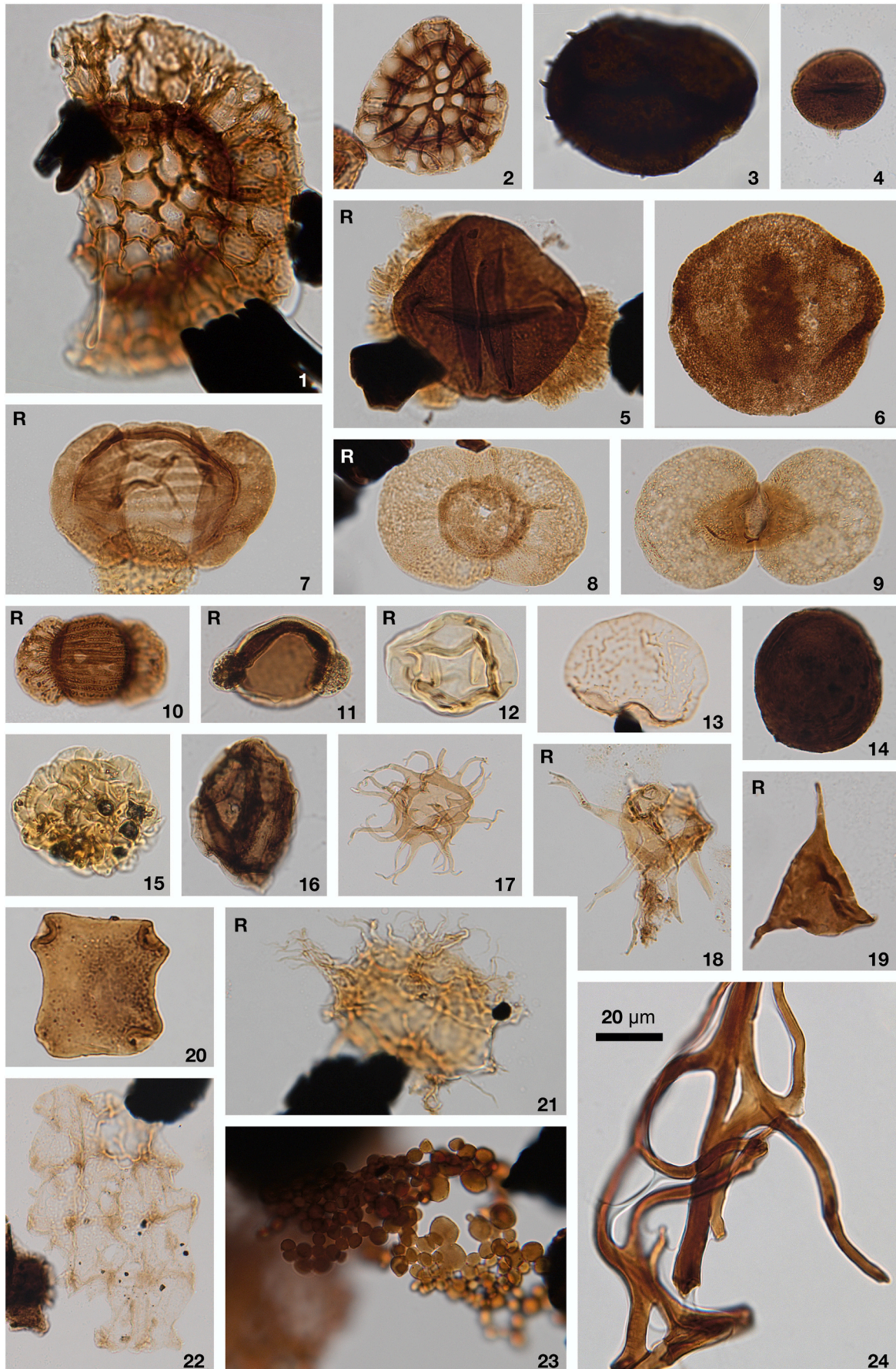
Beds. The Triletes Beds are then characterized by the highest evenness values and richness continuously above 27 genera. After lowest evenness at the top of the RPa sub-zone, evenness increases to the highest evenness value within the section (E5) at around 18.5 m.

At the top of the RP-zone, richness is fluctuating stronger than before and evenness reaches another peak in the last samples (E6), while dominance and Shannon Diversity remain unchanged. Preceding the carbon isotope shift towards more negative values, the last sample of the RP-zone then depicts an abrupt change with evenness and richness continuously decreasing, while dominance increases to diversity values typical for the PiK-zone. With the beginning of the marine ingression, and the base of the PiK-zone richness and evenness are continuously below the median and dominance continuously above.

#### 4.5. Teratology

A striking feature of the section is the recurrent occurrence of aberrant spores and pollen. For instance, some specimens of spores that normally occur as triangular forms occur as squares (e.g. *Perinosporites thuringiacus*) (Fig. 7.31) or depict a chimeric form (Fig. 7.25) showing characteristics made up of two different spores, e.g., mixing the outline of *Cornutisporites seebergensis* and the ornamentation of *Perinosporites thuringiacus*. Lycopytic spores of *Kraeuselisporites reisingeri* normally dispersed as monads, appear more often in tetrads. Diverse aberrant pollen co-occurs at the same intervals as the described aberrant spores. Saccate pollen for instance depicted one or more additional sacci (Fig. 13.20). More rarely, *Classopollis* spp. pollen occur grown together, i.e. not sufficiently separated after microsporogenesis (Fig. 13.10). *Rhaetipollis germanicus* occurs in considerably smaller size or malformed (Fig. 13.11, 14, 15, 21). In addition, pollen like *Classopollis* spp. which regularly co-occur in tetrads show another special condition. In *Geopollis zwolinskae*, *C. torosus* and *C. meyeriana*, one to four grains out of the tetrad are considerably smaller ( $< 24 \mu\text{m}$ , mostly  $< 20 \mu\text{m}$ ) than the 'average' sized (i.e. 25–40  $\mu\text{m}$ , measured for  $n = 500$  in sample BB0) grain (Fig. 13.8–9, 12–13, 16–17, 18–19). Furthermore, the smaller grains often appear much darker and show a lack of ornamentation compared to the 'average' grain and comply with the description of *Classopollis simplex*. The occurrence of smaller (2/3 of the 'normal' size) and darker *Ricciisporites tuberculatus* grains in un-separated tetrads can also be reported (Fig. 13.7), which is similar to the different tetrad conditions in *Classopollis*. Yet, *Classopollis* shows more variation in this state with either one or even all grains of a tetrad being considerably smaller, while a maximal two smaller than average-sized grains were observed in *Ricciisporites*.

The recurrent occurrence of an increased amount of aberrant spores and pollen, especially in different taxa at the same time is not random, but appears only at particular intervals. For instance, aberrant pollen tetrads occur in the middle of the RLa sub-zone in the lower third of the Contorta Beds (coinciding with evenness peak E2), at the transition from the Contorta to the Triletes Beds (coinciding with evenness peak E3 and E4), and at the bottom of the Pilonotenton Fm. Aberrant spores regularly occur along the transition from the Contorta to the Triletes Beds, especially in the grey layer of the detailed sampling. It is also noteworthy that these aberrant palynomorphs occur only at these distinct intervals, and although sometimes co-occurring with high percentages and/or concentrations of the palynomorph in question, they



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**Fig. 8.** Assemblage Impression of the Triletes Beds II. 1. *Semiretisporis maljavkini*, 2. *Semiretisporis gothae*, 3. *Aratrissporites scabratus*, 4. *Classopollis torosus*, 5. bisaccate pollen, 6. *Araucariacites australis*, 7. *Striatoabietites aytugii*, 8. bisaccate pollen, 9. *Platysaccus papilionis*, 10. *Striatoabietites* sp., 11. *Protodiploxipinus gracilis*, 12. sphaeromorph/*Halosphaeropsis* sp., 13. *Lecaniella* sp., 14. *Concentricystes* sp., 15. *Tsugaepollenites pseudomassulae*, 16. *Perinopollenites elatooides*, 17. *Multiplicisphaeridium dendroidium*, 18. *Multiplicisphaeridium* sp., 19. *Veryhachium* sp., 20. *Tetraporina crassa*, 21. indet, 22. *Plaesiodyctyon mosellanum*, 23. cf. *mycorrhizal fungi remain*, 24. *Diktyothalacos* sp. Reworked palynomorphs are indicated with 'R'. Names with full author citation and botanical affinities are given in supplementary Table 1.

do not occur outside the mentioned intervals even in samples with much higher percentages (30–80%) or high pollen concentrations. Nevertheless, it should be considered that the aberrant *Classopollis* tetrads apparently occur at times with most diverse species richness of the Cheirolepidiaceae, i.e. the plant family they belong to. Nevertheless, they do not always occur when this condition is fulfilled. All in all, aberrant palynomorphs were observed in all major land plant groups (moss, ferns and gymnosperms) in Bonenburg, but not in aquatic elements, i.e. aberrant acritarchs or dinoflagellates, which occur in other sections and time-intervals, were not observed, yet. When aberrant palynomorphs occurred here, they were observed in more than one taxon and were most diverse in the grey layer at the base of the Triletes Beds, i.e. at the bottom of the Event Beds.

## 5. Discussion

### 5.1. Implications of palynofacies for reconstructing sea-level changes, depositional environment, and interpreting diversity

Our palynofacies and palynological analyses, indicate three distinct sea-level high stands or marine incursions in the Bonenburg section; namely at the base (F2) and top (F4) of the Contorta-Beds, and across the TJ-boundary (F6).

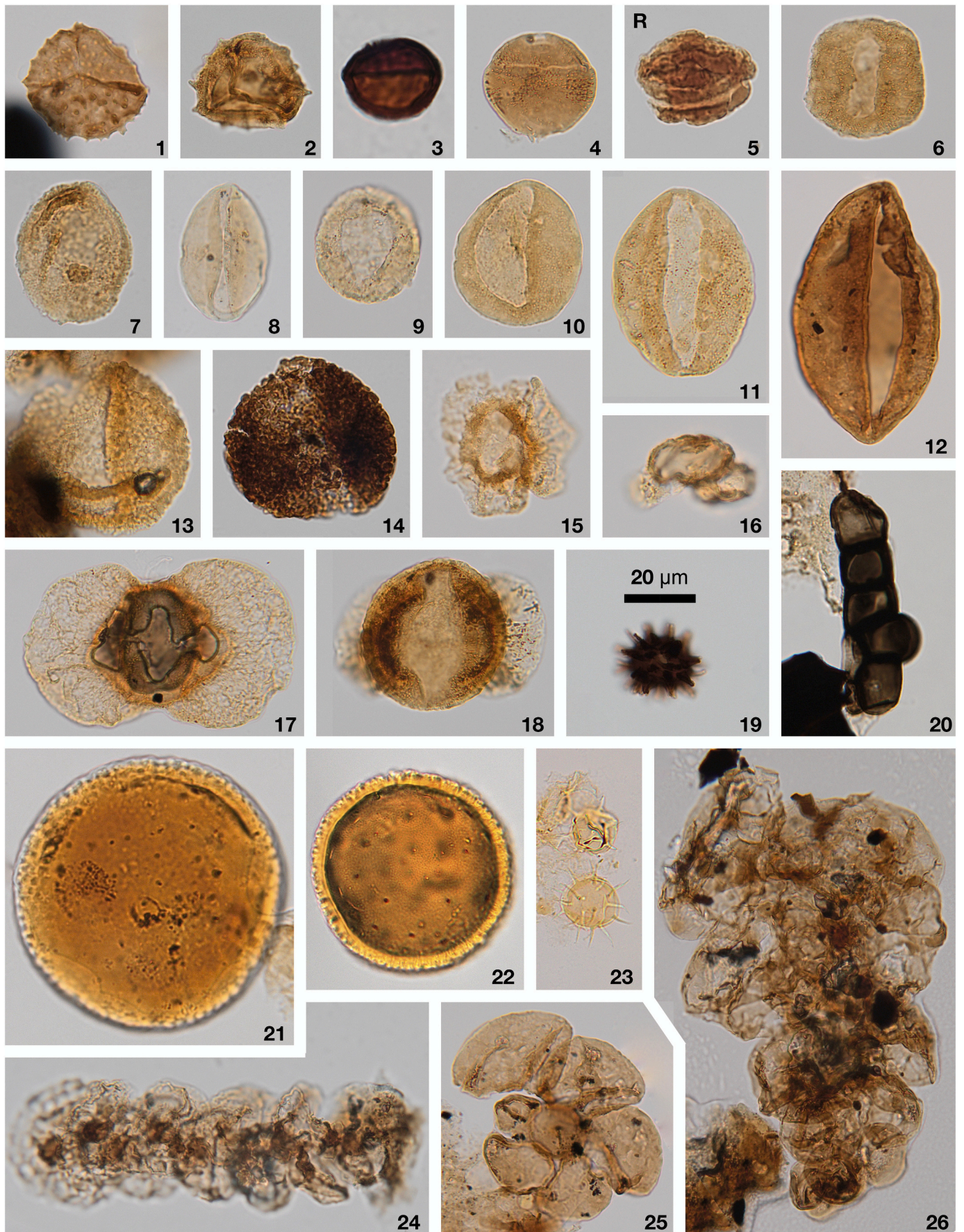
The first marine incursion in the Bonenburg section (F2) occurs at the base of the Contorta-Beds with a sequence of peaks in *Botryococcus*, *Leiosphaeridia* and acritarchs, which indicates the transition to more marine, probably shallow and marginal marine conditions, which acritarchs usually inhabit (Tyson, 1993). The second marine incursion with peak abundances of marine phytoplankton (F4) is characterized by dinoflagellates, especially *Rhaetogonyaulax rhaetica*, which, as opposed to *Dapcodinium priscum*, is more specialized to open marine conditions (Courtinat and Piriou, 2002; Kürschner et al., 2007) and tends to increase offshore (Tyson, 1993). These two incursions correlate with Barth et al.'s reconstruction of the first and second maximum flooding of the Rhaetian sea (MFS Rh1 and 2) for the Germanic Basin and suggests that the second marine incursion extended further than the first (2018). The second maximum flooding event can be recognized in various sections from the Northern hemisphere, beyond the Germanic Basin and seems to have high correlative value (Barth et al., 2018; Lindström and Erilström, 2006).

The continuous low abundances of marine elements, combined with high abundances of freshwater algae and the complete lack of marine fauna throughout the Triletes Beds (Fig. 4) corroborate with signs of a brackish – lacustrine depositional setting for this unit (Will, 1969); i.e. coarsening of the grain size, wave ripples and faint signs of cross-stratification indicates the end-Triassic regression during the latest Rhaetian as also reconstructed by Barth et al. (2018). Alternating higher abundances between *Leiosphaeridia* and *Botryococcus* in the Triletes Beds attest to interchanging episodes of stronger marine influence and increased freshwater influxes leading to more brackish conditions, respectively, suggesting a deltaic environment for the Triletes Beds. The appearance of *Concentricystes*, regarded a freshwater indicator at least in quaternary deposits (Chen et al., 2011; Horton et al., 2005; Norris, 1965), together with the sudden peak of *Botryococcus* at the base of the Triletes Beds and an influx of Chlorophyceae (Fig. 4) coinciding with the appearance of reworked palynomorphs (aquatic and terrestrial) at the top of the Triletes Beds (Figs. 4 and 5) suggests an elevated riverine influx. Given the coincidence with other reworked taxa we cannot exclude that occurrences of *Plaesiodyctyon mosellanum* and *Concentricystes*

are the result of reworking. The latter, however, does not always coincide with other reworked elements which are otherwise a recurrent characteristic. Occurrences of *P. mosellanum* does co-occur with other reworked elements, but it is very fragile and would be potentially heavily damaged in this process, which was not observed. Yet, even if they were only reworked, this would together with the amount of *Botryococcus* still support the interpretation of a changed weathering regime. Enhanced maturation of terrestrial organics delivered to marine sites under a changing weathering regime has previously also been postulated for the Bonenburg section based on stratigraphic patterns in (in)organic geochemistry (Schobben et al., 2019). This is further supported by aquatic palynofloral patterns as described here and by Bonis et al. (2010) for the Eiberg Basin, which suggest an increased riverine influx indicated by terrestrial derived or reworked aquatic elements. The increasing number of aquatic elements in relation to terrestrial palynomorphs constituted by brackish-marine phytoplankton in the uppermost Rhaetian then is the onset to higher sea-level stands in the Jurassic where marine fauna reoccurs in the Germanic Basin (Fig. 4, Barth et al., 2018).

As was pointed out before, changing depositional environments can potentially bias diversity curves. High richness values, like in the Triletes Beds, can be the result of good preservation (see discussion in Barbacka et al., 2017). To limit this effect and allow better comparison with other sections, we compare generic diversity patterns, as otherwise species-rich genera like *Stereisporites* would raise richness levels significantly in the Triletes Beds. In Bonenburg many of the strongly marine influenced samples (e.g. from F4) with very hyaline preservation, still show high richness values, due to the appearances of spores that occur continuously after the transition from the Contorta to the Triletes Beds. Therefore, the generic spore diversity does not seem to be explicable only through good preservation. Moreover, even samples with very poor preservation in the Triletes Beds, e.g. from two sandstone samples at the top of the RP-zone, still depict very high richness values that do not drop beyond the median. Therefore, we interpret values as an increased richness signal for this part of the section, even if partly elevated through a preservation bias.

Given that marine incursions, especially at the top of the Contorta Beds and base of the Psilonotenton Fm. coincide with very high pollen concentration and dominance (Fig. 11), this influences richness and Shannon Diversity as the correlation analysis showed. This influence is logical though, as richness decreases with proximity to the source and dominance increases as a result of the 'Neves Effect'. Both these indices are thus more influenced by changes in the depositional environment. The evenness curve, on the other hand, was shown to not be significantly confounded by facies changes and can thus better attest for diversity. This can be explained by its inherent character as the conceptual inverse of a dominance index. It is sensitive to changes amongst all taxa, also the non-dominant ones. Changes in dominance, although affecting the index, bias the explanatory power of the index less than the other two. Therefore, evenness peaks (e.g. E1 and E4) might thus be attesting to changes of biodiversity, even when coinciding with depositional changes like marine incursions. Nevertheless, caution should be taken, interpreting diversity patterns directly coinciding with palynofacies shifts. Palynomorphs are particles that are also influenced by the sedimentary environment. Yet, depositional changes are in return the result of environmental change, which necessarily influences the plant community. Therefore, diversity patterns are necessarily influenced and should not be dismissed straight away, on this basis of a potential preservation bias.



(caption on next page)

**Fig. 9.** Assemblage Impression of the Pylonotenton Formation. 1. *Foraminisporis jurassicus*, 2. *Kraeuselisporites reissingeri*, 3. *Aratrisporites minimus*, 4. *Classopollis torosus*, 5. *Rhaetipollis germanicus*/reworked, 6. *Quadraeculina anellaeformis*, 7. *Cerebropollenites* cf. *thiergartii*, 8. *Cycadopites* sp., 9. *Chasmatosporites apertus*, 10. *Chasmatosporites hians*, 11. *Chasmatosporites elegans*, 12. *Chasmatosporites major*, 13. cf. *Cerebropollenites thiergartii*, 14. *Cerebropollenites* cf. *macroverrucosus*, 15. Monosaccate pollen indet., 16. *Pinuspollenites minimus*, 17. cf. *Alisporites radialis*, 18. cf. *Podosporites* sp., 19. cf. *Palaeopericonia* sp., 20. Fungal remain, 21. cf. *Tythodiscus faveolus*., 22. *Tasmanites* sp., 23. *Micrhystridium* sp., 24. *Foraminifera* type 3, 25. *Foraminifera* type 1, 26. *Foraminifera* type 2. Reworked palynomorphs are indicated with 'R'. Names with full author citation and botanical affinities are given in supplementary Table 1.

## 5.2. Biostratigraphy

The preliminary biostratigraphic framework that was published in Schobben et al. (2019) is complemented and updated here. Zones are named the same, only the former *Pinuspollenites*-*Heliosporites* zone was renamed as *Pinuspollenites*-*Kraeuselisporites* zone due to taxonomic revision. Also the lower zonation changes slightly, due to a change of chosen thresholds for zones (formerly 7.5 TSS, now 9 TSS), updated quantitative data and cluster analysis. Now the former *Ricciisporites*-*Conbaculatisporites*-zone is part of the RL-zone. While assemblage zones have high correlative value (compare correlation chart of zones in supplementary Fig. 5), sub-zones attest for rather minor assemblage changes and do not correlate well with other sections and are thus likely driven by local, rather than supra-regional vegetation changes.

In general, the identified zones are identical with those identified by Heunisch (1999) and correlate well with other German sections, except for the transitional *Deltoidospora*-*Concavisporites* Zone (Barth et al., 2018). This difference might however be connected to Bonenburg's hiatus at the bottom of the Pylonotenton Fm. (Schobben et al., 2019). The lack of a transitional interval with strong *Deltoidospora*/*Concavisporites* spp. dominance detectable in other Germanic sections (Barth et al., 2018; Lund, 1977), suggests a gap in the record in the uppermost Rhaetian in Bonenburg. Given that changes begin to be visible in the last two samples it is assumed that this gap is rather small because diversity values have already rapidly declined to values typical of the lower Jurassic in Bonenburg (Fig. 11). Moreover, the last sample that is lithologically assigned to the Triletes Beds is palynologically part of the PiK-zone (Fig. 5). Major transitions from the CE-zone to RL-zone and RL- to RP-zone can be observed in all previously published sections (see supplementary Fig. 4) and correlate well with Bonenburg. This facilitates comparison of the Contorta Beds and Triletes Beds and the therein observed changes with all other sections not only in the Germanic Basin (Barth et al., 2018; Heunisch, 1999; Lund, 1977; van de Schootbrugge et al., 2009), Britain (Bonis et al., 2010a; Orbell, 1973), but also Scandinavia (Dybkjær, 1988; Larsson, 2009; Lindström, 2016; Lindström et al., 2017a; Lindström and Erlström, 2006), Greenland (Mander et al., 2010, 2013) and the Northern Calcareous Alps including the GSSP section Kuhjoch (Bonis et al., 2009; Hillebrandt et al., 2013; Kürschner et al., 2007; Morbey, 1975; Schuurman, 1979).

## 5.3. Inferred vegetation patterns and changing environmental conditions

The above studied palynomorph abundance changes in the terrestrial assemblage alone seem rather abrupt, perhaps even dramatic, when comparing the Contorta to the Triletes Beds, i.e. the pre-extinction to the extinction interval, and at the TJ-transition, i.e. the transition from the Triletes to the Pylonotenton Fm. However, the latter might only appear so abrupt because of the hiatus noted for the bottom of the Pylonotenton Fm. (Schobben et al., 2019), although changing diversity patterns and assemblage affiliation of the last samples of the Triletes Beds seem to trace at least part of a change or transition. As for the transition from the Contorta to the Triletes Beds, the impression of an abrupt change is partially owed to the strong dominance of pollen prior to the Triletes Beds. Looking at the pollen and spore assemblage separately and summarized according to their botanical affinity (section 4.3, Fig. 10 and supplementary Fig. 6 for GSSP section Kuhjoch), smaller and more gradual changes become visible.

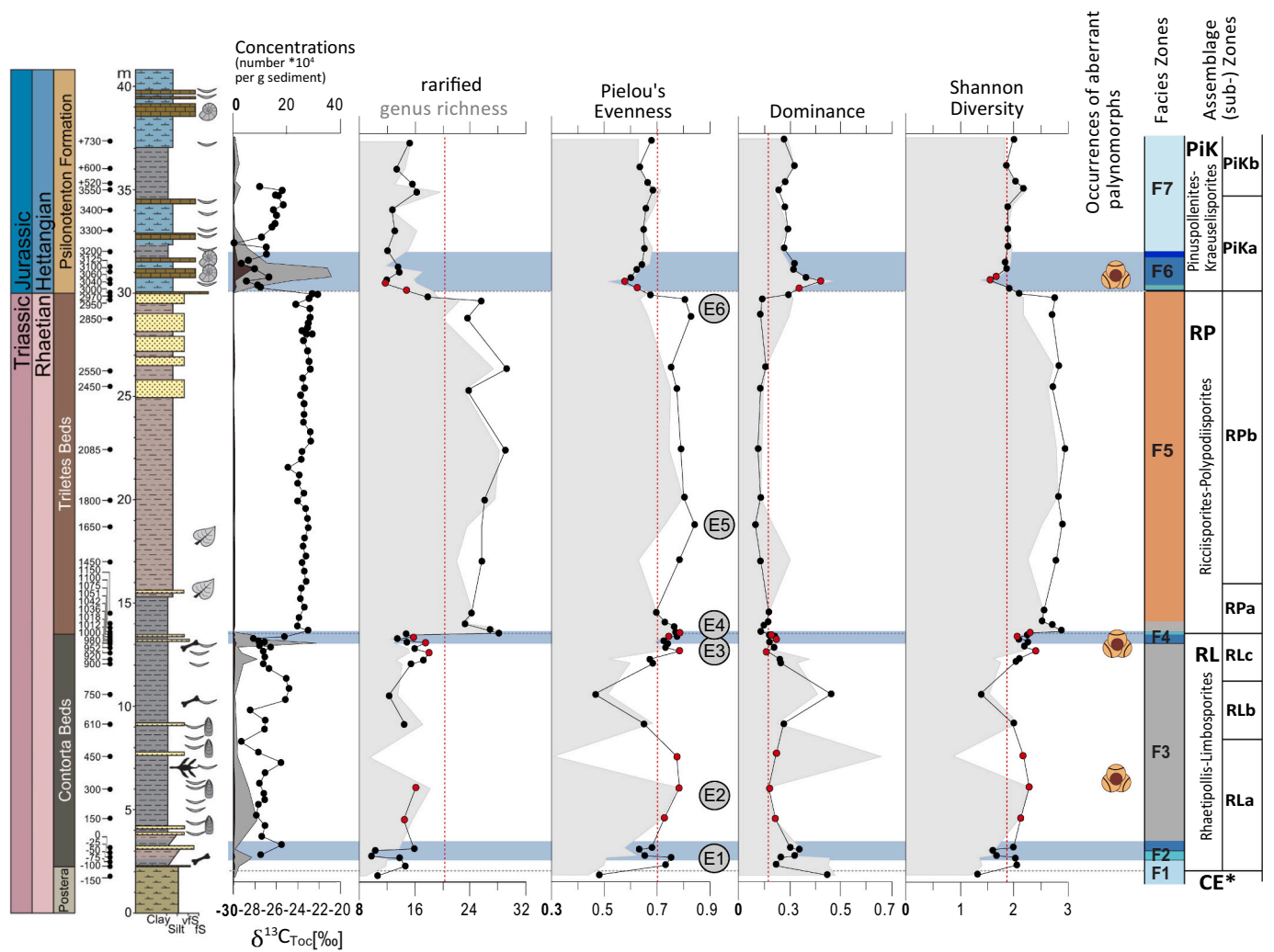
The Cheirolepidiaceae community recorded in the CE-zone just prior to the marine ingression might reflect the coastal community, to which the Cheirolepidiaceae are usually assigned (Alvin, 1982; Watson, 1988), i.e. a community probably fostered by raising sea-levels (compare Uličný et al., 1997) (Fig. 10). In general, Cheirolepidiaceae appear most abundant in the section at times of marine incursions, but this might be a result of a transport effect of this pollen, which is much smaller and supposedly lighter than the other dominating pollen *Ricciisporites tuberculatus*. The latter is not only bigger, with massive ornamentation, but almost obligatory occurs in tetrads, which makes it much heavier and thus likely to be deposited closer to its source (Lindström et al., 2017a; Lindström and Erlström, 2006; Petersen et al., 2013). Even when *Classopollis* spp. occur in tetrads, it is assumed to be still much smaller and thus more easily transported. Given that bisaccate pollen with very good floating capacities (Leslie, 2010), do not show the same increased abundances in times of marine incursions, we interpret the abundant occurrence of Cheirolepidiaceae not as a depositional effect, but as a result of their ecological niche representing a coastal community to which they are typically assigned (Abbink, 1998; Abbink et al., 2001; Batten et al., 1994).

The ensuing mixed gymnosperms forest in the RL-zone then consists of Cheirolepidiaceae, with *Classopollis torosus* strongly dominating over *C. meyeriana*, rivaled by the putative gymnosperm *R. tuberculatus*. While the Austrian sections show a high dominance of the thermophilous *C. meyeriana* over *C. torosus*, indicating a relatively drier and warmer climate in the Tethys realm (Bonis et al., 2009; Bonis and Kürschner, 2012; Kürschner et al., 2007), Bonenburg with the much more dominant *R. tuberculatus* and *C. torosus*, which presumably prefers more humid and cool conditions relative to *C. meyeriana*, probably represents a more temperate gymnosperm forest. This interpretation is also supported by Bonis and Kürschner's (2012) reconstruction of a more humid and warm-temperate reconstruction of the NW-European realm within the overall warm conditions preceding the TJ-transition (e.g. Frakes, 1979; Sellwood and Valdes, 2006). This gradient is continued when comparing Bonenburg with East Greenland (Mander et al., 2013; McElwain et al., 2007). There the Cheirolepidiaceae are even less represented, wherefore Bonenburg with values in between sections from lower and higher paleolatitudes bridges occurrences and indicates a vegetational gradient from the Tethys to Northern Europe.

Associated with the onset of evenness peak two (E2) (ca. 4.5 m) is an increase in *Botryococcus*, Equisetales, Isoetales and ferns (Figs. 4, 10 and 11), suggesting closer proximity to a riverine outlet transporting this association from the banks of the river or temporary more brackish and wetter conditions (Abbink, 1998; Abbink et al., 2004a, 2004b). The associated abundance decline of the more xerophytic Cheirolepidiaceae better adapted to seasonally dry- to semi-arid conditions (Batten et al., 1994; Bonis and Kürschner, 2012) additionally suggests changing water availability. A temporary warmer and wetter interval around E2 is further supported by a slight increase in number of relatively more thermophilous species, such as *C. meyeriana* and *Geopollis zwolinskae* (Bonis et al., 2010a; Lindström, 2016), the wet and warm adapted Osmundales (Abbink, 1998) and the co-occurrence of an increased amount of *Dapcodinium priscum*, which seems to prefer warmer temperatures (Poulsen and Riding, 2003), and a very low *R. tuberculatus* abundance. With declining evenness, the previously mentioned warm elements disappear again, likely as a result of other species thriving in the changed and cooling conditions slowly outcompeting species with higher temperature optima. The assemblage then resembles previous







**Fig. 11.** Palynofloral diversity patterns of Bonenburg plotted against the  $\delta^{13}C_{TOC}$  curve. Genus richness, with non-rarified data given as grey histogram and rarified genus richness as line with circles for respective samples. Pielou's evenness (J), dominance (D), and Shannon Diversity (H) are given for palynomorph clusters (e.g. tetrads) counted as individuals (i.e. 4) in grey histogram and counted as items (i.e. 1) in a line with circles for respective samples. Due to low values, rarefied genus richness cannot be given for sample BB450. The median value for each index is indicated by a red dotted vertical line. Temporary peak abundances of evenness are referred to as E1-E6. Pollen and spore concentrations, as well as carbon isotope values after [Schobben et al. \(2019\)](#) on the left and, palynofacies and informal palynomorph assemblage (sub-) zones identified in this paper on the right. Aberrant palynomorph occurrences are indicated through an aberrant tetrad icon on the right. The corresponding samples are identified through a red circle in the diversity curve. Marine ingressions according to palynofacies analysis are denoted in blue. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

assemblage composition, of the temperate gymnosperm forest, probably representing again the more mature successional stage of this forest community after temporary, temperature-induced community change.

In the spore assemblage (Fig. 10), the continuously more negative carbon isotope values at the top of the Contorta Beds (Fig. 11) is accompanied by a sequence of temporary peak occurrences of (1) horsetails, (2) 'other leptosporangiate ferns', and (3) Osmundales, which probably attest for the shift through temporary successional stages from one prevalent vegetation type to another, and thereby attests to the gradual character of successive vegetation change at the transition from the Contorta to the Triletes Beds and suggests the evolution of another vegetation type and not for an abrupt change with a succeeding "extinction" flora. The reversed order of appearance at the base of the Pilonotenton Fm. in Bonenburg might further support a fragmentary picture of successional shifts despite the hiatus. This interpretation also supports [Barth et al.'s \(2018\)](#) reconstruction of their new *Deltoidospora-Concavisporites* Zone as a transitional interval. It is noteworthy, that the same pattern can be observed in Kuhjoch bracketing the Schattwald Beds, when analyzing the botanical affinities in the spore assemblage in the same way as in this study (see

supplementary Fig. 6). Only there the abundant dominance of *Deltoidospora/Concavisporites* ssp. at the base of the Jurassic is replaced by *Trachysporites* spp., which probably inhabits the same niche as *Deltoidospora/Concavisporites* spp. in the Germanic Basin. Therefore, it might not only be a local, but perhaps a supra-regional development of typical sequences of successional assemblage changes, resulting from changing environmental conditions.

After these short term successional assemblages, the vegetation in times of marine extinction, i.e. in the Triletes Beds, is a shrubby herbaceous community typical also in the Danish Basin for example ([Lindström et al., 2015](#); [Petersen and Lindström, 2012](#)), dominated by seed ferns, and joined by ferns, clubmosses and bryophytes. This spore-dominated assemblage might then also suggests more humid conditions for this interval. Although characterized by a very diverse number of species and genera, with abundances rather evenly distributed amongst them, two taxa have a more prominent role: the Schizaceae *Polipodiisporites polymicroforatus* and the leptosporangiate fern spores *Deltoidospora/Concavisporites* spp. This is a pattern that is found in all sections in the Germanic Basin, Scandinavia and Austria with high correlative value ([Lindström et al., 2017b](#)). It appears questionable what

constitutes the competitive success of these taxa over all others, in a shrubby herbaceous assemblage with long-lasting persistence.

Perhaps the two taxa in question are comparable to extant highly drought and fire resilient ferns like the sword fern (*Polystichum nuttatum*) known to quickly reoccur after fires in North America (Douglas and Ballard, 1971; Dyrness, 1973; Long and Whitlock, 2002), bracken (*Pteridium aquilinum*) which is known to recolonize first and even invasively after disturbance (De Silva and Matos, 2006; Gliessman, 1978), or the climbing fern (*Lygodium microphyllum*) an aggressive colonizer, which even derives from the same family as *P. polymicroforatus*, i.e. the Schizaceae (Madeira et al., 2008). Interestingly, spores of fossil *Lygodium* spp. from Upper Cretaceous and Cenozoic in situ finds would, as dispersed specimens, be referred to as *Cyathidites* (Balme, 1995; Gandolfo et al., 2000; Rozefelds et al., 2017), which belongs to the *Deltoidospora/Concavisporites* spp. complex (see discussion in Lund, 1977). On top of that, Rozenfeld et al. (2017) argue that the smooth to scabrate sporoderm in *Lygodium* is like the ancestral state as opposed to the derived reticulate ornamentation. Also tree ferns, another potential mother plant of *Deltoidospora/Concavisporites* spp. (Balme, 1995), are reported to be more resilient to fires (Blair et al., 2017; Lehn and Leuchtenberger, 2008). Assuming, a recurring fire regime throughout the Triletes Beds, which was proposed for this time interval (Belcher et al., 2010; Petersen and Lindström, 2012; van de Schootbrugge and Wignall, 2016 and see more detailed discussion in 5.4) the competitive advantage of the discussed species might be explained with strategies similar to extant ferns known to be fire resilient. The deeply buried rhizomes are protected from the fire and resprout afterwards, benefiting from the influx of nutrients, freed space and light (Mason et al., 2016; McGlone et al., 2005; Perry et al., 2014). Their often highly flammable fronds, in accordance to the ‘kill thy neighbor hypothesis’ (Bond and Midgley, 1995), then increase the selective pressure against neighboring species. By fueling the fire and thereby damaging other less flammable species burning to death, this can prevent the recolonization of forest trees over a long period of time (Gliessman, 1978). The morphological traits of ferns are tested to be generally more flammable than gymnosperm leaves and therefore fern dominated landscapes, such as those of bracken, create feedback loops, where fires select for flammable vegetation, which in turn increases the likelihood of fires (Mason et al., 2016). In that respect the above given association of our prominent species with extant Schizaceae *Lygodium* is particularly noteworthy (Konijnenburg-Van Cittert, 2002), because the latter forms thick and climbing leaf ‘mats’ over the tops of shrubs and trees that, in cases of wildfires, carry the flames into the canopy, which is destroyed although it would otherwise survive ground fires (Madeira et al., 2008). Independently of its botanic affinity, when comparing *P. polymicroforatus* with its very restricted but abundant occurrence in times which are supposedly crown fire-prone as recorded at least for the Danish Basin (Lindström et al., 2015; Petersen and Lindström, 2012; van de Schootbrugge and Wignall, 2016), could suggest that its mother plant depicted similar adaptive strategy and could explain its consistent dominance, and probably even fueled the contingency of fires throughout this time interval.

Even if other abiotic factors such as strong seasonality with episodic heavy rain, alternating with periods of enhanced drought and fluctuating groundwater tables (Petersen and Lindström, 2012; Weibel et al., 2016), in an overall wet interval, constituted a stressor for the assemblage, their rhizomes would have equally helped them to survive such stressful conditions as laid out before. Together with a potential adaptation to fire, these hypothetical arguments could explain, why *Deltoidospora/Concavisporites* ssp. and *Polypodiisporites polymicroforatus* were so successful in times of biotic crisis, and might compare to strategies of extant representatives of their plant family.

If the vegetation in the Triletes Beds, i.e. in times of marine extinction, depicts such resilient and potential disturbance adapted species, it stands to question whether it was also an extinction interval from a plant perspective. Were conditions hostile enough to cause

actual extinction as some authors argue (Lindström et al., 2015; McElwain et al., 2009; McElwain and Punyasena, 2007) or did changing environmental conditions do nothing more than select for a different type of vegetation as discussed above?

In Bonenburg, many genera and especially many pollen species disappear during the RP-zone (e.g. *Classopollis*, *Quadraeculina*) or occur in very reduced numbers (e.g. *Chasmatosporites*), but re-occur after the TJ-transition (Fig. 5). This suggests, that these taxa, typical of a particular vegetation type and adapted to certain environmental conditions, rather followed their preferred living optima to other regions or refugia, before reestablishing themselves once conditions had changed for the better.

Only the Cheirolepidiaceae *Granuloperculatisporites rudis* does disappear with the shift from the RL to RP-zone and does not return after the TJ-transition. *Ovalipollis* spp. and *Rhaetipollis germanicus*, *Lunatisporites rhaeticus* and *Geopollis zwolinskae* which are supposedly extinct after the TJ-transition (Hillebrandt et al., 2013; Lindström, 2016; Lund, 1977), however, reoccur in Bonenburg's PiK-zone (Fig. 5). Since *L. rhaeticus* and *R. germanicus* only occur as mostly singular occurrences, outside the count and sometimes poorly preserved specimens they may be reworked, indeed. Similar occurrences are also documented for other sections (Kürschner et al., 2007; Mander et al., 2013). Yet, although *R. germanicus* is severely reduced since the RP-zone it lingers on until the top of the section, and temporarily comes back in increased abundances (e.g. 30 and 35 m). More persistent reoccurrences of *R. germanicus* were documented in Hochalplgraben (Bonis et al., 2009) or Kuhjoch East (Hillebrandt et al., 2013).

In the case of *Ovalipollis* spp., which reoccurs in low, but more than singular abundances and rather continuously (Fig. 5), reworking might be a less likely explanation. This is even more true for *Geopollis zwolinskae*, which does not only reoccur continuously, but even in abundances comparable to those of the Contorta Beds, i.e. before the extinction interval. This could also explain the highly abundant reoccurrence of *R. tuberculatus* at the top of our section in the Lower Jurassic after a temporary absence in the PiKa subzone. Even though not reported from the geographically close Mariental (Heunisch et al., 2010), British (Bonis et al., 2010a) and Scandinavian sections (Lindström, 2016; Lindström et al., 2017a; Lund, 1977), it is documented in great abundances from the Eiberg Basin (Bonis et al., 2009; Kürschner et al., 2007), after the TJ-transition (also compare overview in Lindström, 2016; Lindström et al., 2017b). Perhaps the Bohemian Massif (compare Fig. 1) might have served as a refugium for several supposedly extinct taxa to which they migrated, following their preferred climate conditions, a process which is also tested for simulations of the present climate change (Wang et al., 2019). This would also explain the even more abundant reoccurrences in the Lowest Jurassic in Austria compared to Bonenburg, due to its proximity, as well as the time-lag until its return in Bonenburg in the PiKb subzone.

The fact that *R. tuberculatus* still occurs throughout and after the Triletes Beds in Bonenburg, although in reduced abundance compared to the Contorta Beds, and the successively declining abundances towards the RL/RP transition, illustrates a rather gradual ecosystem change. Together with Jurassic occurrences in Austria, this does not attest for its overall, but rather local extinction. Similarly, many other pollen species gradually decline in abundance. Likewise, most spore genera do not occur suddenly after the transition to the RP-zone, but already (occasionally) mix with the assemblage leading up to the RL/RP-transition. Reversely, many spore genera already disappear, or decrease in abundance prior to the RP/PiK transition, and while very few (*Perinosporites thuringiacus*, *Semiretisporis* spp.) actually appear limited to this time interval, most reoccur later in time or in other places (compare e.g. stratigraphic ranges in Schulz, 1967).

All in all, analyzing the changing vegetation patterns and actual disappearances in the Bonenburg section, attests to gradual vegetation shifts from one to another vegetation type, depending on the present environmental conditions, rather than an abrupt turnover as visible in the faunal realm, since our results demonstrate that in Bonenburg, very

few species actually disappear until the top of the lower Hettangian. Different patterns in different sections might then indicate more fragmented populations and local extinction of several taxa. Fragmentation might then have increased the risk of extinction for taxa with reduced population size in the long run after times of marine extinction.

#### 5.4. Environmental disturbances recorded in palynomorph diversity indices

Even though plants seemingly did not face dramatic extinction this does not necessarily mean that plants were not severely affected, and an ecological impact on the floral realm could also manifest itself as community reorganization, irrespective of the taxonomic impact (McGhee et al., 2004; Webb et al., 2009). Given that disturbance events can trigger the establishment of earlier plant successional stages, and since different successional stages are characterized through different diversity patterns (e.g. Connell, 1978; Kimmins, 1997) (e.g. dominant species in pioneer- or end-successions, opposed to richer and more evenly distributed assemblages in intermediate successional stages, etc.), diversity patterns can help us to understand the above discussed vegetational changes from an ecological point of view, and evaluate the ecological impact on plants in times of a major biotic crisis like at the end-Triassic.

Richness is the most frequently used index in paleopalynological studies. Comparative data for diversity patterns beyond richness along the Triassic-Jurassic transition of the Germanic Basin is virtually only available from macroscopic plant remains (McElwain et al., 2009; McElwain and Punyasena, 2007) and molluscs (e.g. Mander et al., 2008). Not only for better comparison of these datasets, there is good reason to also use evenness to complement our palynofloral observations. First of all, because evenness for a microfossil assemblage, is better discernable than dominance, because of temporal compression. A few centimeters of sediment likely contain thousands of years, and even if the sedimentation rate was extremely high, it could be difficult to trace pioneering successions that often last only a couple of years, or few decades at most. Very early successional stages occur thus likely at a timescale, that is difficult to detect in a microfossil assemblage. And while other indices, especially dominance, is potentially confounded by palynofacies shift and the associated Neves Effect (compare section 5.1), evenness appears to be less biased and can be used to also trace intermediate successional stages is therefore helpful to reflect, how much meaning should be given to other diversity indices during such shifts.

Although richness and evenness are two sides of the same coin, they have been shown to be independent parameters, not necessarily responding equally to, but affected differently by different ecological processes and should therefore be considered separately, but concomitantly in studies on diversity (Ma, 2005; Stirling and Wilsey, 2001; Svensson et al., 2012; Wilsey and Stirling, 2007). While species richness, in accordance with the IDH, is shown to be highest at intermediate levels of disturbance (frequency and/or magnitude), i.e. when disturbance excludes competitive exclusion, Svensson et al. (2012) have demonstrated with a theoretical statistical model and metanalysis, that evenness is more likely to further increase at high levels of disturbance, when richness again declines, e.g. as a result of selection. Even though it is still unclear what the exact underlying mechanisms for these responses are, the results are supported by field studies on extant plant and animal communities (Hillebrand et al., 2007; Kimbro and Grosholz, 2006).

Evenness, thus, in the palynological record, might serve as a good relative proxy for disturbance. Assuming the IDH, evenness indicates a continuum of disturbances that includes the intensity as well as the relative time interval between disturbances. Decreasing evenness would then indicate the maturation of the succession, whereas high evenness values together with high richness would indicate intermediate disturbances (i.e. intermediate strength and/or intermediate frequency of disturbance) preserving a highly diverse successional stage. High evenness values, joined with decreasing richness would indicate disturbances beyond the intermediate level and probably triggering substantial ecosystem restructuring (Svensson et al., 2012). Studying

evenness changes in Bonenburg could thus give a new perspective on the strength and frequency of disturbances preceding the extinction interval and after, to understand, when the plant community was most affected by those environmental changes that caused the biotic crisis.

As discussed in section 5.1 (Fig. 11), the first and fourth evenness peaks (E1 and E4) coincided with marine incursions and are potentially driven by palynofacies changes, a common argument in regards to diversity patterns (Peters and Foote, 2001; Raup, 1976; Smith and McGowan, 2005). It should be considered however, that the diversity change itself might be driven by those environmental changes that also drive palynofacies change (Heim and Peters, 2011; Peters, 2005). For example, the shift to a coastal community, typically selecting for Cheirolepidiaceae (Abbink et al., 2004a, 2004b), is fostered by the changed abiotic conditions (especially salt stress), wherefore an ecological signal of increased disturbance caused by changing sea-levels cannot be excluded and would at the same time explain the increased abundance of pollen as a result to the Neves-Effect.

Evenness peaks that are independent of palynofacies or lithological change, such as E2 and 3, cannot be dismissed based on a facies bias at all and are thus even more meaningful to indicate ecological changes and their impact on the plant community. In E2 the joined increase of richness and evenness paired with decreased dominance and Shannon Diversity suggests increased, but probably still intermediate levels of environmental disturbance. Paired with the co-occurrence of aberrant *Classopollis* and *Ricciisporites* tetrads and aberrant *Rhaetipollis germanicus* grains during E2, might further suggest disturbance (compare Fig. 12 and see further discussion in section 5.5).

The only comparative data for diversity patterns leading up to the extinction interval is available from nine plant beds from Astartekløft in East Greenland with a macrofossil record (McElwain et al., 2007; McElwain and Punyasena, 2007). They report relatively high richness and evenness values for plant beds 1–2 in ecozone 1 and decreased evenness and richness values for beds 3–4 from ecozone 2, i.e. within the RL Zone (Mander et al., 2013; McElwain et al., 2007). This is the same pattern as observed in Bonenburg in Evenness peak 2 and afterwards in the RLb sub-zone. The similarity in the macroplant and palynological Evenness records is remarkable, but the exact stratigraphic correlation is yet difficult to constrain and requires further investigation. For Greenland, McElwain and coworkers have used Kempton (1979) employing evenness as a metric for ecosystem health, with high evenness values constituting a more resilient and stable plant community with a bigger pool of genetic/taxonomic variety to draw from if (a) biotic conditions change. Decreased evenness values, like in plant beds 3–4 in Greenland, indicates decreased resilience with fewer taxa monopolizing resources which makes the community more vulnerable towards abiotic perturbations. Accordingly, the community evolving in the Upper Triletes Beds is, like in Greenland, depicting decreased evenness values, with *Ovalipollis* spp. dominating the assemblage. At this stage, it is hard to say whether this development was a result of the first disturbance pulse or a mere adaption to particular environmental conditions, but with one taxon stronger monopolizing resources, the community was more vulnerable for potential changes to come (in E3 and 4). Despite the fragmentary record in Greenland, it is interesting, that there are comparable changes within the pre-extinction interval on a supra-regional scale.

Just after E2, as evenness values decline, we noted a minor *Cymatiosphaera* acme (Figs. 4 and 11). This is a pattern that repeats itself with successively smaller amplitudes after E3 and/or E4, E5 and E6. A similar prasinophyte acme has been documented immediately above the Kössen Formation in Austrian sections, with even higher amplitude (Bonis et al., 2009). However, in Bonenburg, as well as in Mariental (Heunisch et al., 2010) this prasinophyte peak occurs earlier, i.e. before the transition from the RL to RP-zone/RPo Zone and changing carbon isotope values (Fig. 4 and Fig. 11), which diminishes a potential supra-regional correlative value, but suggests a regional application. *Cymatiosphaera* has been suggested as a ‘disaster species,’

opportune to consequences of environmental change (Guy-Ohlson, 1996; Tappan, 1980; van de Schootbrugge et al., 2007), but given its lagged occurrence it might also be explained by a predator-prey relationship (Kürschner et al., 2007) with prasinophytes benefitting from reduced foraging by the preying foraminifera, when the latter suffered from disturbance. The abundant appearance of *Cymatiosphaera* with the disappearance of foraminiferal test linings in Bonenburg is similar to the findings of Kürschner et al. (2007), who can even link their decreasing foraminiferal test linings with decreasing numbers of calcareous foraminifera. By comparison, this could further support our tentative interpretation.

E2 is also followed by the first continuous appearance of *Polypodiisporites polymicroforatus* in Bonenburg (Figs. 5 and 11). It occurs in low quantities, with a temporary absence in the RLc sub-zone. Similarly, in other sections from Germany, England to Austria (Bonis et al., 2010a; Heunisch et al., 2010; Kürschner et al., 2007) it also occurs already shortly prior to the RP-zone, however in smaller and stronger fluctuating abundances. The increasing abundance of *P. polymicroforatus* in the second half of the marine ingression (F4) is a harbinger of the newly establishing vegetation type and coincides with increasing evenness values leading up to E4. In view of these later patterns, this might indicate as early as for E2 and shortly thereafter, that vegetation experienced conditions similar to those that mark the final shift to a new vegetation type, where this taxon dominates the assemblage.

Evenness peak 3 is accompanied by slightly increased richness and together this might indicate increased disturbance, but not beyond an intermediate level. In the succeeding evenness peak (E4) however richness declines, while evenness increases, which suggests, following Svensson et al. (2012), higher disturbance levels than in the previous peak. However, because dominance also decreases, this is not interpreted to be a facies effect caused by more distal conditions, since then we would expect increased dominance values (compare with E1). Moreover, E4 is coinciding with the disappearance of marine fauna and highest number of different taxa depicting aberrations. This suggests a strong disturbance, which would justify the vegetation shift from the RL to the RP-zone. Similarly, a study of bivalve diversity in Southwest England show the same evenness increase towards the transition to the extinction interval, but while marine fauna disappears with drastic richness losses at the transition to the extinction interval (Mander et al., 2008), the palynoflora in Bonenburg increases in richness after this transition. This suggests a supra-regional effect on all communities, but the plant community, although disturbed, is able to adapt, change and thrive in a new form, while fauna faces extinction. A potential cause affecting different communities in different places at the same time might be associated with environmental perturbations caused by CAMP volcanisms just prior to the Event beds (Dal Corso et al., 2014; Davies et al., 2017; Ruhl and Kürschner, 2011). Evenness peaks that succeed each other shortly then might indicate that perturbations occurred in pulses, before reaching a tipping point.

In the context of this supra-regional effect it is particularly remarkable, that peaking evenness and temporarily decreased evenness values in between peaks E3 and E4, just prior to the transition to the Triletes Beds, is not only discernable in Bonenburg, but also in the Eiberg Basin, including the GSSP section Kuhjoch (Fig. 12). Analyzing those datasets that also cover this time-interval shows, that evenness changes are the same as in Bonenburg, but with much higher amplitudes. Correlating these patterns through palynostratigraphy it is also remarkable, that temporarily decreased evenness values coincide with a negative  $\delta^{13}\text{C}_{\text{TROC}}$  excursion as recorded in many of the TJ-sections of the Eiberg basin, however absent in other northwestern European records (Lindström et al., 2017b). This suggests the correlation of floral changes with a major carbon cycle perturbation related to CAMP volcanism through the injection of either magmatic or thermogenic  $^{13}\text{C}$ -depleted carbon or marine methane clathrate destabilization (Ruhl et al., 2011; Heimdal et al., 2018). The lack of an analogues feature in

the  $\delta^{13}\text{C}_{\text{TROC}}$  record of the Bonenburg section might merely reflect the less-than-perfect recording capabilities of total organic carbon in terms of global carbon cycle-forced  $\delta^{13}\text{C}$  anomalies, where changes in the sourced organic matter can skew these bulk-rock derived  $\delta^{13}\text{C}_{\text{TROC}}$  records (Schobben et al., 2019), as opposed to e.g. more-sensitive compound-specific organic C isotope analysis (Ruhl et al., 2011). Nevertheless, our results correlated with similar but much more pronounced disturbances recorded in the Eiberg basin tentatively support a synchronous, supra-regional pattern of disturbance in plant assemblages, associated with carbon cycle perturbation caused by CAMP volcanism as suggested by previous studies (e.g. Hallam and Wignall, 1997; Hesselbo et al., 2002; Kiessling, 2009; Korte et al., 2019; McElwain and Punyasena, 2007; Pálffy, 2003; Pálffy et al., 2001; Tanner et al., 2004).

The intermediate disturbance hypothesis (IDH) also predicts, that those species dominating the assemblage are usually struck hardest by disturbance, when the disturbance is not constituted by intra- or interspecific competition (Connell, 1978). Accordingly, with two evenness peaks E3 and E4, indicating disturbance the Voltziales, Cheirolepidiaceae and *Ricciisporites* having dominated the assemblage before (Figs. 10 and 11), should have been affected most harshly by those changed environmental conditions constituting the disturbance at the transition from the Contorta Beds to the Triletes Beds, i.e. from the pre-to extinction interval. But as discussed in section 5.3. most of them, except for the Voltziales, return in similar abundance in the lower Jurassic, suggesting a shift of vegetation zones, rather than extinction. *Granuloperculatisporites rudis* (Cheirolepidiaceae), which had already almost disappeared after E2, and the Voltziales, represented by *Ovalipollis* spp. might, in accordance with the IDH, represent the few real victims of this change.

The Triletes Beds stand out due to their generally very high and fairly stable richness and evenness values. Nevertheless, after the transition, values are decreasing, which might indicate a maturing succession, prior to renewed disturbance in E5. This evenness peak coincides with a small but distinct *Chasmatosporites* spp. peak in the pollen assemblage, which is detectable from the Germanic Basin to the Tethys shelf (Bonis et al., 2009; Hillebrandt et al., 2013). This illustrates that, despite apparently uniform on first glance, the Triletes Beds still depict assemblage variations.

It is peculiar though, what might explain the continuously high richness and evenness values, despite minor variations. One explanation could be associated to a changed weathering regime that was suggested for the Triletes Beds of Bonenburg (Schobben et al., 2019) but also for stratigraphically equivalent units at many other sites (Ahlberg et al., 2003; Brański, 2014; Michalik et al., 2010; Nystuen et al., 2014; Pálffy and Zajzon, 2012; van de Schootbrugge et al., 2009). An increased terrestrial influx as a result of land wasting in the hinterland which was already suggested by previous authors for the Event Beds (Bonis et al., 2010b; Lindström and Erlström, 2006; Steinthorsdottir et al., 2012), would transport palynomorphs from probably a number of different plant communities. This could explain the extremely diverse assemblage. This view can be supported by the number of reworked specimens found during the Triletes Beds (Figs. 4 and 5). Their origin from a number of different time intervals suggests substantial erosion. Nevertheless, the causes of this changed weathering regime might themselves represent a continued stressor of the assemblage, upholding high evenness values, or they might have caused still other and/or additional abiotic stresses.

One such abiotic factor, which causes cyclic and continued disturbance, and prevents the recolonization by a forest community could be wildfires (Kelly and Brotons, 2017). Even though diversity patterns are dependent on the fire severity (e.g. Burkle et al., 2015 and further references therein), fires can maintain high diversity levels (e.g. Dodson and Peterson, 2010; Abella and Springer, 2015). Previous studies have already discussed the likelihood of crown fires in the Upper Rhaetian, deforesting the previous conifer forest which maintained a rather herbaceous and shrubby vegetation (Petersen and Lindström, 2012). These

wildfires might have been caused by the more humid conditions also increasing storminess and wildfire-inducing lightnings (Belcher et al., 2010; Petersen and Lindström, 2012; van de Schootbrugge and Wignall, 2016). Increased storminess itself could represent a recurrent disturbance in itself, but the particularly high amount of opaque phytoclasts (charcoal) in the Triletes Beds can support this interpretation. Since increasing evenness coincides with decreasing amounts of this material at the bottom, but not at the top of the Contorta Beds, it is difficult to make a link between those two aspects, wherefore wildfires might not be the main driving force as a main stressor (e.g. leading up to E2) it still might still be one factor upholding continuously raised levels of disturbance ensuring continued high richness and evenness. Especially as this sort of deforestation might foster increased erosion and landslides, it is, as a secondary reason, potentially linked with a changed weathering regime upholding high richness and evenness values.

Another explanation might be found in the overall climate regime, which is also connected to the previously said. As a result of greenhouse gas release from CAMP volcanism the global climate regime was warm (Huynh and Poulsen, 2005) and potentially locally more humid (Lindström, 2016; Petersen and Lindström, 2012; Steinthorsdottir et al., 2011, 2012; van de Schootbrugge and Wignall, 2016), which might also foster higher levels of biodiversity, because warmer and wetter environmental conditions are known to harbor increased biodiversity with high evenness (Brown, 2014; Grime, 2006; Wang et al., 2019). Besides overall warm climate, it is assumed, that the CAMP volcanism also caused stronger seasonal extremes between warm and cold (Huynh and Poulsen, 2005), and/or climatic fluctuations on annual to millennial timescales (Landwehrs et al., 2020), which might have as a recurrent, yet intermediate level stressor, potentially upholding high evenness values and richness. In addition, high diversity, known to enhance community stability, might have made the ecosystem more resilient towards disturbances at the same time (Ives and Carpenter, 2007; Loreau and de Mazancourt, 2013; MacArthur, 1955). The highly diverse assemblage described for the Triletes Beds might therefore be a key to the resilience of this system, a diversity which might have been selected for by a continuously changing (local) climate regime representing continued disturbances, preventing the establishment of highly competitive genera and species which would outcompete others in times of more stable conditions.

Evenness Peak 6 (E6), occurring before the palynofacies shift, probably already detects changes in the terrestrial environment which precedes the environmental changes as a result of the Jurassic marine transgression. The latter results in palynofacies changes as well as the assemblage changes occurring from the RP-zone to the PiK-zone. The exact shift and its diversity patterns in the transition from the RP-zone to the PiK-zone are, however, not further discernable due to the present hiatus.

Seen the above discussed diversity patterns, especially evenness as an indicator of disturbance suggests a sequence of probably three main disturbance events prior to the TJ-transition: E2, which was followed by temporary recovery, in which *Polypodiisporites polymicroforatus*, the opportune species of the extinction interval, was recorded for the first time; E3 then represents a renewed disturbance pulse, causing new selective pressure, inducing ecosystem change which is succeeded by a probably even stronger disturbance event beyond the intermediate level, which might have been the final tipping point selecting for a new vegetation type, prevalent thereafter for the remainder of the Germanic Triassic.

### 5.5. Teratology and its ecological significance

Occurrences of malformed palynomorphs have been reported for various palynomorph groups in different time intervals, in phytoplankton in the Lower Triassic (Heunisch and Röhling, 2016), or aberrant saccate bisaccates in the Permian-Triassic (PT) transition (Foster and Afonin, 2005; Hochuli et al., 2017; Mishra et al., 2018;

Prevec et al., 2010) and Norian (Baranyi et al., 2018). Aberrant spores were reported for the end-Devonian, the PT and TJ-transitions (Barth et al., 2018; Filipiak and Racki, 2010; Lindström et al., 2019; Marshall et al., 2020; Visscher et al., 2004) and unevenly sized *Classopollis* pollen tetrads (Kürschner et al., 2013) were reported in the Early Jurassic, respectively. This is the first report of aberrant pollen and unevenly sized *Classopollis* tetrads for the Triassic part of the TJ-transition, and shows that not only ferns, as documented by Lindström et al. (2019) were affected during the transition by a changing environment.

Benca et al. (2018) have effectively demonstrated that the malformations in bisaccate pollen at the PT-boundary could have been induced by UVB-radiation (2018). Other authors have hypothesized a number of potential other stressors causing aberrant palynomorphs such as drought, heat, frost, pCO<sub>2</sub> perturbations, atmospheric pollutions such as SO<sub>2</sub> (Bacon et al., 2013; Baranyi et al., 2018; Barth et al., 2018), or heavy metal pollution (Heunisch and Röhling, 2016; Lindström et al., 2019; Vandembroucke et al., 2015). From extant plants we know, that the male gametophyte and especially the process of microsporogenesis might be considered the 'weakest link' in the plant lifecycle, most easily affected by a stressful environment (Reňák et al., 2014; Zinn et al., 2010) such as high and low temperatures (Higashitani, 2013; Oshino et al., 2007; Tang et al., 2011), water supply (Saini, 1997), and pollutants (e.g. Dixit et al., 2016; Sénéchal et al., 2015) including heavy metals (Kumar and Srivastava, 2011; Lindström et al., 2019; Yousefi et al., 2011). Given that plants are sessile organisms, they are particularly vulnerable to change as they cannot easily escape or temporarily move away. Depending on the strength of the environmental signal and the inherited genetic set of the organism, any cue can act as a stressor.

Given that plants are not as easily able to evade stress through movement like animals do, and have instead evolved a variety of mechanisms to cope fast and efficiently with changing environmental cues like radiation, temperature, moisture, nutrients and heavy metals (Bradshaw, 1972; Huey et al., 2006). Genetic repair mechanisms can prevent the formation of aberrant or aborted microspores (e.g. de Almeida et al., 2012) and if formed, other mechanisms can buffer the potentially fatal effects of such formations (e.g. the sheer mass of microspores of which not all will hand their genetic information to the next generation). Aberrant grains as such are thus a natural feature of microsporogenesis. One could then argue, that we detected such a natural feature only because of overall high pollen concentrations or dominance of the taxa in question. Nevertheless, aberrant tetrads also occur when pollen concentrations are low, but evenness values elevated (e.g. at 8 and 12.5 m) and often do not occur even when *Classopollis* spp. abundance is highest (1.5 m and 2.7–3.1 m) and not even when pollen concentrations as well as *Classopollis* spp. abundances are high (e.g. 2.5–2.7 m and 12 m).

One should also keep in mind that, besides these discussed abiotic effects, there are potential biotic causes for the observed aberration. For example percentages of aberrant pollen can be used as an indicator of hybridism and subsequent polyploids (Bhowmik and Datta, 2012; Chaturvedi et al., 1999; Ickert-Bond et al., 2003). Given that aberrant *Classopollis* spp. tetrads occur when *C. meyeriana* mixes with *C. torosus* or *Geopollis zwolinskae*, could suggest hybridization as one possible explanation. Then we would, however, expect these aberrant tetrads to occur also at the very base or the very top of the studied section, where these taxa occur simultaneously as well. Even if hybridization would explain aberrant *Classopollis* spp. tetrad occurrences, habitat shifts and mixing of previously separated populations in itself might be a result of the changing environment and would thus still indicate times of environmental stress. The temporarily occurring aberrant tetrads, with joined occurrences of aberrations in more than one taxon then suggests a connection with an episodically changing environment as a trigger for these malformations, probably induced by stress beyond the usual baseline.

The co-occurrence of aberrant palynomorphs together with E2, E3 and E4 with most diverse aberrations found in E4 and at the very base

of the Triletes Beds then further supports the interpretation of disturbance during these intervals. Even though plants did not become extinct, this likely indicates that they were severely stressed, nevertheless.

The question then is, whether there are any indications as to the source of the stressor. In section 5.3 it was already discussed, that the aquatic and terrestrial communities up to E2 suggests temporary more warm, brackish and wet conditions. Temperature, water as well as potential salinity stress might have constituted a stressor for the established assemblage, which could explain elevated evenness values and could, according to the arguments laid out above, explain the appearance of aberrant palynomorphs and tetrads.

Similarly, the coincidence with comparably negative  $\delta^{13}\text{C}_{\text{TOC}}$  values may hint at an association of this interval with climatic change. Perturbations in the carbon cycle, which are often interpreted as a result of the release of thermogenic methane as a result of CAMP volcanism (Bernier and Beerling, 2007; Heimdal et al., 2019; Hesselbo et al., 2002; Marzoli et al., 2018; Ruhl et al., 2011) and the occurrence of aberrant palynomorphs and tetrads in the same interval could even be associated to secondary mutagenetic effects of volcanism (e.g. through mercury or  $\text{SO}_2$ ) as suggested by other authors for this time interval (Lindström et al., 2019).

So even, if aberrant palynomorphs here do not directly point at a stressor, they might indicate times of increased environmental stress, which further supports the above given interpretation of increased disturbance around evenness peaks. Even though further, and more quantitative and interdisciplinary studies are needed to distinguish the stressor (Lindström et al., 2019) teratology in palynology might serve as a new potential proxy to identify times of increased disturbance.

### 5.6. Implications for the TJ-extinction

Since we cannot report significant taxonomic losses, the palynoflora did not seem to have faced severe extinction. One should keep in mind however, that a comparative study of plant micro- and macrofossils in Greenland, has discussed conflicting records in both fossil types with higher extinction rates for microfossils, due to underrepresentation of certain pollen types in the palynofloral record (Mander et al., 2010). Our palynological results are very similar to Mander and coworkers and following their arguments, a more severe impact on the floral realm might simply not be detectable in the palynological record due to taphonomic reasons. It should be considered as well however, that it is in the nature of macrofossils to give a temporarily more fragmentary insight and are thus likely to show stronger differences and thus more abrupt changes, which can overrepresent change, where temporarily compressed microfossils give a more gradual and thus apparently less dramatic impression. As with everything, the truth is likely somewhere 'in between'. As for the palynological record in Bonenburg, which is comparable to results from other European sections as well as Greenland, those few species that did get lost rather represent the natural selection over time that facilitates evolution and successive ecosystem change, adapting to changing environmental conditions. This is a very similar observation as what Barbacka et al. (2017) have deduced after analyzing extinction rates excluding sample-related biases for micro- and macrofossils.

Given our observations of gradual shifts of vegetation change from the RL- to RP-zone through intermediate successional stages with temporary peak abundances of lycophytes, leptosporangiate ferns and Osmundales peaks to a new long-lasting vegetation type in the Triletes Beds we also agree, that assemblage changes reflect natural successional stages (Barbacka et al., 2017). And although we also believe that fluctuations of local environmental conditions play a significant role in driving floral changes (Barbacka et al., 2017), we would like to stress, that some of the patterns of changing vegetation might have supra-regional significance, such as the Cheirolepidiaceae abundance bracketing the *Polypodiisporites polymicroforatus* interval and the evenness increase paired with negative carbon isotope excursion prior to that

interval in the Germanic Basin as well as in the Northern Calcareous Alps (including the GSSP section).

In this paper, we have analyzed generic alpha diversity patterns in the classical sense to evaluate the strength of disturbance and magnitude or ecological restructuring indicated by changing diversity patterns. This can however only document a facet of ecosystem change, because extant as well as more and more paleo studies recognize not only the importance of generic diversity, but also functional diversity (e.g. Díaz et al., 2007; Dunhill et al., 2018; Loreau and de Mazancourt, 2013; Schumm et al., 2019). To make inferences on ecosystem functions or morphological traits for plant microfossils is however very difficult, given the scarce knowledge we have about them, especially when the mere botanical affinity is yet unclear even for very dominant taxa like *Riccisporites tuberculatus*. Looking at genus diversity is however the first step in that direction and can complement our understanding of the ongoing processes. Especially evenness patterns, have proved to be rather uniform in the compared sections from the Eiberg Basin and maybe even compared to Greenland and should be further investigated, as excursions in the evenness curve could serve as an additional correlative tool, when studying changes on a supra-regional scale.

Although plants as sessile organism are not able to move in the strictest sense, they indirectly evade unfavorable conditions through a dispersal. As a result, they follow their living optima in a changing environment, resulting in (temporarily) changed geographic ranges, from which they can recolonize once conditions have changed again. This was illustrated in the above studied section by the re-occurrence of Cheirolepidiaceae for example. Therefore, it is particularly important to evaluate plant extinction at the TJ-transition in the context of changing vegetation types and considering their occurrences elsewhere or later, in order to not overestimate extinction.

Having said this, it is also important to consider our observations on diversity patterns together with terrestrial pollen and spore teratology and other recent observations on spore teratology (Barth et al., 2018; Lindström et al., 2019) prior to the TJ-transition. If interpreting evenness as a disturbance indicator and seen its co-occurrence with aberrant palynomorphs, this can indicate that although plants were stressed like the fauna, they did not face major extinction.

Especially aberrant pollen tetrads as direct evidence of malfunctions during microsporogenesis are a very significant side-observation of this paper. Their episodic occurrences, coincidence with raised evenness values, and occurrence in many taxa at the same time suggests an environmental trigger for these occurrences. Recently for example, (Lindström et al., 2019) mercury was discussed as a potential stressor. One should keep in mind however, as was discussed above, that a number of other potential stressors as temperature and moisture changes can also cause such malformations. Even though there might not be a unidirectional relationship allowing to infer a certain stressor based on the malformations, these intervals may however indicate episodes of increased environmental stress. These intervals are very interesting to study further with interdisciplinary approaches, to better understand the causes of environmental change causing faunal extinction.

The quantitative results of aberrant palynomorphs for Bonenburg will be presented in a separate paper. For now, their occurrences indicate those episodes that potentially harbor more information to better understand the events leading up to the end-Triassic biotic crisis, which struck animals much harder than plants. Although plants appear to have been stressed, rather than going extinct, further quantitative studies are needed to better evaluate their level and potential causes of stress.

The mere appearance of aberrant tetrads necessarily resulting from disturbed meiosis, can however already indicate increased mutation rates and recombination, resulting in increased variation, which together with natural selection, is a prime force of speciation (Darwin, 1859). Selection, i.e. a bottleneck event, with shifting environmental conditions is given as well. Therefore, aberrant tetrads indicate a particularly relevant time interval in the phylogeny of those lineages in which they occur. When studying the Cheirolepidiaceae in the future,

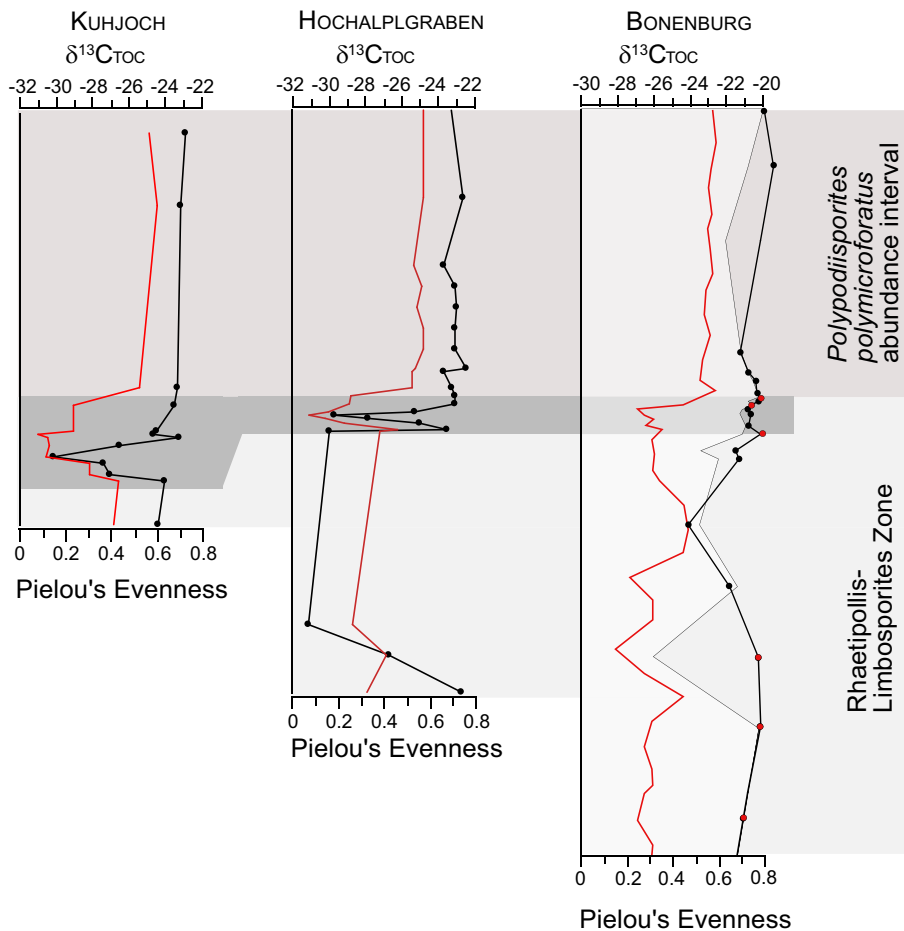


Fig. 12. Comparing diversity patterns from the Germanic Basin (Bonenburg) with the Eiberg Basin (Kuhjoch, Hochalplgraben). Compared evenness curves (black dotted line) in correlation to  $\delta^{13}C_{TOC}$  curves (red line) from the GSSP section Kuhjoch, Hochalplgraben and Bonenburg. Stratigraphically, correlatable assemblage zones given as light grey background, negative CIEs correlating with evenness decreases highlighted with dark grey background. For Bonenburg, evenness is given for palynomorph clusters (e.g. tetrads) counted as individuals (i.e. 4) in light grey histogram and counted as items (i.e. 1) in a line with circles for respective samples. Red circles indicate aberrant palynomorph occurrences. Please note the scale difference for Bonenburg compared to Fig. 11, this is necessary to better compare with samples with much higher amplitudes from the Eiberg Basin. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

greater emphasis should be given to the TJ-transition, as it might play a key role in the evolution and the success of this plant family.

All in all, our study has also shed more light on the character of the Triletes Beds. Continued and/or intermediate disturbance is indicated through high evenness values, which after a third peak reached a tipping point which was followed by a shift in vegetation composition. Even if there are a number of potential abiotic stresses that can individually or jointly explain these values. It should be considered that the effects on land, e.g. weathering influx changes likely would have emanated to the sea, and thereby influenced marine communities for example through eutrophication, anoxia or turbidity. Observations from palynofacies, reworked palynomorphs together with geochemical data (see Schobben et al., 2019) suggest, that the Triletes Beds are, at least partially, a result of disturbance and not (only) sea-level changes. The latter might in fact be only another result of globally changed climate conditions, which had also a number of other, additional, disturbance effects.

## 6. Conclusions

The new Bonenburg section, so far only studied for biostratigraphy, geochemistry and vertebrates, gives now, when studied from a paleopalynological perspective a number of new insights into the TJ-transition, confirms and supports observations of other studies or disciplines and adds new facets to existing discussions and provides the most detailed record to date of vegetational changes leading up to the biotic crisis.

Study of (1) the depositional environment, based on palynofacies data and marine palynomorphs, indicate three marine ingressions in the Bonenburg section and supports earlier paleogeographic reconstructions of three distinct sea-level changes in the Germanic Basin. Moreover, palynofacies analysis together with reworked palynomorphs

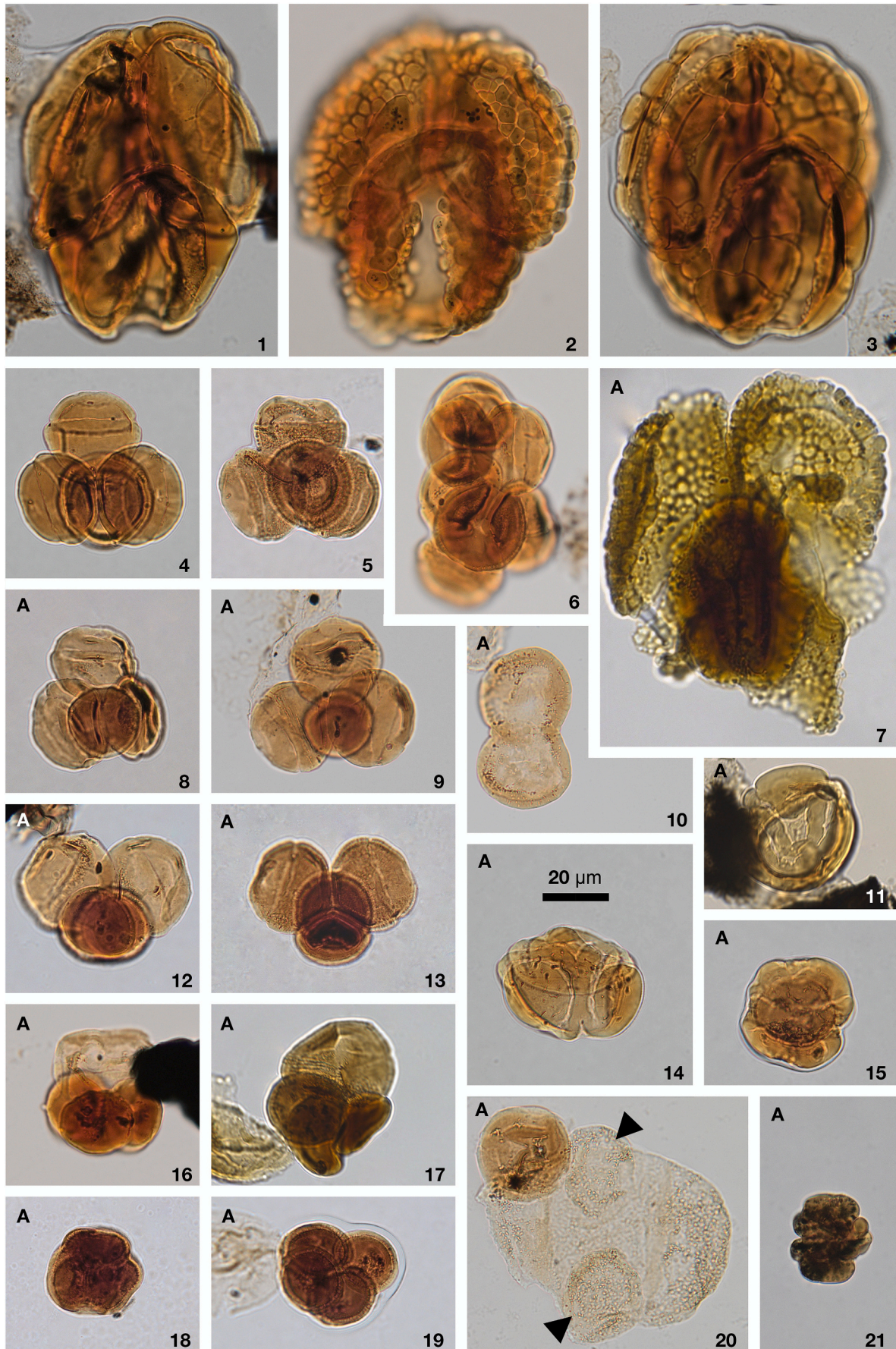
trace riverine influx changes and offer additional support for the assumption of a changed weathering regime during the extinction interval as proposed by previous studies.

A more detailed and quantitative study of palynofloral assemblages with identification of four informal assemblage zones gives a good (2) palynostratigraphic framework for Bonenburg. It also allows a better correlation with other European sections which facilitates comparison of present and future findings. In this process a typographical error of the stratigraphically important taxon *Limboisporites lundbladiae* [published as '*lundbladii*'] under Art. 60.8 (ICBN) was corrected and should be used in this corrected form, henceforth.

When studying (3) the vegetation history, we illustrated the gradual transition through different successional stages. The pre-extinction interval is characterized by a Conifer forest with Cheirolepidiaceae, Voltziales and the botanically unassigned *Ricciisporites*. After successional abundances of lycophytes, leptosporangiate ferns (*Deltoidospora* spp.) and Osmundales, the vegetation changes to a shrubbier and more herbaceous Cycad and fern assemblage, with a diverse cryptogam flora. The lowest Jurassic is thereafter characterized by a conifer forest of Pinaceae, Podocarpaceae and Cheirolepidiaceae with abundant Selaginellales.

Although the vegetational changes at first glance suggest a less dramatic effect for the floral realm, the study of diversity pattern gave a more detailed insight into (4) plant ecosystem response. Using evenness as a disturbance indicator, three disturbance pulses (E2, E3 and E4) leading up to the extinction interval can be identified. While the first one occurs already in the lower half of the Contorta Beds (top of RL<sub>a</sub>), the next two follow on one another shortly. Nevertheless, all of them co-occur with aberrant palynomorphs which could support that most plants, although stressed by the changing conditions, did not go extinct. In fact, the mutagenic stressor might even have facilitated the variation necessary to adapt to changing





(caption on next page)

**Fig. 13.** Aggregated pollen and aberrant pollen from the Bonenburg section. Aberrant pollen or pollen tetrads are indicated with an 'A'. 1.-3. *Ricciisporites tuberculatus* with different types of ornamentation. 4. *Classopollis meyeriana* tetrad 5. *Classopollis torosus* tetrad 6. *Classopollis* sp. cluster of seven grains. 7. *R. tuberculatus* tetrad with one underdeveloped grain. 8. + 9. *C. meyeriana* and *C. torosus* tetrads with one underdeveloped grain. 10. two *C. sp.* grown together. 11. aberrant *Rhaetipollis germanicus* 12. + 13. *C. meyeriana* and *C. torosus* tetrads with two underdeveloped grains. 14. + 15. malformed *R. germanicus* 16. + 17. *C. meyeriana* and *C. torosus* tetrads with three underdeveloped grains. 18. + 19. *C. meyeriana* and *C. torosus* tetrads with all grains underdeveloped. 20. Bisaccate pollen indet. With two additional sacci (black arrowheads). 21. Abnormally small *R. germanicus*. Names with full author citation and botanical affinities are given in supplementary Table 1.

conditions. The last pulse of disturbance (E4) bridging the pre- to the extinction interval depicts evenness values increasing beyond richness, which probably indicates the most severe disturbance, and is supported by the most diverse appearance of aberrant palynomorphs. This severity apparently was a tipping point, as vegetation thereafter shifts towards a new long-lasting type. *Polypodiisporites polymicroforatus* already occurring after the first disturbance pulse (E2) and increasing in abundance between E3 and E4 seems to be the harbinger of the new vegetation type. Given that the abundance interval of this species can be correlated between all major European sections, this pattern seems to be more than a local event, most likely driven by supra-regional environmental change and not (only) by local changes.

The observation of teratology of terrestrial palynomorphs is a significant side observation of this study. We document aberrations not only in spores, but for the first time also in Cheirolepidiaceae pollen with different size coordinations in one tetrad prior to the TJ-transition. Although aberrations are known in saccate pollen from the PT and TJ-boundary and *Classopollis* tetrads in the Jurassic, mainly spores and aberrant saccate pollen have been documented for the pre-extinction interval of the TJ-transition so far. The study of teratology is an evolving field at the moment, potentially serving as a disturbance proxy for plants, which can help to identify episodes of severe environmental stress and thereby to better understand the drivers of faunal extinction not only during the TJ-transition. Moreover, by providing circumstantial evidence of cell divisionary processes, they open a new window into the genetic past and hint at intervals of high evolutionary significance for the phylogeny of the plant lineages in question.

#### Data availability

The palynofacies and palynological slides are stored in the collections of the University of Oslo. Datasets related to this article can be acquired from the corresponding author upon request.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gloplacha.2020.103286>.

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#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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