Schneebeli-Hermann and Kustatscher *Swiss Journal of Palaeontology* (2023) 142:13
https://doi.org/10.1186/s13358-023-00278-2

Swiss Journal of Palaeontology

RESEARCH ARTICLE

Open Access

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

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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 were carried out more than 50 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 were 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, acritarchs, and spore taxa not described so far. Especially the spores 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.

Keywords Carnian, Switzerland, Aquatic palynomorphs, *Aratrisporites*, *Porcellispora*, *Naiadita*

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. Although Scheuring studied only few samples from the base of this episode, it is one of the best places in Switzerland to study the Carnian Pluvial Episode (CPE; e.g., Dal Corso et al., 2020; Simms and Ruffell, 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). In Swiss successions, this time interval 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

Handling editor: Susanne Feist-Burkhardt.

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especially *Aulisporites astigmosus* and/or *Leschikisporis adunctus*, both species were not encountered in the Belchentunnel samples (e.g., Franz et al., 2019; Orłowska-Zwolińska, 1985; Paterson and Mangerud, 2015; Roghi et al., 2010; Vigran et al., 2014).

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 assemblages are dominated by cycadophytes, ferns, sphenophytes with rare ginkgophytes and conifers (Brongniart, 1825; Heer, 1865; Leuthardt, 1903, 1904; Kräusel, 1955; 1959; Kräusel and Schaarschmidt, 1966; Schlotheim, 1822). 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 Fanezfurgga (GR), and Iberger Klippen (Sz) (Hochuli and Frank, 2000; 2006). They are, however, characterized by a high thermal maturity and low diversity of sporomorphs. Well-preserved Carnian palynomorphs are rare in Swiss successions. The sandstone-dominated lithology in Northwest Switzerland and the predominantly dolomitic facies with high thermal maturity in the Austroalpine nappes are unfavorable for the preservation of palynomorphs.

The exceptional preservation and detailed description of the sporomorphs from the Belchentunnel and from Monte San Giorgio has made the publications by Scheuring (1970; 1978) reference papers 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.

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 50 years. Despite the fact that 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.

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. 1a), 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. 1c).

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. Vertebrate fossils are known to occur in bonebeds in the argillaceous marls (Pietsch et al., 2016), which are predominantly deposited under marine conditions. Only in the upper part of the Asp Member, increased continental influence is documented by plant fossils (Merki, 1961). The Bänkerjoch Formation consists of an alternation of shales, sulphates, sulphate shale, and shale with nodular sulphate. These sediments were deposited under arid to semiarid conditions in a peri-marine to terrestrial environment (Jordan et al., 2016). 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 deposited in large fluvial system from the Fennoscandian shield to the Tethys. From its lithological equivalent in southwest Germany, the Stuttgart Formation lacustrine deposits are known to occur near the top of the otherwise predominantly fluvial deposits (Beutler et al., 1999). It is overlain by the dolomites of the Gansingen Member, which were deposited in a restricted marine environment with brackish conditions developing into evaporitic sabkha and siliciclastic marginal environments towards the east (Jordan et al., 2016). The succession of the following Gruhalde Member is heterogeneous, consisting of marls, dolomitic marls, and dolomites with varying contribution of sand deposited in a coastal playa (Jordan et al., 2016).

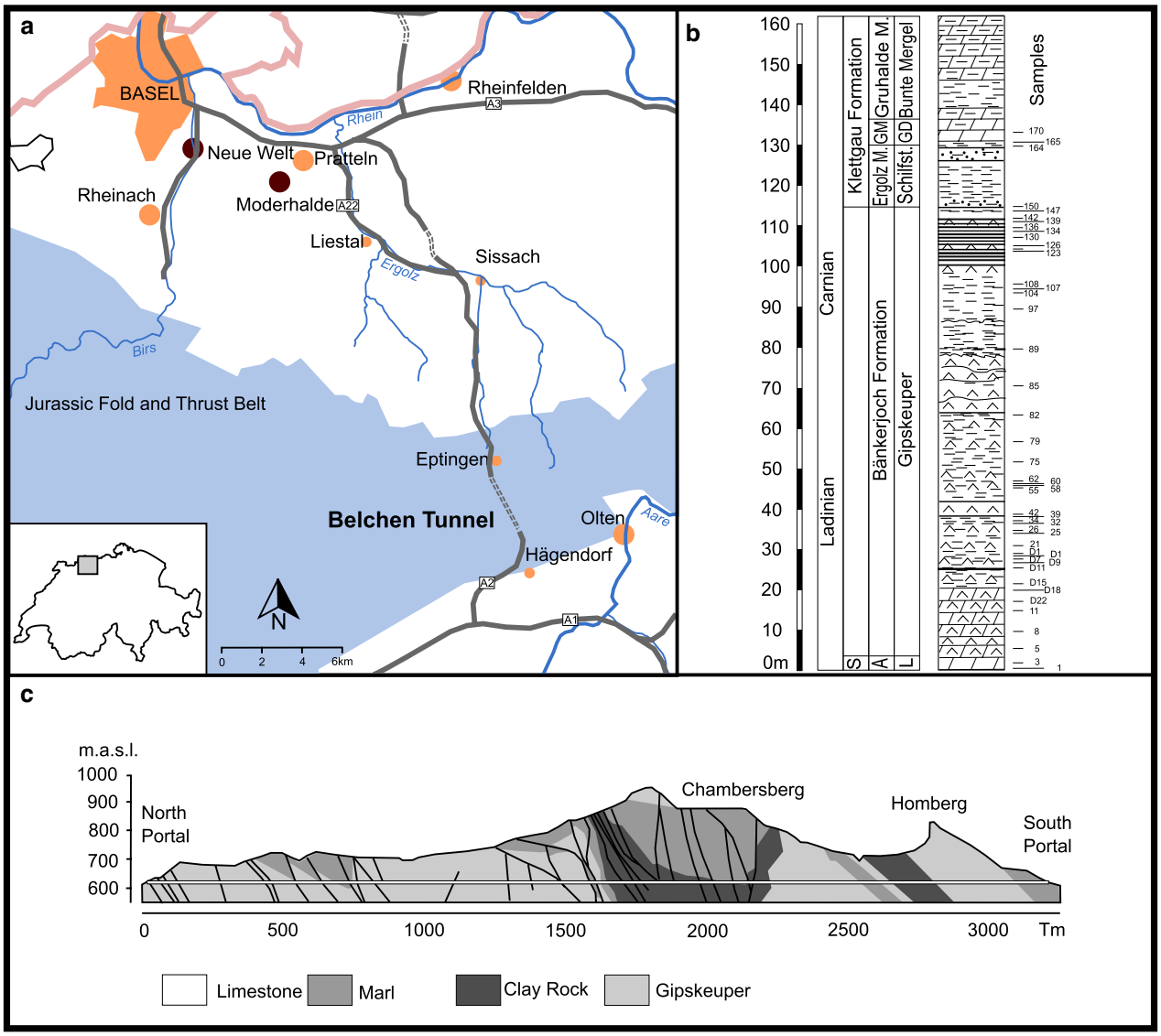

Fig. 1 Geographic and geological overview. **a** Geographical overview of the Belchentunnel location. Blue area indicates roughly the extend of the Jurassic thrust and fold belt. **b** simplified stratigraphic and lithologic log of the Belchentunnel succession studied by Scheuring (1970). S: Schinznach Formation, A: Asp Member, L: Lettenkohle: GM: Gansingen Member, GD: Gansinger Dolomit. **c** Geological cross section along the Belchentunnel after Amann et al., (2014)

Materials and methods

For this study, Scheuring's productive palynological slides, stored in the palaeontological collection at Eidgenössische Technische Hochschule Zurich (ETHZ), were re-examined. The original Belchentunnel samples were processed according to the following scheme: (1) crushing, washing, and soaking, (2) HCl (warm-up if necessary), washing, (3) HF (in a copper pot, warm-up if necessary), washing, (4) HCl (hot), washing, (5) Chlorination (warming up Na_2ClO_3 in glacial acetic acid with a few droplets of concentrated HCl in a water bath) to remove pyrite and organic residuals, washing (6) Acetolyze (concentration as required), washing, (7) Density separation to remove mineral remains using bromoform or a saturated mixture of $CdJ + KJ + H_2O$, washing. Strew mounts were prepared using glycerine jelly and nail polish (Scheuring, 1970, p. 8).

According to Scheuring (1970), 89 out of 200 original samples were processed and 45 of them were productive. 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 was too low. Samples with counts < 100 are marked by a gray bar in Fig. 5. Miscellaneous palynomorphs, i.e., fungal remains and marine palynomorphs, have been counted along with spores and pollen. For the relative abundance of the phytoplankton fraction, the total amount of marine palynomorphs, spores, and pollen was calculated. Figures 5 and 6 display all samples studied by Scheuring (1970), despite the fact that 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. 5 and 6, because no exact stratigraphic position was given in the original paper.

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

Results and facies interpretation

Over the past 50 + years, the microscope slides have suffered from degradation. Seventeen out of 46 of Scheuring's original strew mounts could be quantitatively 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 ~ 53% of the holotypes could be located on intact slides. Especially holotypes described from strew mounts could not be allocated or are degraded (Additional file1: Table). Holotypes are illustrated in Figs. 2, 3 and 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* (= here recorded as *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 poor; 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. *Jugasporites* spp., including *Jugasporites conmilvinus,* have been described to occur in Lower Triassic alpine sediments (Klaus, 1964), although no difference in preservation is apparent, these forms might be reworked. 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 sample, *Micrhystridium* accounts for almost 40% of the total palynomorph count, excluding fungal remains and *Reduviasporonites* spp. (Figs. 6, 7). *Leiosphaeridia* spp., *Micrhystridium* spp., and *Veryhachium* spp. are generally regarded as marine acritarchs, whereas *Tasmanites* spp. represent marine prasinophytes. *Micrhystridium* spp. have also been reported from Permian–Triassic fluvial deposits of the Karoo (Cole & Barbolini, 2019). A taxon even more controversially discussed is *Reduviasporonites*, which has been regarded either as fungal remains or algae (Foster et al., 2002; Visscher et al., 2011). In recent studies, the attribution of *Reduviasporonites* tends to a zygnematalean affinity, which is mostly found in freshwater (Lei et al., 2013; Heunisch and Röhling, 2016). *Reduviasporonites* spp. are commonly found in marine Permian–Triassic successions (Lei et al., 2013; Heunisch and Röhling, 2016). The combination of several marine acritarch taxa in the Belchentunnel indicates marine influence during deposition of Association A. *Botryococcus* spp. and *Plaesiodictyon mosellanum,* which are affiliated with chlorococcale green algae and indicate brackish to freshwater influx.

Association B is described as being similar to association A in composition, with sporadic occurrences of *Eucommiidites 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. The re-studied 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*

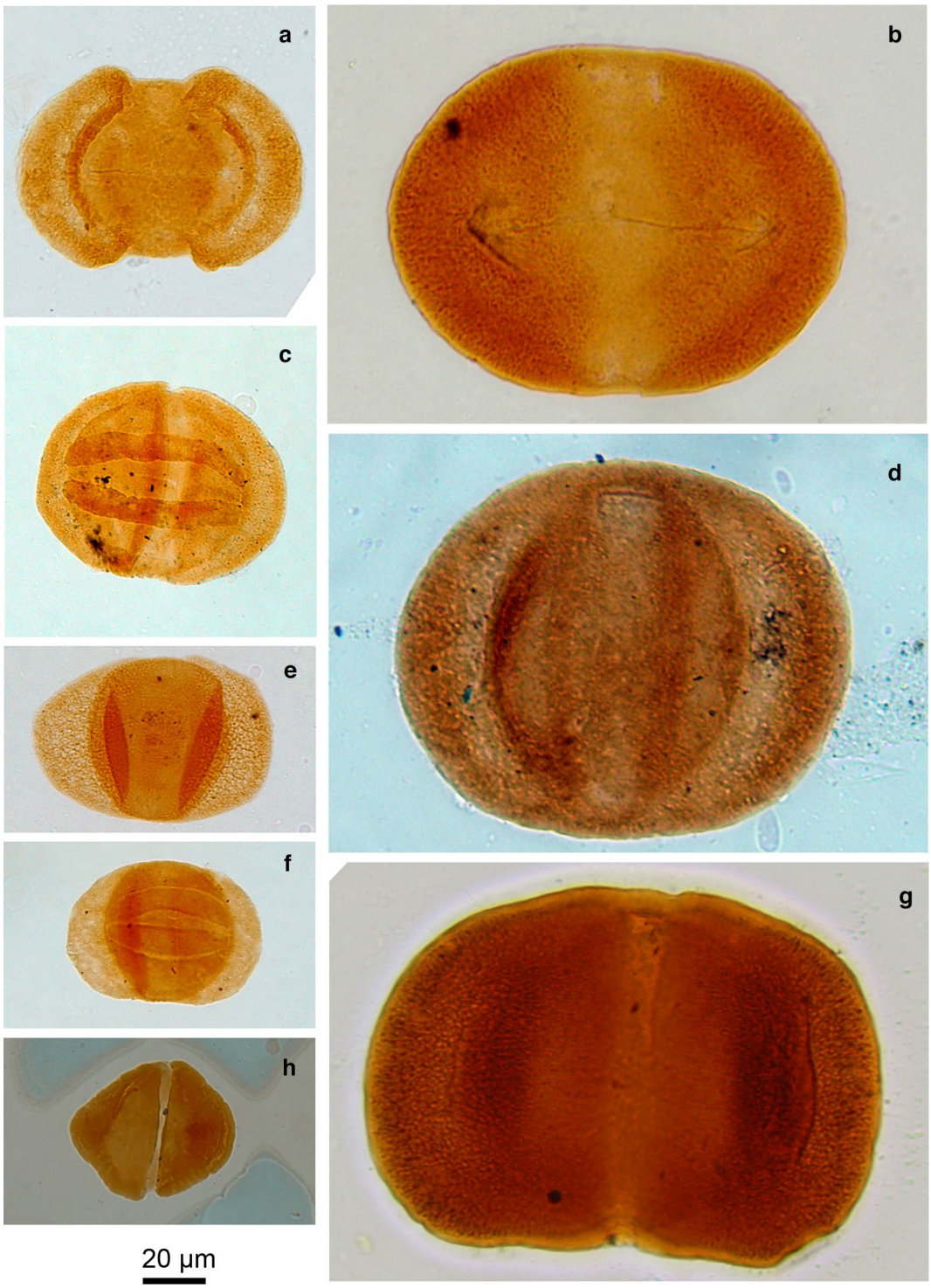

Fig. 2 Palynomorphs from the Belchentunnel. Palynomorph followed by three-part number identifying single mounts (number of box/slide number/sample number) after Scheuring (1970) or by Englandfinder coordinates on strew mounts. **a** *Ovalipollis lepidus*, 3/66/5; **b** *Ovalipollis molestus* (holotype), 3/80/97; **c** *Lunatisporites noviaulensis var. mollis* (holotype), 3/25/5; **d** bisaccate pollen grain on single mount in box 4, position 25, which should contain the slide of the holotype of *Parillinites eiectus*, which has not been found; **e** *Lunatisporites acutus var. regalis* (holotype), 3/41/3; **f** *Lunatisporites acutus var nudus* (holotype), 3/55/5; **g** *Parillinites callosus* (holotype), 4/6/34; **h** *Cucullispora cuneata* (holotype), 7/85/05

spp., *Plaesiodictyon mosellanum, Reduviasporonites catenulatus,* and *Tytthodiscus* sp. Aquatic palynomorphs never exceed 10% of the total terrestrial and aquatic miscellaneous palynomorph count. For the terrestrial and aquatic miscellaneous palynomorph count, the equivocal *Reduviasporonites* spp. was excluded because of its enigmatic affinity (e.g., Heunisch and Röhling, 2016). The mixture of chlorococcale green algae, acritarchs, and prasinophytes (*Tytthodiscus* sp.) indicates a mixed marine to brackish-freshwater environment.

The assemblage in sample 11 is marked by several first occurrences (FOs) and last occurrences (LOs). *Retusotriletes* spp., *Ellipsovelatisporites plicata*, *Sulcatisporites* spp., *Protodiploxypinus decus*, and *Parillinites* spp. have their FOs in D11. The LOs recorded include those of *Striatoabieites* spp., *Cucullispora cuneata*, *Lunatisporites acutus*, *Perinopollenites* cf. *elatoides*, *Osmundacidites* spp., and *Apiculatisporis* spp. In addition, *Sulcosaccispora 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 generally resembles associations A and B, but *Cucullispora cuneata* is absent. Instead, *Duplicisporites*, *Camerosporites*, *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 species list provided by Scheuring (1970) can be complemented here by the presence of *Cordaitina* sp. (D9), *Platysaccus* spp. (D100), *Cycadopites* spp. (D100), *Doubingerispora filamentosa* (D100), and *Echinitosporites iliacoides* (D100), and the LO 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 elements are *Enzonalasporites* spp. and *Fossapollenites* cf. *moderatus*, *Aratrisporites scabratus*, *A. paraspinosus*, *Retusotriletes* spp., *Lycospora* sp., and *Punctatisporites* spp., whereas *Infernopollenites* spp. were not recorded. In addition, algal colonies, algal cysts, *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 for > 50% of the total palynomorph count, excluding fungal remains and *Reduviasporonites* spp. (Fig. 5). Aquatic palynomorphs indicate a depositional environment ranging from brackish-freshwater to marine facies. The dominant taxon has been associated with green algae and yellow–green algae, respectively, the latter grows in freshwater and marine environments today (Butterfield, 2004; Wall, 1962).

Association D is marked by a 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,* and *T. suspecta* are absent (Scheuring, 1970). Only samples 82 and 85 were still intact and could be analyzed. The assemblages in these two samples agree with Scheuring's description. LOs recorded in Association D are those of *Striatoabieites balmei*, *Parillinites* spp., and *Chordasporites* spp. *Staurosaccites* spp. has its first occurrence, and a single occurrence of *Infernopollenites* sp. is recorded. *Tasmanites* is the only aquatic palynomorph recorded, indicating marine influence during the deposition of Association D.

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 LOs 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 for ~ 30% of the total terrestrial and aquatic miscellaneous palynomorph count, excluding fungal remains and *Reduviasporonites* spp. *Micrhystridium* spp. and *Leiosphaeridia* spp. are mostly regarded as marine palynomorphs; however, affinity to freshwater algae cannot be

(See figure on next page.)

Fig. 3 Palynomorphs from the Belchentunnel. Palynomorph followed by threepart number identifying single mounts (number of box/slide number/sample number) after Scheuring (1970) or by sample number and Englandfinder coordinates on strew mounts. **a** *Triadispora aurea* (holotype), 5/6/D100; **b** *Parillinites solidus* (holotype), 4/23/97; **c** *Triadispora triradiata,* 5/8/D100; **d** *Triadispora suspecta* (holotype), 5/82/3; **e** *Parillinites vanus,* 4/72/150, the holotype is missing, this specimen is another example (Scheuring, 1970 plate 7, picture 32); **f** *Triadispora vilis* (holotype), 6/70/D9; **g** *Triadispora verrucata,* 5, T28/3; **h** *Protodiploxypinus decus* (holotype), 1/16/D11; ***i*** *Protodiploxypinus gracilis* (holotype), 7/83/03; **j** *Triadispora obscura* (holotype),6/40/3; **k** *Triadispora verrucata,* 5, U27/2; **l** *Triadispora modesta* (holotype), 6/29/5

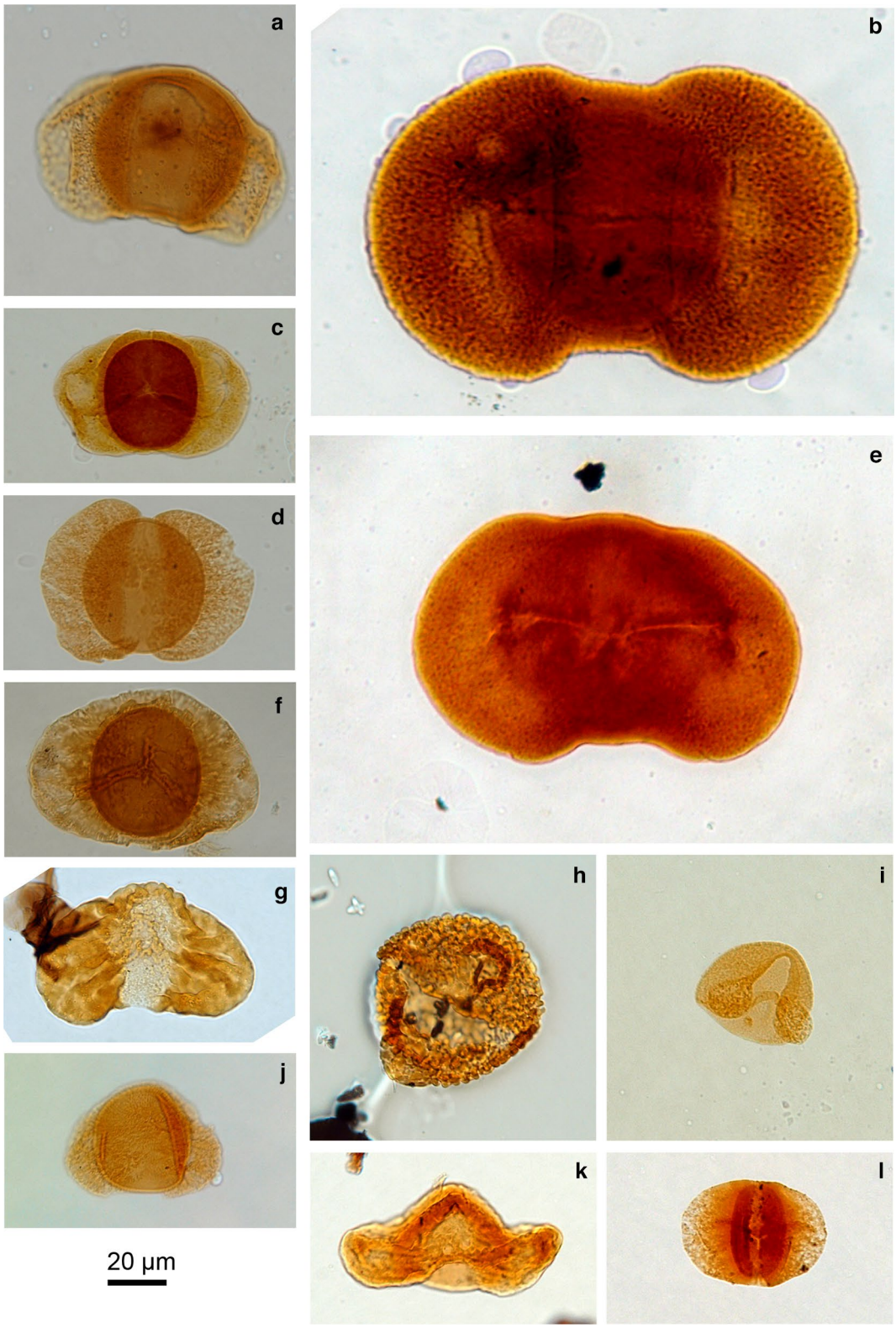

Fig. 3 (See legend on previous page.)

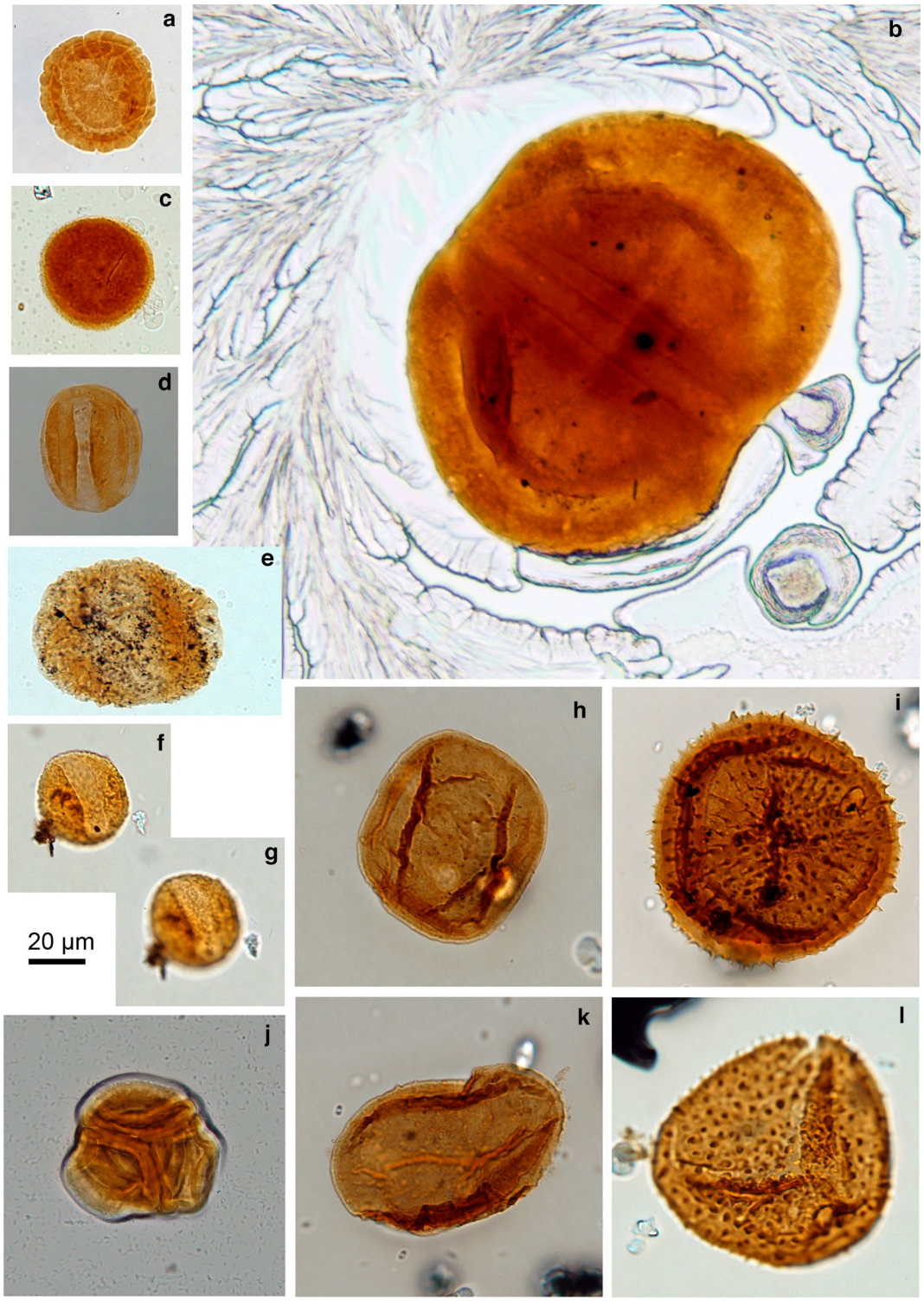

Fig. 4 Palynomorphs from the Belchentunnel. Palynomorph followed by threepart number identifying single mounts (number of box/slide number/sample number) after Scheuring (1970) or by Englandfinder coordinates on strew mounts. **a** *Camerosporites pseudoverrucatus* (holotype), 8/19/58, (*C. secatus* in Scheuring, 1978); **b** *Parillinites pauper* (holotype) threatened by degradation,4/55/58; **c** *Paracirculina tenebrosa* (holotype), 8/23/58; **d** *Eucommiidites microgranulatus* (holotype), 7/54/55; **e** *Ellipsovelatisporites rugosus* (holotype), 7/9/126; **f, g** *verrucate monosulcate pollen grain,* D11, M34/2; **h** *Porcellispora longdonensis*, 142, O37/3; **i** *P. longdonensis*, 142, Q35/1; **j** *Paracirculina quadruplicis* (holotype), 2/36/136; **k** *P. longdonensis*, 142, R39; **l** *P. longdonensis*, 142, S37

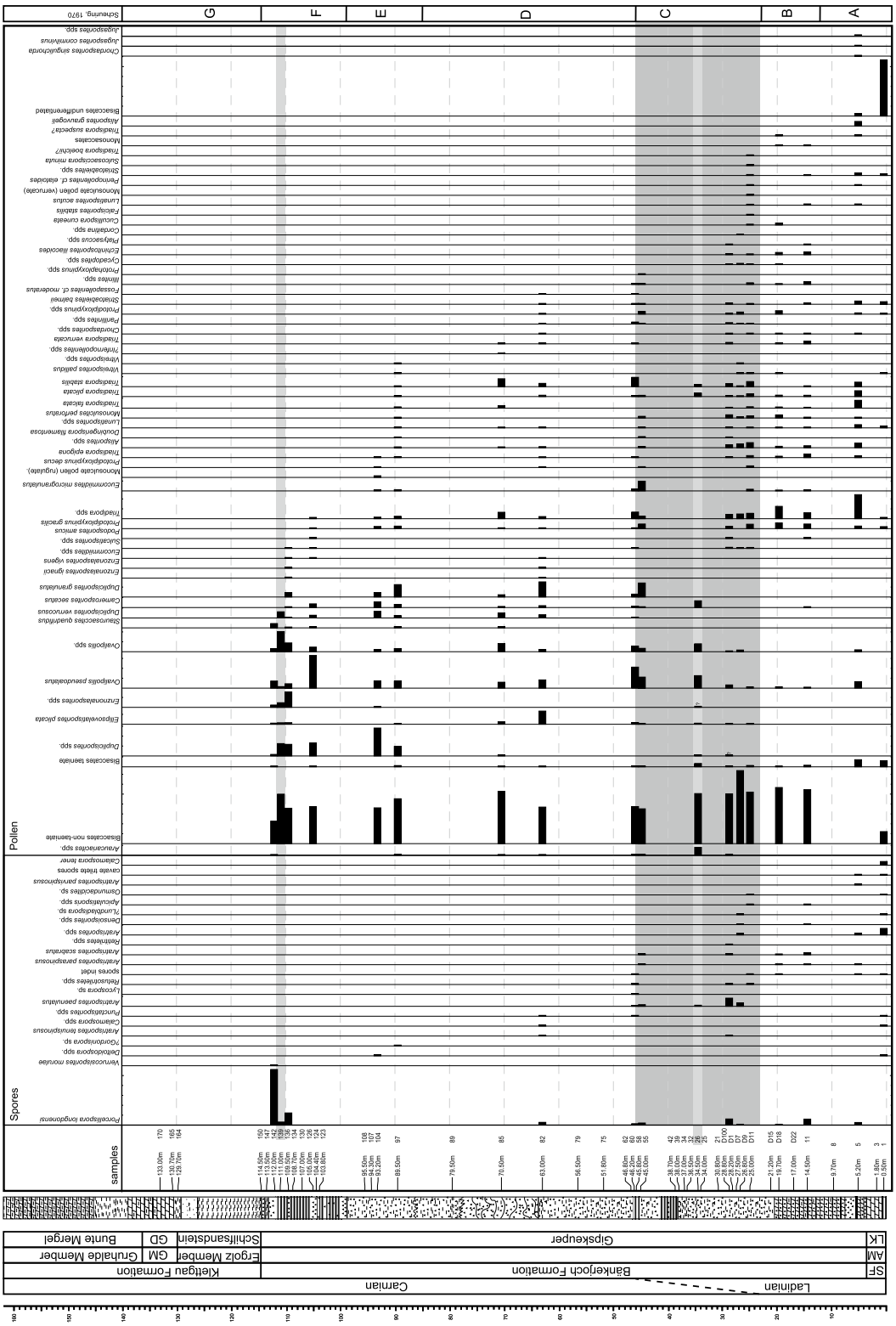

Fig. 5 Relative abundances of terrestrial palynomorphs in the Belchentunnel samples. Arranged according to the stratigraphic last occurrence of the taxa. Broad dark gray band illustrates Ladinian–Carnian transition. Samples with total counts < 100 are marked light gray

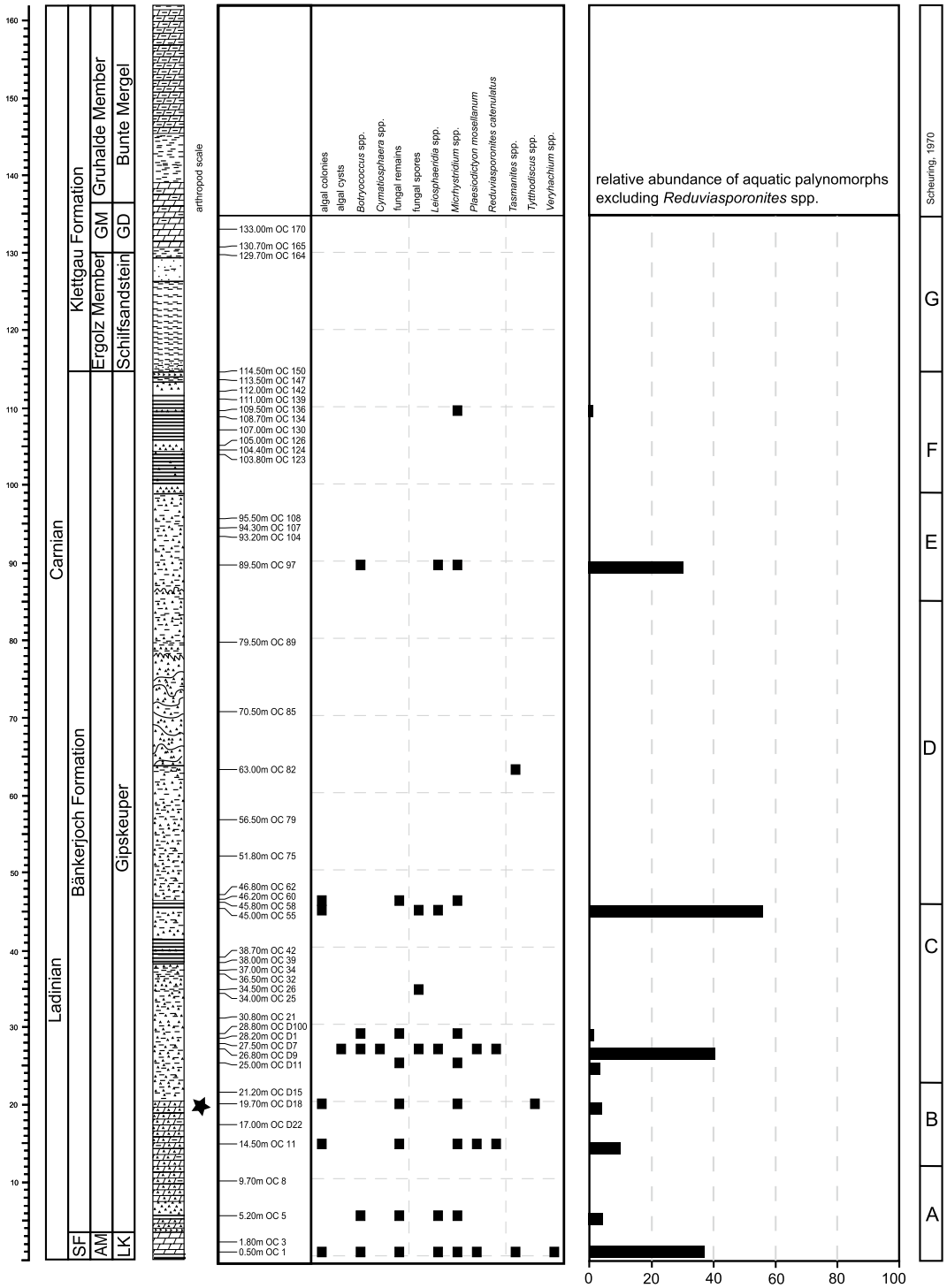

Fig. 6 Miscellaneous palynomorphs in the Belchentunnel samples calculated using the total of palynomorphs counted excluding *Reduviasporonites*

excluded (see above), whereas *Botryococcus* spp. indicates brackish to freshwater conditions.

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 (Scheuring, 1970) (Fig. 5). *Paracirculina* was later revised by Scheuring (1970) and included in *Duplicisporites* (Scheuring, 1978); therefore, *Paracirculina quadruplicis* is included in *Duplicisporites* spp. in this study. In contrast to Scheuring's range of *Triadispora verrucata*, the taxon is present in associations B to D of the Gipskeuper (Bänkerjoch Formation), 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* occur commonly. Just one *Micrhystridium* sp. was found in sample 136. The ecological meaning of the *Porcellispora longdonensis* acme is discussed in Chapter 5.1.

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

Discussion

The spores in the assemblages

More than 50 years ago, Bernhard Scheuring described the assemblages of the Belchentunnel with a strong focus on the 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 being neither diverse 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 *Porcellispora longdonensis*. Its botanical affinity has long been regarded as bryophytic and is thus considered indicative of rather humid climatic conditions (Baranyi et al., 2019; Visscher and Van der Zwan, 1981). Currently, *P. longdonensis* is regarded as derived from aquatic liverworts growing in hypersaline settings (Hauschke and Heunisch, 1990). Relatively high abundances of *P. longdonensis* have been documented from Muschelkalk sediments (Brückner-Röhling and Heunisch, 2004), which represent hypersaline sedimentary basins. The parent plant of *P. longdonensis* is the fossil liverwort taxon *Naiadita lanceolata* (Heunisch, personal communication) which is known to occur in different Middle to Upper Triassic successions in Europe (Kleber, 2019). The modern relative of *Naiadita lanceolata* is *Riella.* Morphological similarities exist between the fossil spore species *P. longdonensis* and the spores of the modern liverwort taxon *Riella* (Reinhardt and Riecken, 2000). *Riella* grows as submerged plants in fresh-water 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 et al., 2008; Djamali and Segarra-Mortegues, 2021). Spores are accumulated in spore banks, remaining viable during times of desiccation and germinating when conditions ameliorate (i.e., freshwater influx into saline lakes) (Djamali et al., 2008; Kelber, 2019). Based on these considerations, in recent publications on Late Triassic palynology, *P. longdonensis* has been regarded as a xerophytic element (Fijałowska-Mader et al., 2021). A xerophytic affinity seemingly contrasts with the former interpretation of *P. longdonensis* as an indicator for humidity. However, the spores can endure and stay viable for several years under arid conditions and germinate only if water is available again. 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 emphasize its palaeoecological significance and its potential as an environmental indicator of ephemeral lakes to a greater extent and to group it with aquatic palynomorphs, as has been demonstrated for *P. longdonensis* occurrences in Muschelkalk and Keuper (Brückner-Röhling and Heunisch, 2004; Hauschke and Heunisch, 1990). Further paleoecological evidence comes from sedimentology. In wide areas of the Central European Basin, the CPE is marked by widespread deposition of sandstone units (e.g., Arden Sandstone in the UK, Stuttgart Formation

(See figure on next page.)

Fig. 7 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; **l** *Aratrisporites tenuispinosus*, 82, Q 41/2; **m, n** immature spore masses?, 1, M 39, M44/3; **o** arthropod scale, D18, V41/1

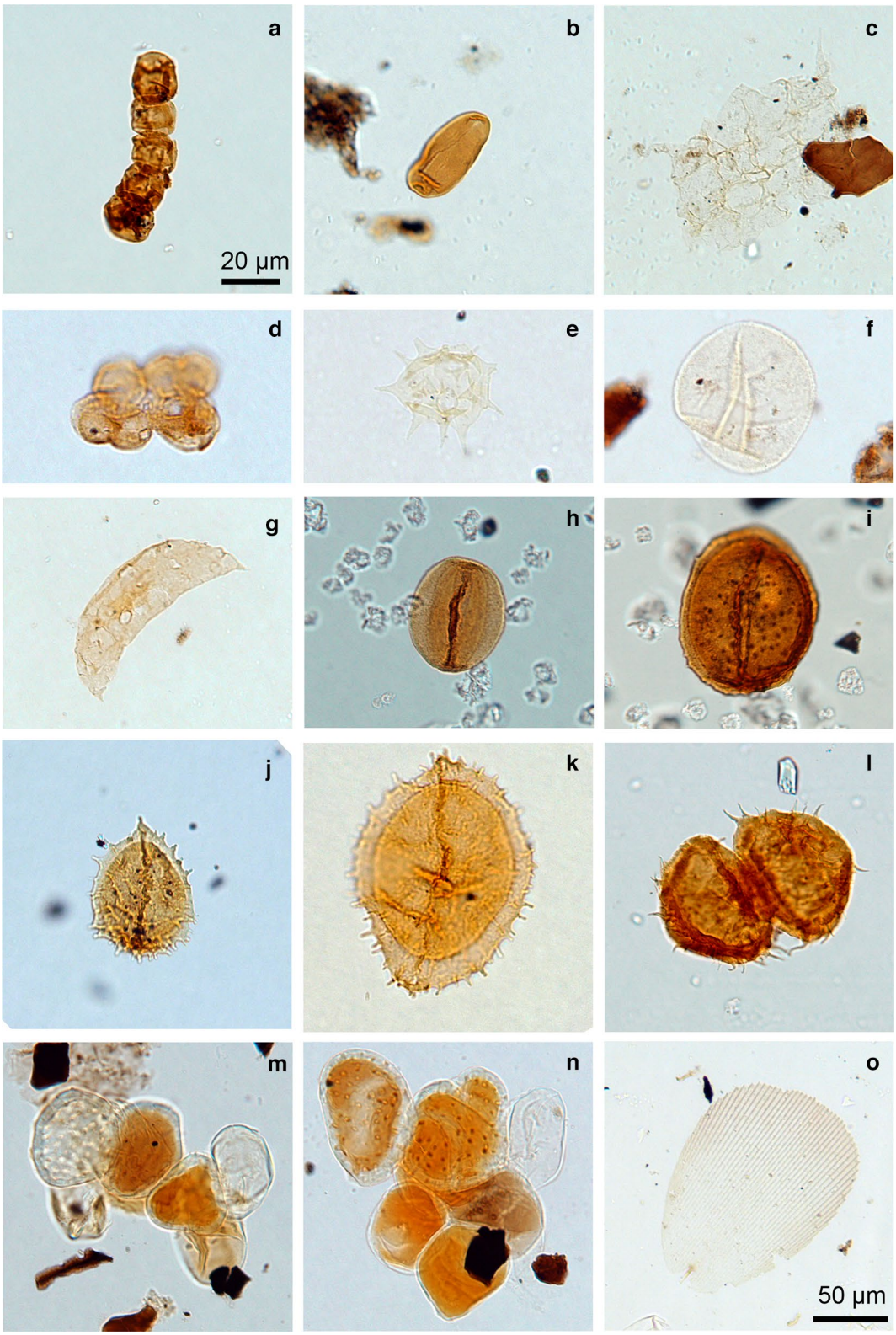

Fig. 7 (See legend on previous page.)

	Central European Basin								Alpine Triassic		Boreal Triassic		
	Stratigraphy Germany (STGC 2022)	Kürschner & Herngreen 2010		Heunisch & Wierer, 2021	Scheuring 1970 and this study	Stratigraphy Switzerland old	Stratigraphy Switzerland Jordan et al., 2006	Orłowska-Zwolińska 1985	Roghi et al., 2010	Roghi et al., 2004	Vigran et al., 2014	Paterson & Mangerud, 2019	Hochuli et al., 1989
Carnian			subzone										
Carnian	Schilfsand-stein (Stuttgart Fm)	*Camero-sporites secatus*	*Aulisporites astigmosus*	GTr 14	G	*Schilfsand-stein*	Ergolz Mb, Klettgau Fm	*Aulisporites astigmosus*	*Aulisporites astigmosus*	*Duplici-sporites continuus*	*Aulisporites astigmosus*	*Leschiki-sporis adunctus*	D,E
Carnian	Grabfeld Fm		*Triadispora verrucata*	GTr 13	D, E, F?	Gipskeuper and Lettenkohle	Bänkerjoch Fm and Asp Mb, Schinznach Fm	*Porcellispora longdonensis*		*Concentrici-sporites bianulatus*		*Podo-sporites vigraniae*	F
Carnian	Grabfeld Fm			GTr 12	C?							*Semireti-sporis hochulii*	G
Ladinian	Erfurt Fm	*Heliosaccus dimorphus*		GTr 11	A-B?			*Heliosaccus dimorphus*			*Echinito-sporites iliacoides*	*Echinito-sporites iliacoides*	H
Ladinian	Warburg Fm			GTr 10									

Fig. 8 Correlation of the Belchentunnel assemblages with palynozones from the Central European Basin, Tethys, and the Barents Sea

in SW Germany), indicating increased precipitation and runoff in an otherwise arid climate (Howard et al., 2008; Simms and Ruffell, 2018). These sandstone-dominated units include marl lenses, which have been interpreted as temporary lakes (Clarke, 1965) that would provide habitat for the *Riella*-related *Naiadita lanceolata* plants during the Late Triassic.

Correlation of assemblages with Upper Triassic palynostratigraphic schemes

The palynostratigraphic subdivision of Ladinian and lower Carnian deposits by Scheuring (1970) is to date unmatched in terms of resolution (Fig. 8). In the following, we compare the Belchentunnel associations with neighboring palynostratigraphic schemes from the Central European Basin and the Alpine area. Because taxon ranges (FOs and Los) differ significantly, the comparison with boreal palynostratigraphic schemes is only loosely outlined.

Associations A and B

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 and Wierer, 2021: *Heliosaccus dimorphus* Zone sensu Kürschner and Herngreen, 2010) and the *Heliosaccus dimorphus* Zone described from Poland (Orłowska-Zwolińska, 1985) (see also Nowak et al., 2018), which would correspond to Assemblages A to B of Scheuring (1970) in the Belchentunnel (Fig. 8). *Heliosaccus dimorphus* and *Echinitosporites iliacoides* are also characteristic elements of the *secatus–dimorphus* phase sensu Van der Eem (1983), and their LOs are the markers 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. Diverse *Aratrisporites* and abundant non-taeniate bisaccate pollen are also common features of the *Echinitosporites iliacoides* Zone of the Barents Sea area (Paterson and Mangerud, 2020; Vigran et al., 2014) 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.

Association C

The base of the following younger Zone in the Germanic Basin, which has been described from the Ladinian–Carnian Grabfeld Formation (*Camerosporites secatus* Zone sensu Kürschner and Herngreen, 2010), is marked by the FOs of *Enzonalasporites vigens* as well as the nominate species, and the first common occurrences of *Ovalipollis pseudoalatus*. The latter two features are observed in assemblage C in the Belchentunnel, whereas *E. vigens* was recorded in assemblage D. Palynological assemblages from the Kalkschieferzone of Meride (Ticino, Switzerland) were described as comparable with Association C of the Belchentunnel (Scheuring, 1978). Based on the comparison with palynological assemblages of the Reiflinger Kalke (Grossreifling, Northern Calcareous Alps) and the occurrence of a Longobardian bivalve *Daonella lommeli* there (Mostler and Scheuring, 1974), Scheuring assigned a Longobardian (late Ladinian) age to the assemblages from Meride (Scheuring, 1978; Stockar et al., 2012). In the Global Boundary Stratotype Section and Point for the base of the Carnian (Prati di Stuores/Stuores Wiesen, Italy), *Vallasporites ignacii* (*Enzonalasporites ignacii* Scibiorski et al., 2022) and *Patinasporites densus* in association with *Enzonalasporites vigens* are regarded as indicative for the base of the Carnian (Mietto et al., 2012). The genus *Enzonalasporites* occurs in Association C, whereas *P. densus* was recorded only from Association F onward (Scheuring, 1970). *Enzonalasporites ignacii* and *E. vigens* occur from Association D onward (see "Associations D–F"); therefore, the Ladinian–Carnian boundary is tentatively located between associations C and D.

Associations D–F

The *C. secatus* Zone is subdivided into two subzone: the base of the lower *Triadispora verrucata* Subzone is marked by the FO 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 perforates* by Scheuring, 1970) 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) (Fig. 8). Regular occurrences of *P. longdonensis*, diverse *Triadispora* species and circumpolles pollen are also characteristics of the *P. longdonensis* Zone in Poland (Orłowska-Zwolińska, 1985). 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 include the nominative species and *Kyrtomisporis ervei* as well. The only species in common is *Duplicisporites verrucosus* (Roghi et al., 2004). 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 FOs 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 is 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).

Association G

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 also include 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 compositions. A resampling would be necessary to understand whether the palynological assemblage resembles the *A. astigmosus* Subzone sensu Kürschner and Herngreen, 2010, the *A. astigmosus* Zone sensu Orłowska-Zwolińska, 1985 (Vigran et al., 2014; Roghi et al., 2010), or the *L. adunctus* Zone sensu Paterson et al. (2017) and Paterson and Mangerud 2020).

The Carnian Pluvial Episode

The Carnian Pluvial Episode is marked by changes in lithology and vegetation composition due to higher relative humidity in middle Carnian successions in the low latitudes (e.g., Dal Baranyi et al., 2019; Corso et al., 2015). However, records from the Germanic Basin seem to contradict this (Franz et al., 2019; Visscher et al., 1994), since 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 cropping out.

The typical marker taxa for the Carnian Pluvial episode in Europe are *Aulisporites astigmosus* and *Leschikisporis adunctus*. These are not present in the palynological samples from the Belchentunnel, 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. A similar coincidence of a *P. longdonenesis* increase in combination with the absence of *A. astigmosus* and *L. aduncus* has been documented for the Carnian Pluvial Episode from the Mercia Mudstone Group of southwest England (Baranyi et al., 2018). In the event that *P. longdonensis* is confirmed to be related to *Riella* plants and the preferred growing environment is the same, the increase in relative abundance of *P. longdonensis* spores could be correlated with lake level highs that allow for brackish to freshwater conditions, i.e., the conditions that favor *Riella* spore germination. Lake level rises during glacial episodes promoting *Riella* spore germination, have been explained more 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 favored 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).

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 just before the deposition of the Schilfsandstein, the sediment facies representing the Carnian Pluvial Episode.

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 Carnian Pluvial Episode in Swiss successions.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13358-023-00278-2.

Additional file 1. Palynological data of the Belchentunnel Switzerland.

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. Carmen Heunisch, an anonymous reviewer, and Susanne Feist-Burkhardt are thanked for their constructive comments.

Author 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.

Funding
Not applicable.

Availability of data and materials
Palynological slides are stored in the Palaeontological Collection of ETH Zurich. All other data are included in the text and in the Additional files.

Declarations

Competing interests
The authors declare that they have no competing interests.

Received: 16 March 2023 Accepted: 12 June 2023
Published online: 18 July 2023

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