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**Ultrastructure and probable botanical affinity of the enigmatic sporomorph
Froelichsporites traversei from the Norian (Late Triassic) of North America**

Short title: Wall-ultrastructure of Froelichsporites traversei

Viktória Baranyi^{1*}, Charles H. Wellman†, Wolfram M. Kürschner*

*Department of Geosciences, University of Oslo, P.O. Box 1047, Blindern, Oslo 0316,

Norway; † Department of Animal and Plant Sciences, University of Sheffield, Western Bank,
Sheffield S10 2TN, United Kingdom

¹Author for correspondence; e-mail: viktoria.baranyi@geo.uio.no

Abstract

Premise of research. *Froelichsporites traversei* is a prominent palynomorph in the Upper Triassic of North America which ~~is always occurs~~ ~~permanently found~~ in ~~—~~ tetrahedral ~~permanent~~ tetrads. It is an important regional biostratigraphic marker in the Norian ~~of~~ North America and its abundance rises around 215 Ma associated with a significant floral and faunal turnover. Its most striking morphological features are the well-developed distal pores (ulci) ~~on each grain~~ and ~~the~~ annulus-like exine thickening around them ~~on each grain~~. Previous works suggested it was produced by spore-~~—~~producing plants or Cheirolepidiaceae, but its botanical affinity is still unclear.

Methodology. The ~~wall~~ ultrastructure of *F. traversei* was analysed by TEM in order to reveal more information on the botanical affinity of the palynomorph.

Pivotal results. The sporoderm consists of two layers and ~~an~~ inner faint discontinuous lamination. The outermost exine layer has homogenous texture (tectum), while the inner layer has granular texture (infratectum). The laminae below the granular layer are not continuous, but directly contiguous with the granules.

Conclusions.

An explanation for the lack of the well-developed lamellate nexine is that it might represent an immature pollen grain, but the outer layers of the sporoderm, indicates full development. The ultrastructure studies have ambiguous results ~~and~~; the botanical affinity could not be revealed with certainty, ~~although~~ the most likely candidates are Gnetales or Bennettitales based on the ~~wall~~ ultrastructure. The unusual morphological and ultrastructural features ~~may~~ represent experimentation with angiosperm-related features and functions. The dispersal ~~ion~~ as permanent tetrads ~~may have~~ provided ~~probably~~ adaptive advantages to the parent plant of *F. traversei* ~~related to~~ ~~explained by~~ polyembryony or polyploidy.

Keywords: Froelichsporites traversei, ultrastructure, permanent tetrad

Introduction

Froelichsporites traversei is an enigmatic palynomorph in the Upper Triassic of North America ~~that always occurs as permanently found in~~ tetrahedral permanent tetrads (Litwin et al. 1991, Litwin et al. 1993; Reichgelt et al. 2003). It has peculiar angiosperm-like morphological features, including distal pores on each grain and an annulus-like thickening around each pore. Unambiguous remains of angiosperm related pollen are known from the Cretaceous onwards (Friis et al. 2011), but in the Late Triassic several pollen types existed among the gymnosperm pollen that show angiosperm like features (e.g., Afropollis, Crinopollis group) (Cornet 1989; Doyle 2005, 2009; Hochuli and Feist-Burkhardt, 2013). This period is apparently marked with experimentation with new morphological features and functions that ~~have become~~ later became extinct during the evolution of seed plants. In addition, dispersed palynomorphs occurring in tetrads have been often associated with sterility caused by environmental stress or environmental mutagenesis (e.g., Visscher et al. 2004; Looy et al. 2005). ~~PEventually p~~ permanent tetrads might represent a special reproductive strategy (e.g. polymebryony, Mander et al. 2012) that provided adaptive advantages for the parent plant during environmental perturbations by increasing the chance for producing viable offspring.

Froelichsporites traversei was first described as Pyramidosporites traversei by Dunay and Fisher (1979) from ~~+++~~

Later Litwin et al (1993) erected the new genus Froelichsporites to replace the generic assignment to Pyramidosporites. The distribution of the taxon is restricted to Upper Triassic formations of North America (e.g. Dunay and Fisher 1979; Fisher and Dunay 1984; Litwin et al. 1991, 1993; Cornet 1993, Fowell and Olsen 1993, Fowell et al. 1994) (Fig. 1, Table 1) and similar forms ~~have been~~ described from Upper Triassic continental strata of Portugal

(Adloff et al. 1974). *Froelichsporites traversei* has been recorded from the Chinle Formation in the SW USA (Arizona, Utah, New Mexico) (Gottesfeld 1972; Dunay and Fisher 1979; Fisher and Dunay 1984; Litwin et al. 1991; Reichgelt et al. 2013; Lindström et al. 2016), Dockum Group (Texas, New Mexico), the Chatham Group (North Carolina) (Litwin and Ash 1993) and the Newark Supergroup (Cornet 1993) (Table 1). It can be considered as a regional biostratigraphy marker of the middle Norian in North America (Litwin et al. 1991; Reichgelt et al. 2013). In the Chinle Formation in Arizona and New Mexico peaks of its abundance are associated with a floral and faunal turnover and severe environmental perturbations including a shift towards arid climate, and increased seasonality (Reichgelt et al. 2013; Whiteside et al. 2015; Lindström et al. 2016). The highest abundance of *F. traversei* is coeval with the maximum abundance of the *Patinasporites* group (*Patinasporites*, *Enzonasporites*) (Lindström et al. 2016) and *Klausipollenites gouldii* which is probably associated with an opportunistic Voltzialean parent plant.

Despite the significance of the species in the Upper Triassic of North America and its peculiar morphological features the botanical affinity is still unclear. Previous works suggested it was produced by spore-producing plants (Litwin et al. 1993), alternatively it could be a prepollen (REF) or it was proposed that it was probably produced by Cheirolepidiaceae, based on due to the resemblance of the tetrads to the *Classopollis* tetrads (Litwin et al. 1993).

In order to clarify its botanical affinity, we document its morphology using scanning electron microscopy (SEM) and transmission electron microscopy (TEM). This is the first documentation of the wall ultrastructure of *F. traversei*. The exine ultrastructure analyses can provide useful insight into the botanical affinity of dispersed palynomorphs and reveal relationship between plant groups (e.g., Doyle 2009). The precise botanical assignment of *F. traversei* is also crucial in understanding the role of the taxon during the environmental perturbation recorded in the Norian of North America.

Material and methods

The Froelichsporites tetrads investigated here ~~were~~ collected from the Chinle Formation, at the Petrified Forest National Park, Arizona (PEFO), USA (Fig. 1). Samples BL 1-BL 7 were taken from the Badlands section, in the upper Jim Camp Wash beds, in the upper part of the Sonsela Member from the Badlands locality in the SE corner of the PEFO (Fig. 1). Samples MLM 1-MLM 4 were collected from the Mountain Lion Mesa section in the upper part of the Sonsela Member, in a higher stratigraphic position compared to BL samples (Fig. 1). The SEM and TEM studies were carried out on tetrads from one palynological sample, BL 7, from the Badlands section ~~of the Petrified Forest National Park (PEFO)~~ in Arizona (GPS coordinates of the locality: 34°50'36.3120"N 109°47'59.0541"W) (Fig. 1). ~~The sample Bl 7 is dark grey mudstone with organic material, it comes from a low energy, environment possibly lacustrine horizon or marsh/floodplain, environment.~~ Preparation of the palynological samples follows the protocol from Kuerschner et al. (2007). About 10 g of sediment was crushed and ~~to dissolve~~ the carbonates and silicates ~~dissolved in~~ 10% HCl and concentrated HF ~~were used~~. The organic residue was sieved with a 250 µm and a 15 µm mesh. Heavy liquid separation or further oxidation of the organic residue was not necessary. Palynological slides were mounted using epoxy resin (Entellan) ~~as a mounting medium~~. The organic residues are stored at the Department of Geosciences, University of Oslo. Microscopy analysis was carried out with Zeiss No. 328883 microscope connected to an AxioCam ERc5s camera and Zen 2011 software.

The Froelichsporites *traversei* tetrads were handpicked with an eyelash ~~tool~~ from the organic residue and dehydrated in a series of ethanol solutions with increasing concentration (50%, 70%, 90% and 100% ethanol solution). The tetrads stayed in each solution at least 30 minutes, before transferring them into the next solution with higher concentration. The tetrads were placed on stubs and coated with gold with a Quorum Q150RS sputter coater. SEM

photographs were taken with a Hitachi SU5000 SEM at the Department of Geosciences, University of Oslo. SEM stubs are stored in the SEM labor of the Department of Geosciences, University of Oslo.

For ultrastructure analysis handpicked *Froelichsporites traversei* tetrads were embedded in 0.1% strength agar (0.1g agar ~~agar~~ dissolved in 10 ml Milli-Q water) and dehydrated with 100% ethanol and propylene oxide. As embedding medium, Spurr replacement ERL 4221 was applied and the infiltrated blocks were polymerized at 60° for at least 48h. Sectioning and ~~the following~~ TEM analysis were carried out at the Department of Animal and Plant Sciences, University of Sheffield. Approximately 85 nm thick sections were cut by a diamond knife and a Leica UC-6 ultramicrotome. The sections were picked up on 400 mesh copper grids.

Additional blocks were sectioned at the Electron Microscopy Laboratory of the University of Oslo, where machine types was used. Approximately 85 nm thick sections were cut by a diamond knife and a Leica UC-6 ultramicrotome. The sections were picked up on 75 mesh copper grids. The sections have not been stained. Check with Antje

Results

Systematic palynology

In the morphological description no interpretative terminology was applied to avoid premature conclusions.

Genus *Froelichsporites*, Litwin, Smoot, Weems 1993

Froelichsporites traversei (Dunay and Fisher 1979) Litwin, Smoot, Weems, 1993

1979 *Pyramidosporites traversei* n. sp.; Dunay and Fisher: pl. I, figs 6-9.

1984 *Pyramidosporites traversei* Dunay and Fisher; Fisher & Dunay: pl. 2. fig. 4.

1991 *Pyramidosporites traversei* Dunay and Fisher; Litwin et al.: pl. II, fig. 7.

1993 *Froelichsporites traversei* (Dunay and Fisher) nov. comb. emend.; Litwin et al.: pl. I
figs 1-6, pl. 2, figs 1-6, pl. 3, figs 1-12.

2016 *Froelichsporites traversei* (Dunay and Fisher) Litwin et al.; Lindström et al.: pl. VI, figs
1-4.

Description. *Froelichsporites traversei* specimens are obligate tetrahedral tetrads with slightly to moderately thickened and fused contact areas. The specimens are permanently united in tetrads. The proximal face of each sporomorph is in complete contact with all others and they are joined at an oblique angle (in polar view). Two wall layers (11, 12, fig.2A) are distinguished, but the outermost layer (11, Fig.2A) is not always present (fig). The tetrads occasionally exhibit only the inner wall-layer (12, Fig. 2A) on the distal hemisphere of each member, and the remnant of the outermost layer is visible only along ~~and~~ the sutures between the members. The outer wall layer is thin, psilate, and diaphanous. This layer is thickened towards the contact area of the grains to form a thick contact area. The inner layer is thin and scabrate. On the distal face of each member a distinct pore structure, ulcus (u, Fig. 2A) is present. The ulcus is rimmed by a slight thickening of the inner wall layer to form an annulus-like structure, and it is usually 2-4 µm in diameter (observed range 1-7 µm) (Fig. 3). On the proximal face of the spores a distinct (but perhaps non-functional) trilete laesurae is present. Individual members of the *F. traversei* tetrads cannot be separated, they are firmly bonded. Specimens from the PFNP were well preserved. The colour of the palynomorphs varies between pale yellow to golden brown, their SCI index ranges from 2 to 7 (Batten, 2002). The specimens from the Newark Supergroup showed increased thermal alteration, their SCI index ranges between 8 and 9.

Dimensions. Thirty specimens of *F. traversei* tetrads were measured. The tetrad diameter ranges between 40µm and 94µm (average 58µm) (Fig. 3). Equatorial diameter of the single grains ranges between 29µm and 48µm (with an average of 30µm) (Fig. 3). The diameter of

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Commented [g2]: Place the comments on SCI in the methods part where we discuss oxidation?

the ulcus is between 3µm and 10µm (with an average of 5.6µm) (Fig. 3). The width of the contact area (curvatura perfecta) is 2-7µm with an average of 4µm (Fig. 3). There was no difference in size range between the specimens from the PFPN, or the Newark basin.

Ultrastructure

The preserved sporoderm of *F. traversei* consists of two distinct layers and innermost faint discontinuous laminae (Figs 5-6). The outermost layer (L1; Figs 5-6) is a thin electron dense spongy layer with homogenous texture. It contains no discernible internal structures and measures 0.2µm and thickens gradually towards the contact areas (Fig. 5G-H). The boundary between the outer and inner layer is sharp, no gradation is observed. The layer below (L2, Figs 5-6) has granular texture with small cavities. This layer is 0.4-0.6 µm thick and similarly to the outermost layer it thickens gradually towards the triple junction areas of three individual grains (Fig. 5 G-H). The tetrads are flattened due to compression therefore the granules and cavities in this layer might be bigger. Occasionally the cavities seem to increase in size towards the boundary between L1 and L2 (Figs 5-6). Below the granular layer indication of faint lamination is observed (L3) (Figs 5-6), however the laminate layer is not continuous. The granules in L2 are directly contiguous with the underlying, dark-staining laminae. The individual grains within the tetrad are connected by the outer layer and the inner granular layer and they are firmly bonded (Fig. 7).

DISCUSSION

Sporoderm preservation and maturity

A variety of both abiotic and biotic effects such as preservation state, developmental stage, can influence the observed ultrastructure in spores and pollen grains (Osborn and Taylor 1995). The studied *F. traversei* tetrads are well-preserved and the colour of the wall (SCI index) does not indicate significant thermal alteration. Besides preservation and thermal maturity, palynomorph wall-ultrastructure may also be obscured or damaged by the processes of embedding or sectioning during preparation for TEM examination (e.g. [knife marks and](#)

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[ChatterWellman et al. 2003](#)). The preserved layers of the sporoderm can be interpreted as follows: the outer spongy and inner granular layer can be interpreted as the sexine (Fig. 6). The homogenous outer layer represents the tectum and the granular layer is the infratectum (Fig. 6). The faint lamination below the granular layer represents either the remnants or the first indication of a nexine (Fig. 6). The lack of a well-developed nexine might imply that circumstances under which an intact nexine would be detectable may have not been encountered, although multiple grains were sectioned and all of them show only faint laminae. Alternatively, the lack of nexine might suggest that the *F. traversei* tetrads represent an early stage of pollen ontogeny and are not fully developed. In the Gnetales (group with granular infratectum) the nexine forms in a later tetrad stage during ontogeny (Doores et al. 2007). Similarly, in the pollen of the cycad *Ceratozamia* the nexine develops after sexine development is well advanced (Audran, 1981). The early developmental stage was also suggested by Taylor and Alvin (1984) for explaining the permanent tetrads of *Classopollis*. However, in certain groups such as angiosperms and certain pollen with Bennettitalean affinity, the nexine (or endexine) is strongly reduced (or absent) even at maturity. However, both sexine layers are present in the contact areas that suggest that the tetrad members are likely to be fully developed according to Mander et al. (2012). In addition, no individual grains of *Frohlichsporites traversei* have ever been found in the samples from the Chinle Formation or the Newark Supergroup. Therefore, the specimens of *F. traversei* investigated here can be most likely considered as fully developed and dispersed as tetrads at maturity from the parent plant.

Botanical affinity

Litwin et al. (1993) assigned the tetrads to spores based on the presence of a distinct but probably non-functional trilete mark on the proximal face of the tetrad members. However,

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the presence of trilete mark is not necessarily an unambiguous feature of spores (e.g. Triadispora). The affinity to spore-producing plants is challenged by its occurrence as permanent tetrads, the granular ultrastructure and the presence of a distal pore. In the case of spores, the occurrence of permanent tetrads is usually the result of mutagenesis and it represents sterile or immature specimens (Visscher et al. 2004). [Various bryophyte groups disperse permanent tetrads \(reviewed in Gray 1985 and Edwards et al. 1999\). However, these all have very different wall ultrastructure compared to F. traversei \(for example in the Andreaopsida as described by Brown and Lemmon 1984\). Only one bryophyte group \(Andreaopsida\) \(Brown and Lemmon 1984\) is known to shed as permanent tetrads. The Andreaopsida have different sporoderm structure compared to F. traversei \(Table 2\).](#) In the Permian increased abundances of fused lycophyte spore tetrads [have been interpreted as](#) was an indication of environmental mutagenesis due to the destruction of the ozone layer, but even in that case single specimens were also found (Visscher et al. 2004; Looy et al. 2005). [Such occurrences of unusual abundances of trilete spores dispersed as permanent tetrads have also been reported from the Devonian \(e.g. Lavender and Wellman 2002\).](#) In contrast, permanent tetrads can normally occur among the gymnosperms e.g., Classopollis ~~spp. and~~ Riccisporites tuberculatus (Mander et al. 2012, Kürschner et al. 2013) (Table 2). According to the observation of Litwin et al. (1991) Froelichsporites possesses a distal thinning similar to Classopollis but he also noted that it differs from the members of the Circumpolles group by the lack of a ring tenuitas, the high degree of proximal contact of tetrad members, and by possession of a double-layered wall. Ultrastructure studies can help identifying the botanical affinity of dispersed spores and pollen grains but it should not be considered as the basis for assigning sporomorphs to any botanical groups (e.g., Doyle 2005, 2009). The double layered exine and the faint lamination suggest that the parent plant of F. traversei was a gymnosperm. The homogenous tectum and granular infratectum observed in F. traversei occur in non-

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saccate conifers such as the Araucariaceae and Cupressaceae, as well as in Gnetales, Pentoxiales, Bennettiales, and certain angiosperms (Doyle 2009). The majority of Mesozoic gymnosperms have a stratified sporoderm (Kurmman 1992; Osborn and Taylor, 1994; Osborn 2000) and possess a laminate nexine, while nexine ~~or~~ (or equivalent laminated inner layer of the sporoderm) might be reduced and discontinuous or absent in angiosperms (Doyle 2005). The [wall ultrastructure analysis](#) ~~US studies~~ of *F. traversei* provides ~~ed~~ ambiguous results, as there is no well-developed nexine layer while the spongy outer and the granular middle layer indicate an affinity within the gymnosperms. However, there are several Mesozoic pollen grains that show extraordinary ultrastructure patterns, e.g. Mesozoic bennettitalean pollen grains. They exhibit various ultrastructure patterns and in several cases deviate from the typical stratified pattern of the gymnosperm pollen grains (e.g., Zavada 1990; Zavialova et al. 2009). A thin lamellate inner layer is present in the bennettitalean pollen *Granamonocolpites luisae* from the Chinle Formation, while its ultrastructure is otherwise homogenous (Zavada 1990). The pollen grains found in situ in *Williamsoniella coronata* (Zavialova et al. 2009) have also a homogenous ultrastructure. The wall of the pollen found in situ in *Cycadeoidea dacotensis* possess stratified pattern characteristic for other gymnosperms (Osborn and Taylor 1995) with homogenous tectum and granular infratectum and a thick darker-staining homogenous nexine with only faint indication of lamellae.

Another exception is *Cyclusphaera psilata* (Taylor et al. 1987) a diporate pollen grain with affinity within Araucariaceae (Del Fueyo and Archangelsky 2005) that has columellar ultrastructure which is unusual in the Araucariaceae.

Based on the results of the ultrastructure study the precise botanical affinity still remains ambiguous, but at least the assignment to the Cheirolepidiaceae as suggested previously by Litwin et al. (1993) can be excluded. The members of the Circumpolles group possess completely different exine stratification and characteristic columellar infratectum (e.g., Taylor

and Alvin 1984; Zavialova, 2003; Zavialova and Roghi 2005; Zavialova et al. 2010) in contrast to the granular texture in *F. traversei*. The most likely candidates are Gnetales, or Bennettitales, but *F. traversei* cannot be precisely assigned to any groups based ~~on~~ solely on ~~the~~ morphology or wall-ultrastructure.

The Reproductive Biology of the parent plant of *Froelichsporites traversei*

The morphology of pollen grains and some aspects of exine organization may relate functionally to pollination mechanism (e.g. Bolinder et al. 2015). Dispersal~~ion~~ of mature pollen grains as tetrads or other compound units is widespread among angiosperms (e.g. Cyperaceae, Juncaceae) but very rare in gymnosperms (Shukla et al. 1998; Blackmore et al. 2007). In angiosperm the dispersal of pollen grains as permanent compound units (tetrads, dyads) is a common phenomenon in order to fertilize several ovules during one fertilization event (Shukla et al. 1998). In the case of the gymnosperm pollen *Riccisporites tuberculatus* Mander et al. (2012) suggested that simple polyembryony (Webber 1940) is the explanation for ~~the~~ dispersal as permanent tetrads. Polyembryony is the formation of more than one embryo within a single ovule due the fertilization of more than one archegonia by different pollen grains (Shukla et al. 1998). This type of fertilization is present in the life cycle of several conifers (e.g., *Picea*, *Larix*, *Pseudotsuga*, *Pseudolarix*), and in *Gnetum* (Gnetales) the process is especially common (Sporne 1974; Williams 2007). Mander et al. (2012) argued that the simple polyembryony provided the parent plant of *R. tuberculatus* an adaptive strategy to avoid self-fertilization and increasing the chances of producing viable offspring.

~~In the original description Litwin et al. (1993) reported the occurrence of *F. traversei* triads, but i~~In the present material only tetrads ~~were have been found, but in the original description Litwin et al. (1993) reported the occurrence of *F. traversei* triads however, no example was~~ documented. The presence of permanent tetrads and the occurrence as triads together with aberrant uneven tetrads was explained by polyploidy (unreduced 2n pollen) in the case of

Classopollis (Kürschner et al. 2013). Polyploidy increases the fitness of the offspring which tends to be more vigorous and healthier than the diploid parent plants

This process is common in flowering plants, but a rare phenomenon in gymnosperms (e.g. Li et al. 2015), with the exception of Ephedra (Gnetales) where it can be prevalent (Ahuja, 2005). In addition to the dispersal as compound units, the exine structure and thickness have been proposed to relate to transport mechanisms (e.g., Bolinder et al. 2015). The granular exine with no or very thin endexine is an early specialization trend in some Magnoliales in order to reduce exine thickness (Doyle 2009). The reduction of exine thickness was explained as an adaptation to beetle pollination (Doyle 2009). By contrast, switching to granular exine in Fagales was most likely a response to wind pollination and exine reduction (Doyle 2009). As the parent plant of *F. traversei* is not precisely known, its the pollination mechanism of the parent plant is unknown. Among the potential candidates for the parent plant of *F. traversei*, the Bennettittales are considered to be primarily insect- pollinated based on the huge pollen size and thick granular infratectum (Bolinder et al. 2014). In the case of fossil Gnetales entomophily was suggested to be the main pollination mechanism, but Bolinder et al. (2015, 2016) observed a shift to anemophily in several modern Ephedra species which is also evident in the slight differences in ultrastructure: entomophilous species have a thicker infratectum and the granules in the infratectum are more densely spaced compared to the anemophilous species. The thickness of the infratectum in *F. traversei* is uneven and the surface is smooth that could probably enable wind pollination. However, the granules are densely spaces in the infratectum of *F. traversei* and during the routine light microscopy analysis *F. traversei* seemed to have high settling velocity which is more characteristic of rather for insect-transported pollen. The revelation of the pollination mechanism is beyond the scope of this paper as the parent plant is uncertain. Most likely the exine structure and the

previously listed special fertilization strategies (polyembryony and/or polyploidy) provided advantages in the transport and reproduction of the parent plant of *F. traversei*.

The distal ulcus is a conspicuous feature of the morphology of *F. traversei*. Generally, the aperture plays an important role in the reproductive biology of the plant as this is the place where the fertilization starts (Furness and Rudall 2004). Spores of bryophytes, lycophytes and ferns have a single proximal trilete or monolete aperture that forms at the contact area between four spores in the tetrad (Rudall and Bateman 2007). By contrast, apertures are predominantly distal in extant seed plants, e.g. Ginkgo, most conifers, most cycads, and basal angiosperms (Rudall and Bateman 2007). The shift from proximal to distal germination aperture has been regarded as one of the key innovation of seed plant evolution (Furness & Rudall, 2004). The distal pore is derived from the reduction of a monosulcate germination aperture (Furness and Rudall 2004; Rudall and Bateman 2007). The number, position and orientation of pollen apertures are considered to be related to the meiotic cytokinesis in the anther (e.g. Ressayre et al. 2002, 2005). The orientation of the distal sulci in *F. traversei* resembles the aperture pattern that forms in the case of monosulcate angiosperm pollen grains during simultaneous cytokinesis. Similarly, the tetrahedral tetrad configuration, as observed in *F. traversei*, is more common in simultaneous cytokinesis (Furness and Rudall 20014). This microsporogenesis type characterizes the majority of extant gymnosperms with the exception of the cycads where different sporogenesis types are present (successive, simultaneous, intermediate) (Furness and Rudall 2004).

Angiosperm like features

The earliest cladistics analyses already indicated that the angiosperm line, or at least some angiosperm features, originated in the Triassic (Doyle and Donoghue 1986). More recently, various works have showed that several Late Triassic gymnosperm pollen types exhibit angiosperm-like morphological features (e.g. Afropollis, Hochuli and Feist-

Burkhardt, 2013; Crinopollis group, Cornet 1989). *Froelichsporites traversei* ~~also possesses~~ ~~also~~ a series of angiosperm like features, such as a distal pore (ulcus), annulus, reduced discontinuous nexine and ~~the dispersal~~ as compound units (permanent tetrads). Dispersal as permanent tetrads and a distal ulcus are also observed in the early angiosperm *Walkeripollis gabonensis* (Doyle et al. 1990), even if the ultrastructure and pollen morphology (Doyle and Hotton 1991) differ. On the basis of these unusual features of *F. traversei*, the question arises whether *F. traversei* is related to the predecessors of the angiosperms, or these morphological and ultrastructure features merely represent an extinct evolutionary pathway. Previously, boat-shaped monosulcate pollen and granular exine was considered as the ancestral pollen type among angiosperms (Doyle 2005, 2009). However, contrary to these previous views, the globose monosulcate pollen and columellar exine were ancestral in almost all basal angiosperms (Doyle 2005, 2009). The granular infratectum developed in angiosperms secondarily in the Magnoliales, Nymphaeales and Laurales (Doyle 2005, 2009). The Annonaceae within the Magnoliales represents the only exception, as in this group granular exine is considered to be the ancestral exine structure (Doyle 2005, 2009). These recent developments refute the previous hypothesis that linked Gnetales, Bennettitales, Pentoxylales and angiosperms. It is equally likely that the angiosperms are related to Caytoniales with alveolar exine and/or the Triassic Crinopollis group which has columellar exine (Doyle 2005, 2009). Therefore, the relation between early angiosperm, or angiosperm related pollen grain and *F. traversei* is unlikely. The morphological features of this species most likely represent extinct evolutionary pathways among gymnosperms.

Paleoenvironmental significance

Froelichsporites traversei has a long stratigraphic range in the Chinle Formation ~~where~~ it is present in Zone II and III of Litwin et al (1991). Lindström et al. (2016) found it in the topmost part of the Petrified Forest Member in New Mexico (Zone III) and it is also present in

the Newark Basin (Cornet 1993; Fowell and Olsen 1993, Fowell et al. 1994). Its ~~abundance ratio~~ considerably increases after a faunal and floral turnover in the Sonsela Member in the PEFO around 215 Ma (Reichgelt et al. 2013) (Fig. 8) and at the floral turnover in the upper part of the Petrified Forest Member in New Mexico about 4 Ma years later (ca. 211.9 Ma ago) (Whiteside et al. 2015; Lindström et al. 2016). During both turnovers the high abundance of *F. traversei* is accompanied by an increase in Klausipollenites, which is a bisaccate pollen with Voltzialean affinity, and the Patinasporites group (Patinasporites spp., Enzonasporites vicens, Daughertyspora chinleana). Whiteside et al. (2015) explained the abundance of these groups ~~as a consequence of~~ harsh environmental conditions and climatic extremities. Most likely *Froelichsporites traversei* belonged to a plant group which had greater stress tolerance and thrived in disturbed areas, or ~~during~~ arid periods. The unusual morphological features together with the proposed reproductive biology provided adaptive advantages for the parent plant of *F. traversei* that made it successful during the environmental perturbation. Among the plant groups that can be related to *F. traversei*, the fossil Gnetales are often regarded as an indicator of extremely dry climate (Hoorn et al. 2012). However, modern Gnetales inhabit various environments and live under various climatic conditions therefore their ~~occurrence does not~~ ~~abundance cannot be reduced to~~ represent one ecological signal (dry climate).

Concluding remarks

More and more palynological data from the Late Triassic provide evidence for the “experimentation” with angiosperm related morphological features and probably functions in gymnosperm pollen. The enigmatic palynomorph, *Froelichsporites traversei* from the Norian of North America exhibits a number of angiosperm like features such as distal pore (ulcus) with annulus like thickening, simple granular wall-ultrastructure with discontinuous nexine lamination. The sporoderm structure suggests that the *F. traversei* grains were mature at

dispersion and shed as permanent tetrads. The wall-ultrastructure and the palynomorph morphology provided ambiguous results and the botanical affinity of *F. traversei* could not be determined precisely. The prevailing information suggests that the parent plant was probably related to the Gnetales, or Bennettiales. Dispersal as permanent tetrads provided probably adaptive advantage of the parent plant of *F. traversei*.

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Figure captions

Figure 1: A, Position of the Petrified Forest National Park within North America. The numbers indicate the *Froelichsporites traversei* occurrences: 1) Texas (Tecovas Formation) holotype locality, 2) Utah (Chinle Formation), 3) Arizona (Chinle Formation) (present study), 4) New Mexico (Chinle Formation), 5) Texas (Eagle Mills Formation), 6) South Carolina (South Georgia Basin), 7) North Carolina (Deep River Basin), 8) Virginia (Culpeper Basin), 9) Maryland (Gettysburg Basin), 10) Pennsylvania (Gettysburg Basin), 11) New Jersey (Newark Supergroup). Modified from Litwin et al. (1993). B, Location of the sampling sites within the Petrified Forest National Park. Map modified from Parker and Martz (2011). C, Paleogeographic position of the Chinle sedimentary during the Late Triassic. Map modified from Trendell et al. (2013). D, Stratigraphic position of the studied palynological samples. Logs modified from Reichgelt et al. (2013).

Figure 2 LM photoplate

Figure 3 SEM Photoplate

LM photoplate: A bl 2_2, B Bl 7_2, D MLM 2-2, E Bl 7_2, F Bl 7_1, G bl 4_1, H MLM 2-2, I Bl 6_1, J BL 7-2, K Newark 1, L Newark 1. Scale bars represent 20µm.

Figure 4: Abundance distribution of the measured morphological characters based on 30 specimens.

Figure 5: TEM images of *Froelichsporites traversei* showing the ultrastructure of the palynomorph wall.

Figure 6: TEM images showing the inner tetrad structure and the wall-US in a series of sections from the outside toward the center of the tetrad. Position of the section within the tetrad is marked in Fig. 7.

Figure 7: Schematic interpretation of the sporoderm of *Froelichsporites traversei*.

Figure 8: Simplified pollen diagram with the abundance distribution of *Froelichsporites traversei* and selected ecologically important pollen taxa in the Chinle Formation during the Norian. The dashed line indicates the horizon of the faunal and floral turnover, after Parker and Martz (2011).