

Preprints are preliminary reports that have not undergone peer review. They should not be considered conclusive, used to inform clinical practice, or referenced by the media as validated information.

Triassic palynology of the Swiss Belchentunnel - a restudy of the Scheuring samples

Elke Schneebeli (Zelke.schneebeli@pim.uzh.ch)

Paleontological Institute and Museum, University of Zurich https://orcid.org/0000-0002-1552-4785

Evelyn Kustatscher

Museum of Nature South Tyrol

Research Article

Keywords: Carnian, Switzerland, aquatic palynomorphs, Aratrisporites, Riella

Posted Date: March 23rd, 2023

DOI: https://doi.org/10.21203/rs.3.rs-2695655/v1

License: (c) This work is licensed under a Creative Commons Attribution 4.0 International License. Read Full License

Version of Record: A version of this preprint was published at Swiss Journal of Palaeontology on July 18th, 2023. See the published version at https://doi.org/10.1186/s13358-023-00278-2.

Abstract

Well-preserved Carnian (Late Triassic) palynomorphs are rare in Switzerland, despite sediments include one of the important plant fossil localities, Neue Welt near Basel. Modern detailed palynological studies on Triassic palynomorphs in general and especially in the Carnian are scarce, most palynological studies have been carried out more than fifty years ago. Nevertheless (Late) Triassic sediments still yield surprises for palynological research. Here, we present the results of the re-study of the famous Belchentunnel samples that have been studied and published by Bernhard Scheuring in 1970. The less cheerful result concerns the preservation of slides: more than 60% of the slides are degraded. On the other hand, the restudy of the well-preserved slides showed an unexpected number of algae, acritarch and spore taxa, not described so far. The latter facilitate the correlation with the well-known biostratigraphic schemes established for the Germanic Basin. The distribution of *Porcellispora longdonensis* throughout the Belchentunnel succession is especially striking. The acme just below the Schilfsandstein might suggest the presence of ephemeral ponds.

1. Introduction

The first two Belchen (Bölchen in Scheuring, 1970) tunnels through the Swiss Jura mountains between Hägendorf, Solothurn and Eptingen, Basel-Land were constructed between 1963 and 1966. The opening of a third rehabilitation tunnel recently (July 1, 2022) gave the impetus to re-examine the palynological samples described by Scheuring (1970), taken during the tunnel construction in the 1960s. The succession that had been tunnelled through is one of the few Ladinian–Carnian successions yielding palynomorphs in Switzerland. It is, thus, one of the best places to study the Carnian Pluvial Episode (Simms and Ruffel, 1989), a time of substantial climate and environmental changes accompanied by changes in the composition of the terrestrial and marine ecosystems as well as major originations and radiations among land plants (e.g., Dal Corso et al., 2020). Sedimentologically, this time period is marked by a shift towards siliciclastic dominated facies, as reflected in the Ergolz Member of the Klettgau Formation (Jordan et al., 2016). Palynological assemblages across the Carnian Pluvial Episode are marked by an increase in relative abundance of spores especially *Aulisporites astigmosus* and/or *Leschikisporis adunctus* (e.g., Heunisch, 1999; Paterson and Mangerud, 2015; Vigran et al., 2014; Orłowska-Zwolińska, 1985; Roghi et al., 2010).

In Switzerland the Carnian crops out only in few areas. Some of the most famous Carnian plant fossil localities are Neue Welt near Basel and Moderhalde near Pratteln (ca. 20 km NW of Belchentunnel). The plant fossil assemblage are dominated by cycadophytes, ferns, sphenophytes with rare ginkgophytes and conifers (Schlotheim, 1822; Brongniart 1825; Heer, 1865; Leuthardt 1903; 1904; Kräusel 1955; 1959; Kräusel and Schaarschmidt, 1966). Leschik (1955) described numerous spores and pollen (148 species) from Neue Welt. Other Carnian sediments yielding palynomorphs are the Raibl Group of the austroalpine nappes at Fanezfurga (GR), and Iberger Klippen (Sz) (Hochuli and Frank 2000; 2006). They are, however, characterized by a high maturity and low diversity of sporomorphs.

The exceptional preservation and detailed description of the sporomorphs from the Belchentunnel has made the publication by Scheuring (1970) a reference paper for Middle to early Late Triassic palynological taxonomical studies. Scheuring (1970) described in a very detailed and meticulous way various pollen taxa with a special attention also to the variability within single pollen taxa. As detailed his taxonomic work was, the distribution of the various taxa was provided only by simplified information on the vertical distribution of the described forms, including inaccuracies with respect to sample distance and relative abundance (Scheuring, 1970, p. 19). This means that some palynomorph taxa are not included and that the stratigraphic resolution of palynomorph occurrences is vague. In a short biostratigraphic chapter, seven associations (A–G) are described summarily but the exact stratigraphic positions of the boundaries between these associations were not given.

In order to link the palynological assemblages of the Belchentunnel to modern palynological schemes in the Central European Basin and the alpine Triassic, Scheuring's samples are restudied after over fifty years. Despite the preservation of the slides is concerning, the new inventory shows that the curation of fossils, in this case palynological slides, offers the opportunity to discover more taxa and to interpret old and new data on fossils in new contexts.

2. Geological Setting

In northern Switzerland Middle to Upper Triassic sediment outcrops are rare. However, drill cores, such as those drilled by the NAGRA (National Cooperative for the Disposal of Radioactive Waste) provide additional insight and allowed for the formal definition of the Schinznach Formation, the Bänkerjoch Formation, and the Klettgau Formation (Jordan et al., 2016; Pietsch et al., 2016). During construction of the Belchentunnel under the Swiss Jura fold and thrust belt between Hägendorf and Eptingen (Fig. 1), the sedimentary succession of the uppermost part of the Schinznach Formation, the Bänkerjoch Formation and the lower part of the Klettgau Formation was encountered several times due to the tectonic repetition. Especially the northern part is characterized by thrusts. Therefore Scheuring (1970) sampled the Middle and Upper Triassic succession in the southern part of the tunnel which is less affected by thrusts (Fig. 2).

The Asp Member, the uppermost member of the Schinznach Formation, formerly "Lettenkohle" consists of argillaceous marls in the lower part and dolomites in the upper part. Plant and vertebrate fossils are known to occur in the argillaceous marls (Pietsch et al., 2016). The Bänkerjoch Formation consists of an alternation of shales, sulphates, sulphate shale, and shale with nodular sulphate. The Klettgau Formation is subdivided into Ergolz Member, Gansingen Member, Gruhalden Member, and the Belchen Member, the latter was not encountered in the Belchentunnel. The Ergolz Member consist of fluvial sand- and siltstone and is overlain by the dolomites of the Gansingen Member. The succession of the following Gruhalde Member is heterogeneous, consisting of marls, dolomitic marls, and dolomites with varying contribution of sand (Jordan et al., 2016)

3. Materials And Methods

For this study Scheuring's palynological slides, stored in the palaeontological collection at ETHZ, were reexamined. The original Belchentunnel samples were processed according to the scheme in Fig. 3 (Scheuring, 1970, p.8).

According to Scheuring (1970), 89 out of 200 original samples were processed and 45 of them were productive. Productive samples are stored in slides boxes in the palaeontological collection at ETHZ. During a first inspection of the slides, those samples were identified that are still intact enough for a qualitative and quantitative analysis. The target count of 250 sporomorphs was not reached for every sample, because in a few samples the intact area was too small and the spore-pollen yield too low. Samples with counts < 100 are marked by a grey bar in Fig. 4. Miscellaneous palynomorphs, i.e. fungal remains and marine palynomorphs have been counted along spores and pollen. For the relative abundance of the marine fraction, the total amount of marine palynomorphs, spores and pollen was calculated. The Figs. 4 and 5 display all studied by Scheuring (1970), despite not all could be counted. The distribution of the zones or assemblages provided by Scheuring (1970) and their boundaries are given only approximately in Figs. 4 and 5, because no exact stratigraphic position was given in the original paper. Also, all holotype slides were check for their state of preservation.

The log has been redrawn and simplified for this study. Results are presented along the current Triassic stratigraphy and chronostratigraphy (Jordan et al., 2016).

4. Results

Over the past 50 + years the microscope slides suffered from degradation. Seventeen out of 46 of Scheuring's original slides could be re-studied. Degradation of microscope slides is an issue not only for palynostratigraphic samples but especially for microscope slides with holotypes (Gravendyck et al., 2021). Therefore, all slides with holotypes were checked for their state of preservation. Preservation of holotype slides is similarly concerning, only ~ 59% of the holotypes could be allocated on intact slides. Especially holotypes described from strew mounts could not be allocated or are degraded (supplementary table, and example in Fig. 4).

For simplicity Scheuring's scheme of 7 distinct palynomorph associations A–G is used here as a basis to present the results. First Scheuring's palynological assemblages are re-called, followed by additional observations and discrepancies encountered during this study.

Association A is dominated by *Triadispora* spp., with prominent contribution of *Striatoabieites aytugii* (*S. balmei* after Scheuring, 1978) and *Protodiploxypinus gracilis*. Rare elements are *Ovalipollis* spp., and *Lunatisporites acutus*. Sporadically *Echinitosporites iliacoides, Cucullispora cuneata* and *Retisulcites perforatus* (= *Monosulcites perforatus* Mädler 1964) are recorded (Scheuring, 1970). Samples 1 and 5 could be restudied. The general description given by Scheuring is verified (Fig. 5). The preservation in sample 1 is rather low, therefore most bisaccate pollen grains could not be identified to genus or species level. Additional elements occurring in low abundances in these assemblages are *Jugasporites* spp.,

including Jugasporites conmilvinus, Alisporites grauvogelii, Chordasporites spp., Perinopollenites cf. elatoides. and a variety of spore taxa, such as Deltoidospora spp., Calamospora spp., including C. tener, Punctatisporites spp., Aratrisporites spp., ?Lundbladispora sp., Osmundacidites sp., and undifferentiated spores. Miscellaneous palynomorphs are represented by algal colonies, Botryococcus spp., fungal remains (hyphae), Leiosphaeridia spp., Micrhystridium spp., Plaesiodictyon mosellanum, Tasmanites spp. and Veryhachium spp. In the lowermost samples 1 Micrhystridium accounts to almost 40% of the total palynomorph count, excluding fungal remains and *Reduviasporonites* spp. (Fig. 6, 7). **Association B** is similar to association A in composition with sporadic occurrences of *Eucommildites* microgranulatus and Podosporites amicus. Ovalipollis spp., Retisulcites perforatus (= Monosulcites perforatus Mädler 1964), and Echinitosporites iliacoides are commonly recorded (Scheuring, 1970). The position of the upper boundary is unclear. Samples 11 and D18 are included, whether D11 and D9 were originally included in Association B is concealed. Samples 11 and D18 provided spore and pollen taxa as mentioned by Scheuring (1970), but also additional taxa such as Illinites spp., Platysaccus spp., Cycadopites spp., monosaccate pollen grains and Camerosporites secatus. Scheuring (1970) recorded the latter only from Association C onward. Spores are very rare including Aratrisporites paraspinosus, A. scabratus, Densoisporites spp., and Apiculatisporis spp. Additional palynomorphs include algal colonies and fungal remains (hyphae), Micrhystridium spp., Plaesiodictyon mosellanum, Reduviasporonites *catenulatus*, and *Tytthodiscus* sp. Marine palynomorphs never exceed 10% of the total palynomorph count, excluding fungal remains and *Reduviasporonites* spp. The assemblages in sample 11 is marked by several first appearance data (FAD) and last appearance data (LAD). The LAD's recorded include those of Cucullispora cuneata, Lunatisporites acutus, Perinopollenites cf. elatoides, Osmundacidites spp. Apiculatisporis spp., Sulcosacispora minuta, Falcisporites stabilis, Triadispora boelchii?, and verrucate monosulcate pollen grains occur only in sample D11. The presence of *Cucullispora cuneata* suggests that D11 is probably assignable to Association B (see below). First occurrences are recorded from Ellipsovelatisporites plicata, Sulcatisporites spp., and Parillinites spp. in this sample.

Association C resembles generally associations A and B, but *Cucullispora cuneata* is absent. Instead *Duplicisporites, Camerosporites,* and *Paracirculina* (included in *Duplicisporites* Scheuring 1978), and *Infernopollenites* are new elements in this association. The abundance of *Ovalipollis* spp. increases throughout Association C (Scheuring, 1970). Samples D9, D100, 26, 55, and 58 are included in Association C. The list provided by Scheuring (1970) can be complemented by the presence of *Cordaitina* sp. (D9), *Platysaccus* spp. (D100), *Cycadopites* spp. (D100), *Doubingerispora filamentosa* (D100) and *Echinitosporites iliacoides* (D100), and the LAD in sample 58 of *Protohaploxypinus* spp. and *Illinites* spp. *Aratisporites paenulatus* reaches relative abundances of up to ~ 8% in the basal part of Association C. Additional rare element are *Enzonalasporites* spp. *Lycospora* sp., and *Punctatisporites* spp. whereas *Infernopollenites* spp. was not recorded. In addition, algal colonies, algal cysts of *Botryococcus* spp., *Cymatiosphaera* spp., *Leiosphaeridia* spp., *Micrhystridium* spp., *Plaesiodictyon mosellanum*, and fungal remains (hyphae and spores) are present. *Leiosphaeridia* spp. are especially abundant in sample 55

accounting to > 50% of the total palynomorph count, excluding fungal remains and *Reduviasporonites* spp. (Fig. 5).

Association D is marked by reduction in *Ovalipollis* spp. and an increase in *Triadispora* spp. (especially *T. aurea* and *T. epigona*). *Echinitosporites iliacoides, Retisulcites perforatus* (= *Monosulcites perforatus* Mädler 1964), *Podosporites amicus, T. suspecta* are absent (Scheuring, 1970). Only sample 82 and 85 were still intact to be analysed. The assemblages in these two samples agree with Scheuring's description. LAD's recorded in Association D are those of *Striatoabieites balmei, Parillinites* spp., and *Chordasporites* spp. *Staurosaccites* spp. has its first appearance and a single occurrence of *Infernopollenites* sp., is recorded.

Association E is similar to Association D, but *Eucommiidites microgranulatus* is absent in the former. *Ovalipollis* spp. is again more abundant compared to *Triadispora* spp. (Scheuring, 1970). In addition to the palynomorphs described by Scheuring (1970), assemblages of the two analyzed samples, 97 and 104, included also *?Gordonispora* sp. and *Deltoidospora* sp. Contrastingly, *Eucommiidites microgranulatus* is present in both samples. Numerous LAD's are recorded: the aforementioned *Eucommiidites microgranulatus*, together with *Protodiploxypinus decus, Triadispora epigona, T. stabilis, T. falcata, T. plicata, Monosulcites perforatus, Lunatisporites* spp., and *Doubingerispora filamentosa. Vitreisporites* spp., and *Alisporites* spp. disappear as well. Aquatic palynomorphs include *Botryococcus* spp., *Micrhystridium* spp., and *Leiosphaeridia* spp., the latter accounting to ~ 30% of the total palynomorph count, excluding fungal remains and *Reduviasporonites* spp.

Association F is characterized by new elements such as *Patinasporites densus, Triadispora verrucata,* and *Paracirculina quadruplicis.* The uppermost part of Association F is marked by a *Porcellispora longdonensis* acme, which disappears thereafter (Scheuring, 1970) (Fig. 5). *Paracirculina* was later revised by Scheuring (1970) and included in *Duplicisporites* (Scheuring, 1978), therefore *Paracirculina quadruplicis* in included in *Duplicisporites* spp. in this study. *Triadispora verrucata* is present in Association B to D, but was not found in assemblages of samples 126, 136,139, and 142. Instead of *Patinasporites densus, Enzonalasporites* spp., including *E. vigens* and *E. ignaii* occurs commonly. Just one *Micrhystridium* sp. was found in sample 136.

In the uppermost **Association G***Striatoabieites aytugii* (*S. balmei* after Scheuring, 1978) and *Porcellispora longdonensis* are missing, whereas *Ovalipollis* spp. is dominant. Unfortunately, there are no samples preserved in what is considered the Schilfsandstein. All samples were degraded and could not be reanalysed. The description here is based on data from Scheuring (1970) only.

5. Discussion

5.1 The spores in the assemblages

More the fifty years ago, Bernhard Scheuring described the assemblages of the Belchentunnel with a strong focus on taxonomy of gymnosperm pollen. Only one spore taxon was then described,

Porcellispora longdonensis, which is abundant in the topmost part of the Bänkerjoch Formation (Association F). Despite spores are neither diverse and nor abundant, there are several taxa present in the lower half of the section. These offer additional stratigraphic and ecological information. Sporomorph assemblages are dominated by conifer pollen such as *Triadispora* spp. and *Protodiploxypinus* spp. throughout the studied interval. Pollen of seed ferns (e.g. *Platysaccus* spp.) and pollen with cycadalean affinity (e.g. *Eucommiidites* spp.) are less common. Rare elements are lycophyte spores (e.g. *Aratrisporites* spp.) sphenophyte spores (*Calamospora* spp.), and fern spores (*Punctatisporites* spp.).

The most prominent spore taxon in the assemblages of the Belchentunnel is surely *Porcellispora* longdonensis. Its botanical affinity has long been regarded bryophytic and thus indicating rather humid climatic conditions (Visscher and Van der Zwan, 1981; Baranyi et al., 2019). Currently the affinity of P. longdonensis to Riella is based on morphological similarities between the fossil spore species P. longdonensis and spores of the modern liverwort taxon Riella (Reinhardt and Riecken, 2000). In late Pleistocene-early Holocene palaeoecological studies the concentration of Riella spores has been used as indication of lake level highs (Djamali et al., 2008). During the last glacial episodes higher spore concentration were deposited in lake sediments of the semi-arid to arid region of Iran. The increase in *Riella* spore concentration could be correlated with lake level highs that allow for brackish to freshwater conditions, i.e. the conditions that favour *Riella* spore germination. The lake level rise during glacial episodes has been explained rather by a reduction in evaporation due to reduced summer temperatures than by an increase in precipitation (Djamali et al., 2008). Riella grows as submerged plants in freshwater to brackish, mostly ephemeral ponds in semi-arid climatic conditions with distinct seasonality in precipitation and in rather disturbed environments (Cirujano et al., 1988; Djamali and Segarra-Mortegues, 2021). The plant would, thus, have a very low preservation potential based on their preferred growing environment, whereas the spores have a higher fossilisation potential. Based on these considerations, in recent publications on Late Triassic palynology, P. longdonensis has been regarded a xerophytic element (Fijałowska-Mader et al., 2021). In the present study, we included *Porcellispora longdonensis* within the spores, based on its bryophytic affinity. However, for future studies it might be reasonable to emphasis its palaeoecological significance and its potential as an environmental indicator of ephemeral lakes to a greater extent and to group it with aquatic palynomorphs.

5.2 Correlation of assemblages with Upper Triassic palynostratigraphic schemes

Despite the Carnian Pluvial Episode was not recorded by Scheuring (1970), his palynostratigraphic subdivision of Upper Triassic deposits is to date unmatched in terms of resolution (Fig. 8)

Aratrisporites species are especially present in the upper part of the Middle and lower part of the Upper Triassic deposits in the Germanic Basin (Erfurt Formation, and lower part of Grabfeld Formation; Zone GTr 10 and GTr 11 *sensu* Heunisch, 1999, *Heliosaccus dimorphus* Zone *sensu* Kürschner and Herngreen, 2010) and the *Heliosaccus dimorphus* Zone described from the Poland (Orłowska-Zwolińska, 1985) (see also Nowak et al., 2018), which would correspond to Assemblages A to B of Scheuring (1970) in the Belchentunnel. Diverse *Aratrisporites* and abundant non-taeniate bisaccate pollen are also a common feature of the *Echinitosporites iliacoides* Zone of the Barents Sea area (Vigran et al., 2014, Paterson and Mangerud, 2020), and the assemblage H *sensu* Hochuli et al. (1989). Of the typical elements in the Barents Sea assemblages *Schizaeoisporites worsleyi, Staurosaccites quadrifidus, Protodiploxypinus ornatus, Triadispora verrucata, Ovalipollis pseudoalatus*, and monosaccate pollen, the latter three are also present in assemblages A–B in the Belchentunnel. *Heliosaccus dimorphus* and *Echinitosporites iliacoides* are also a characteristic element of the *secatus-dimorphus* phase *sensu* Van der Eem (1983) and their FAD are the marker of the late Fassanian *Heliosaccus dimorphus* zone *sensu* Roghi (1995) of the Dolomites, whereas they have not been described from the Carnian successions of the Julian Alps (Roghi, 2004). This suggests that the assemblages A and B belong to the late Ladinian.

The base of the following younger Zone in the Germanic Basin (Camerosporites secatus Zone sensu Kürschner and Herngreen, 2010) is marked by the FADs of Enzonalasporites vigens as well as the nominating species, and the first common occurrences of Ovalipollis pseudoalatus. The latter two feature are observed in assemblage C in the Belchentunnel, whereas E. vigens was recorded later in assemblage D. The C. secatus Zone is subdivided into two subzone, the base of the lower Triadispora verrucata Subzone is marked by the FAD of the nominating species, although in the Swiss section T. verrucata is already present in the older assemblage B. Assemblages of the T. verrucata Subzone have been correlated with Zones GTr 12 and GTr 13, which are marked by the presence of E. iliacoides and M. perforatus (recorded as Retisulcites perforatus) and numerous Protodiploxypinus species, T. verrucata and Ovalipollis pseudoalatus, Porcellispora longdonensis and C. secatus. The T. verrucata Subzone sensu Kürschner and Herngreen (2010) and GTr 12 and GTr 13 sensu Heunisch (1999) are, thus, comparable with assemblages D-F sensu Scheuring (1970, and this study). Regular occurrences of P. longdonensis, diverse Triadispora species and Circumpolles are also characteristics of the P. longdonensis Zone in Poland (Orłowska-Zwolińska, 1985). The Aulisporites astigmosus Composite Assemblages Zone in the Barents Sea (Vigran et al., 2014) includes Echinitosporites iliacoides, Triadispora verrucata, Enzonalasporites vigens, and Camerosporites secatus and is, thus, also comparable with the assemblages D-F sensu Scheuring (1970). However, there are also differences. The A. astigmosus Zone is defined by the FADs of A. astigmosus, Ricciisporites tuberculatus, Camarozonosporites rudis, and Uvaesporites argentaeformis. These species are not present in the Belchentunnel samples. A refinement of the *A. astigmosus* Zone are provided by the *Semiretisporis* hochulii and Podosporites vigraniae zones (Paterson and Mangerud, 2020). These correlate with the Zones G and F of Hochuli et al. (1989). A correlation with the palynological assemblages of the Southern Alps is difficult and based on lithostratigraphic correlation (Roghi et al., 2010). The Concentricisporites bianulatus assemblages includes the nominative species, and Kyrtomisporis ervei, as well. The only species in common is *Duplicisporites verrucosus* (Roghi et al., 2004).

The assemblage G *sensu* Scheuring (1970), corresponds stratigraphically to the Schilfsandstein-facies in the Germanic Basin. However, Scheuring (1970) mentioned only two samples,150 at the base and 164 at the top of the Schilfsandstein. Unfortunately, both samples are too degraded for a re-assessment. This interval could potentially include also the Carnian Pluvial Episode. In this case a high abundance of either

Aulisporites astigmosus or *Leschikisporis adunctus* or a combination of both would be expected. However, Scheuring (1970) did not mention any specific divergent composition. A resampling would be necessary to understand whether the palynological assemblage resembles the *A. astigmosus* Subzone *sensu* Kürschner and Herngreen, 2010, A. *astigmosus* Zone *sensu* Orłowska-Zwolinska, 1985 (Vigran et al., 2014; Roghi et al., 2010) or *L. adunctus* Zone *sensu* Paterson et al. (2017; Paterson and Mangerud, 2020).

5.2 The Carnian Pluvial Episode

Carnian Pluvial Episode is marked by changes in lithology and vegetation composition due to higher relative humidity in mid Carnian successions in the low latitudes (e.g., Dal Corso et al., 2015; Baranyi et al., 2019). However, records from the Germanic Basin seem to contradict this (Franz et al., 2019; Visscher et al., 1994), since there palaeoclimate proxies indicate rather continuous semi-arid to arid conditions throughout the Carnian. The lithology of Belchentunnel is closely comparable to the Germanic Basin stratigraphy, with some Schilfsandstein-type successions crop out.

The palynological samples from the Belchentunnel do not include the typical marker taxa of the Carnian Pluvial Episode in Europe (*Aulisporites astigmosus* and *Leschikisporis adunctus*), but the spore *Porcellispora longdonensis* has a striking distribution, with a substantial increase in abundance just below what would be considered the Schilfsandstein facies in the Belchentunnel succession. In case *P. longdonensis* would be confirmed to be related to *Riella* plants, and the preferred growing environment would be the same, the increase in relative abundance of *P. longdonensis* spores could be correlated to lake level highs that allow for brackish to freshwater conditions, i.e. the conditions that favour *Riella* spore germination. Lake level rises during glacial episodes have been explained rather by a reduction in evaporation due to reduced summer temperatures than by an increase in precipitation (Djamali et al., 2008). The general climatic conditions between the late Pleistocene-early Holocene and the Late Triassic differ significantly. Climate proxies indicate arid to semi-arid conditions during the latest Longobardian (late Ladinian, Middle Triassic) and the early Carnian with rather high evaporation rates.

Transgressions into the Central European Basin accelerated the hydrological cycle which led to increased runoff and higher groundwater tables (Franz et al., 2019). This favoured the formation of lakes in lowland areas, ideal conditions for plants adapted to grow in ponds under semi-arid conditions, such as *Riella*. The most extensive transgression occurred just before the deposition of the Schilfsandstein (Franz et al., 2019), which would correspond to the *P. longdonensis* acme in the Belchentunnel. These lakes or backswamps created the taphonomic window necessary for the preservation of the pristine fossil flora of e.g., Neue Welt (Franz et al., 2019).

6. Conclusions

With the description of palynomorphs from the Belchentunnel, Bernhard Scheuring published a reference work for Late Triassic palynomorph taxa in 1970. The restudy of his samples shows that the preservation of numerous slides, including the slides with holotypes, is concerning, over 60% are degraded. A positive

aspect, however, is the discovery of aquatic palynomorphs and spores, especially several *Aratrisporites* species that were previously not recorded. The possible botanical affinity of the spore taxon *Porcellispora longdonensis* with *Riella*, a submerged liverwort in semi-arid regions, might indicate ephemeral ponds during deposition of the Schilfsandstein, the sediment facies representing the CPE.

Resampling and restudy at high resolution with special attention to the upper part of the succession are important to get insights into the traces left by the CPE in Swiss successions.

Declarations

Acknowledgements

We are thankful for valuable information and help in both collections Naturhistorisches Museum Basel and Geological and palaeontological collection of ETHZ by Walter Etter and Iwan Stössel. Torsten Wappler is thanked for valuable information on arthropod scales.

Availability of data and material

Palynological slides are stored in the Palaeontological Collection of ETH Zurich. All other data are included in the text and in the supplementary material.

Competing interests

The authors declare that they have no competing interests.

Funding

Not applicable.

Authors' contributions

ESH had the idea to restudy Scheuring's slides from the Belchentunnel and analysed the slides. EK added palaeogeographic and palaeoclimatic context. Both authors wrote and proofread various versions of the text and approved the final manuscript.

References

- Amann, F., Ündül, Ö., & Kaiser, P. K. (2014). Crack initiation and crack propagation in heterogeneous sulfate-rich clay rocks. Rock Mechanics and Rock Engineering, 47(5), 1849–1865. https://doi.org/10.1007/s00603-013-0495-3
- Baranyi, V., Rostási, Á., Raucsik, B., & Kürschner, W. M. (2019). Palynology and weathering proxies reveal climatic fluctuations during the Carnian Pluvial Episode (CPE) (Late Triassic) from marine successions in the Transdanubian Range (western Hungary). Global and Planetary Change, 177(April), 157–172. https://doi.org/10.1016/j.gloplacha.2019.01.018

- 3. Brongniart, A. (1825). Observations sur les végétaux fossiles renfermés dans les grès de Hoer en Scanie. Annales des Sciences Naturelles, 4, 200-224.
- 4. Cirujano, S., Montes, C., Martino, P., Enríquez, S., & García, P. (1988). Contribución al estudio del género *Riella* Mont. (Spaerocarpales, Riellaceae) en España. *Limnética*, *4*, 41–50.
- Dal Corso, J. D., Bernardi, M., Sun, Y., Song, H., Seyfullah, L. J., Preto, N., Gianolla, P., Ruffell, A., Kustatscher, E., Roghi, G., Merico, A., Hohn, S., Schmidt, A. R., Marzoli, A., Newton, R. J., Wignall, P. B., & Benton, M. J. (2020). Extinction and dawn of the modern world in the Carnian (Late Triassic). Science Advances, 6(eaba0099), 1–13.
- 6. Dal Corso, J., Roghi, G., Kustatscher, E., Preto, N., Gianolla, P., Manfrin, S., & Mietto, P. (2015). Ammonoid-calibrated sporomorph assemblages reflect a shift from hygrophytic to xerophytic elements in the late Anisian (Middle Triassic) of the Southern Alps (Italy). Review of Palaeobotany and Palynology, 218, 15–27. https://doi.org/10.1016/j.revpalbo.2014.02.010
- Djamali, M., & Segarra-Moragues, J. G. (2021). Palaeoecology and conservation of endangered hidden species; example of the liverwort Riella (Riellaceae). *Biodiversity and Conservation*, *30*(10), 2731–2750. https://doi.org/10.1007/s10531-021-02218-3
- Djamali, M., Kürschner, H., Akhani, H., de Beaulieu, J. L., Amini, A., Andrieu-Ponel, V., Ponel, P., & Stevens, L. (2008). Palaeoecological significance of the spores of the liverwort Riella (Riellaceae) in a late Pleistocene long pollen record from the hypersaline Lake Urmia, NW Iran. *Review of Palaeobotany and Palynology*, *152*(1–2), 66–73. https://doi.org/10.1016/j.revpalbo.2008.04.004
- 9. Fijałkowska-Mader, A., Jewuła, K., & Bodor, E. (2021). Record of the Carnian Pluvial Episode in the Polish microflora. *Palaeoworld*, *30*(1), 106–125. https://doi.org/10.1016/j.palwor.2020.03.006
- Franz, M., Kustatscher, E., Heunisch, C., Niegel, S., & Röhling, H. G. (2019). The schilfsandstein and its flora; arguments for a humid mid-carnian episode? *Journal of the Geological Society*, *176*(1), 133– 148. https://doi.org/10.1144/jgs2018-053
- 11. German Stratigraphic Commission (Ed.) (2022): Stratigraphic Table of Germany Compact 2022 (STGC 2022), (Stratigraphische Tabelle von Deutschland), Potsdam: GFZ German Research Centre for Geosciences, 2 p. https://doi.org/10.48440/dsk.stgc.2022
- 12. Heer, O., 1865. Die Urwelt der Schweiz. Schulthess Editor, 622 pp., Zürich.
- Heunisch, C. (1999). Die Bedeutung der Palynologie f
 ür die Biostratigraphie und Fazies in der Germanischen Trias. In N. Hauschke & V. Wilde (Eds.), Trias, eine ganz andere Welt (pp. 207–220). Verlag Dr. Friedrich Pfeil, M
 ünchen.
- 14. Hochuli, P.A., Frank, S.M. (2000). Palynology (dinoflagellate cysts, spore-pollen) and stratigraphy of the Lower Carnian Raibl Group in the Eastern Swiss Alps. Eclogae Geologicae Helvetiae 93, 429-443.
- Hochuli, P.A., Frank, S.M. (2006). Palynomorphe und organisches Material aus den Raibler Schichten einer oberostalpinen Schuppe der Iberger Klippen (Kanton Schwyz, Schweiz). Eclogae Geologicae Helvetiae, 99(1), 131-136.
- 16. Jordan, P., Pietsch, J.S., Bläsi, H., Furrer, H., Kündig, N., Looser, N., Wetzel, A., Deplazes, G. (2016a). The middle to late Triassic Bänkerjoch and Klettgau formations of northern Switzerland. Swiss

Journal of Geosciences 109(2), 257-284.

- 17. Kräusel, R. (1955). Die Keuperflora von Neuewelt bei Basel. I. Koniferen und andere Gymnospermen, Schweizerische Paläontologische Abhandlungen 71, 1-27.
- 18. Kräusel, R. (1959). Die Keuperflora von Neuewelt bei Basel. III. Equisetaceen, Schweizerische Paläontologische Abhandlungen 77, 1-19.
- 19. Kräusel, R., Schaarschmidt, F. (1966). Die Keuperflora von Neuewelt bei Basel. Schweizerische Paläontologische Abhandlungen 84:1-79.
- 20. Kürschner, W. M., & Herngreen, G. F. W. (2010). Triassic palynology of central and northwestern Europe: a review of palynofloral diversity patterns and biostratigraphic subdivisions. *Geological Society, London, Special Publications, 334*, 263–283. https://doi.org/10.1144/SP334.11
- 21. Leschik, G. (1955) Die Keuperflora von Neuewelt bei Basel. II. Die Iso- und Mikrosporen, Schweizerische Paläontologische Abhandlungen 72, 1-270.
- 22. Leuthardt, F. (1903). Die Keuperflora der Neuen Welt bei Basel, Teil I. Abhandlungen Der Schweizerischen Paläontologischen Gesellschaft, 30, 1-23.
- 23. Leuthardt, F. (1904). Die Keuperflora der Neuen Welt bei Basel, Teil II. Abhandlungen Der Schweizerischen Paläontologischen Gesellschaft, 31, 25-46.
- 24. Mädler, K. (1964). Die geologische Verbreitung von Sporen und Pollen in der deutschen Trias. Beih. Geol. Jb. 65, 1–147.
- 25. Nowak, H., Schneebeli-Hermann, E., & Kustatscher, E. (2018). Correlation of Lopingian to Middle Triassic Palynozones. Journal of Earth Science, 29(1), 755–777.
- 26. Orłowska-Zwolińska, T. (1985). Palynological zone of the Polish epicontinental Triassic. Bulletin of the Polish Academy of Sciences, Earth Sciences, 33, 107–117.
- 27. Paterson, N. W., & Mangerud, G. (2015). Late Triassic (Carnian–Rhaetian) palynology of Hopen, Svalbard. Review of Palaeobotany and Palynology, 220, 98–119.
- Paterson, N. W., & Mangerud, G. (2020). A revised palynozonation for the Middle-Upper Triassic (Anisian-Rhaetian) Series of the Norwegian Arctic. Geological Magazine, 157(10), 1568–1592. https://doi.org/10.1017/S0016756819000906
- 29. Pietsch, J. S., Wetzel, A., & Jordan, P. (2016). A new lithostratigraphic scheme for the Schinznach Formation (upper part of the Muschelkalk Group of northern Switzerland). Swiss Journal of Geosciences, 109(2), 285–307. Heunisch, C. (1999). Die Bedeutung der Palynologie für die Biostratigraphie und Fazies in der Germanischen Trias. In N. Hauschke & V. Wilde (Eds.), Trias, eine ganz andere Welt (pp. 207–220). Verlag Dr. Friedrich Pfeil, München.
- Reinhardt, L. & Ricken, W. (2000). Climate cycles documented in a playa system: comparing geochemical signatures of subbasins (Triassic, Middle Keuper, German Basin). Zentralblatt für Geologie und Paläontologie 1, 315–340.
- 31. Roghi, Guido. (1995). Analisi palinologica della sezione di Stuores Wiesen (Prati di Stuores, Dolomiti): dati preliminari. Ann Univ Ferrara. 5. 37-40.

- 32. Roghi, G. (2004). Palynological investigations in the Carnian of the Cave del Predil area (Julian Alps, NE Italy). Review of Palaeobotany and Palynology, 132(1–2), 1–35. https://doi.org/10.1016/j.revpalbo.2004.03.001
- Roghi, G., Gianollo, P., Minarelli, L., Pilati, C., Preto, N. (2010). Palynological correlation of Carnian humid pulses throughout western Tethys. Palaeogeography, Palaeoclimatology, Palaeoecology, 290, 89-106. Doi: 10.1016/j.palaeo.2009.11.006
- 34. Scheuring, B.W. (1970). Palynologische und palynostratigraphische Untersuchungen des Keupers im Bölchentunnel (Solothurner Jura). Schweizerische Paläontologische Abhandlungen 88, 1-119.
- 35. Scheuring, B.W. (1978). Mikrofloren aus den Meridekalken des Mte. San Giorgio (Kanton Tessin). Schweizerische Paläontologische Abhandlungen 100, 1-100.
- 36. Schlotheim, E.F. von (1822). Nachträge zur Petrefactenkunde. Becker'sche Verlagsbuchhandlung, Gotha
- 37. Simms, M. J., Ruffell, A.H. (1989). Synchroneity of climatic change and extinctions in the Late Triassic. Geology, 17, 265-268.
- 38. Stockar, R., Baumgartner, P. O., & Condon, D. (2012). Integrated Ladinian bio-chronostratigraphy and geochrononology of Monte San Giorgio (Southern Alps, Switzerland). Swiss Journal of Geosciences, 105(1), 85–108. https://doi.org/10.1007/s00015-012-0093-5
- 39. van der Eem, J. G. L. A. (1983). Aspects of Middle and Late Triassic palynology. 6. Palynological investigations in the Ladinian and lower Karnian of the western Dolomites, Italy. Review of Palaeobotany and Palynology, 39, 189–300.
- 40. Visscher, H., Van der Zwan, C.J., 1981. Palynology of the circum-Mediterranean Triassic phytogeographical and palaeoclimatological implications. Geol. Rundsch. 70, 625–636.
- 41. Visscher, H., van Houte, M., Brugman, W. A., & Poort, R. J. (1994). Rejection of a Carnian (Late Triassic) "pluvial event" in Europe. *Revtew of Palaeobotany and Palynology*, *83*, 217–226.



Geographical overview of the Belchentunnel location. Blue area indicates roughly the extend of the Jurassic thrust and fold belt.



Geological cross section along the Belchentunnel after Amann et al., 2014.

- 1) Zerkleinern (< 1 mm), Vorwaschen und Aufweichen
- 2) HCl (wenn nötig: Aufwärmen), Waschen
- 3) HF (in Kupfertiegel, wenn nötig: Aufwärmen), Waschen
- 4) HCl (heiss), Waschen
- 5) Chlorieren (Na₂ClO₃ in Eisessig und mit einigen Tropfen HCl conc. im Wasserbad erwärmen). Zum Entfernen von Pyrit und organischen Resten, Waschen
- 6) Azetolysieren (Konzentration je nach Bedarf), Waschen
- Schweretrennung der mineralischen Überreste mittels Bromoform oder einem gesättigten Gemisch von CdJ + KJ + H₂O, Waschen.

Die Streupräparate wurden – wie üblich – mit Glyzeringelatine hergestellt. Nagellack diente zu ihrer Umrandung.

Über die Haltbarkeit solcher Präparate liegen uns noch keine Erfahrungen vor. LESCHIKS Präparate von Neuewelt bei Basel sind zum Teil mit Kanadabalsam verdichtet worden. Dieser wird nach einer gewissen Zeit brüchig, weshalb einzelne seiner Präparate schon unter Luftzutritt stehen.

Figure 3

Preparation scheme applied by Scheuring. 1) crushing, washing, and soaking, 2) HCl (warm-up if necessary), washing, 3) HF (in copper pot, warm-up if necessary), washing, 4) HCl (hot), washing, 5) Chlorination (warming up Na2ClO3 in glacial acetic acid with few troplets of conc. HCl in water bath) In order to remove pyrite and organic residuals, washing 6) Azetolyze (concentration as required), washing, 7) Density separation to remove mineral remains using bromoform or a saturated mixture of CdJ+KJ+H2O, washing. Strew mounts prepared using glycerine jelly and nail polish.



Holotype of *Parillinites pauper* (Scheuring, 1970) threatened by degradation.



Relative abundances of terrestrial palynomorphs in the Belchentunnel samples. Arranged according to the stratigraphic last occurrence of the taxa.



Miscellaneous palynomorphs in the Belchentunnel samples calculated using the total of palynomorphs counted excluding *Reduviasporonites*.



Palynomorphs from the Belchentunnel, scale bar 20 µm except otherwise indicated. Palynomorph followed by sample number and Englandfinder coordinates. **a** *Reduviasporonites catenulatus*, 11, L 29; **b** fungal remain «jelly bean», D9, S 36/3; **c** *Plaesiodictyon mosellanum*, D9, Q 38/3; **d** algal cluster, 11, H 34; **e** *Micrhystridium pentagonale?*, 26, N39/1; **f** *Thyttodiscus*sp., 1, T37/4; **g** algal cyst, D9, R44/1; **h** *Aratrisporites scabratus*, D100, 2. slide, K 49; **i** *Aratrisporites paenulatus*, D100, 2. slide Q 34; **j**

Aratrisporites paraspinosus, 11, J 46/1; **k** *Aratrisporites parvispinosus*, 5, Q28/4; **I** *Aratrisporites tenuispinous*, 82, Q 41/2; **m**, **n** immature spore masses?, 1, M 39, M44/3; **o** arthropod scale, D18, V41/1

Stratigraphy				Scheuring		Stratigraphy	Orłowska-			Paterson &			
Germany	Kürschner & Herngreen		Heunisch,	1970 and	Stratigraphy	CH Jordan et	Zwolinska	Vigran et al.,	Paterson	Mangerud,	Hochuli et	Roghi et al.,	Roghi et al.,
(STGC 2022)	2010		1999	this study	CH old	al., 2006	1985	2014	et al., 2017	2019	al., 1989	2010	2004
		subzone											
Schilfsand-													
stein									Leschiki-	Leschiki-			Duplici-
(Stuttgart		Aulisporites			Schilfsand-	Ergolz Mb,	Aulisporites		sporis	sporis		Aulisporites	sporites
Fm)		astigmosus	GTr 14		stein	Klettgau Fm	astigmosus		adunctus	adunctus	D,E	astigmosus	continuus
									Podo-	Podo-			
									sporites cf	sporites			
			GTr 13	D, E, F?					amicus	vigraniae	F		
	Camero-				1					Semireti-			Concentrici-
upper	sporites	Triadispora				Bänkerjoch	Porcellispora	Aulisporites		sporis			sporites
Grabfeld	secatus	verrucata	GTr 12	C?		Fm and Asp	longdonensis	astigmosus		hochulii	G		bianulatus
lower					Gipskeuper	Mb,		Echinito-		Echinito-			
Grabfeld and					and	Schinznach		sporites		sporites			
Erfurt Fm	Heliosaccus		GTr 11	A-B?	Lettenkohle	Fm	Heliosaccus	iliacoides		iliacoides	н		
	dimorphus		GTr 10				dimorphus						

Figure 8

Correlation of the Belchentunnel assemblages with palynozones from the Central European Basin, Tethys, and the Barents Sea.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

• DataTable.xlsx