Palynology of the upper Chinle Formation in northern New Mexico, U.S.A.:
implications for biostratigraphy and terrestrial ecosystem change during the Late
Triassic (Norian–Rhaetian)

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Abstract

A new densely sampled palynological record from the vertebrate-bearing upper Chinle
Formation at Ghost Ranch in the Chama Basin of northwestern New Mexico provides insights
into the biostratigraphy and terrestrial ecosystem changes during the Late Triassic of
northwestern Pangaea. Spore-pollen assemblages from the Poleo Sandstone, Petrified Forest,

and 'siltstone' members are dominated by pollen of corystospermous seed ferns (*Alisporites*) and voltziacean conifers (*Enzonasporites*, *Patinasporites*). Other abundant taxa include *Klausipollenites gouldii* and the enigmatic fused tetrad *Froelichsporites traversei*, whereas spores of ferns and fern allies are generally rare. The assemblages are correlated with Zone III Chinle palynofloras of previous authors. The lower assemblages contain rare occurrences of typical Zone II taxa, namely *Cycadopites stonei*, *Equisetosporites chinleanus* and *Lagenella martini*, that may either be reworked or represent relictual floral elements. Marked step-wise losses of species richness, along with only minor appearances of new taxa, led to a total 50% drop in range-through diversity during the late Norian of the Chama Basin. Correlations with other Chinle records in the western U.S. reveal differences in the stratigraphic ranges of some spore-pollen taxa, likely attributable to local/regional differences in environmental conditions, such as groundwater availability, precipitation, nutrients, and temperature, rather than stratigraphic miscorrelation. This is interpreted as a consequence of environmental stress resulting from increased aridity coincident with the northward movement of Pangaea. Similarly, major differences between the western and eastern U.S. and northwest Europe can be attributed to floral provincialism governed by climatic zones during the Late Triassic.

Keywords: Late Triassic; Norian–Rhaetian; Chinle Formation; palynology; palynostratigraphy; palaeoecology

1. Introduction

The Upper Triassic Chinle Formation of the western United States preserves some of the most widely exposed and well-studied Late Triassic non-marine deposits in the world. It is famous for its fossil faunal and floral assemblages that document this important interval in the history of life on Earth (e.g., Litwin et al., 1991; Long and Murry, 1995; Good, 1998; Ash, 2005a; Irmis, 2005; Parker, 2006; Parker and Martz, 2011). The Chinle Formation has been

particularly instrumental in documenting the early Mesozoic transition in terrestrial ecosystems, including early dinosaurs and their close relatives (e.g., Parker et al., 2005; Nesbitt et al., 2007, 2009a; Irmis et al., 2007, 2011). Faunal differences across Pangaea are believed to be an effect of latitudinal climate zones (e.g., Ezcurra, 2010; Irmis, 2011), such as those documented from strata coeval with the Chinle Formation in eastern North America (Whiteside et al., 2011). The diverse macrofloral assemblages of the Chinle Formation also record this shifting climate (Ash, 1980, 1987a, 2005a), consistent with sedimentological evidence of a transition from subhumid seasonal conditions in the lower portions of the Chinle Formation, to more arid seasonal conditions in the upper part of the formation (Dubiel et al., 1991; Dubiel, 1994; Therrien and Fastovsky, 2000; Dubiel and Hasiotis, 2011). These climatic changes may be driven by the northward drift of Pangaea throughout the Late Triassic (Kent and Tauxe, 2005; Kent and Irving, 2010; Whiteside et al., 2011).

Although the Chinle Formation is most famous for its macrofloral and vertebrate record, these sediments also preserve a diverse suite of palynomorphs (e.g., Gottesfeld, 1975; Litwin et al., 1991), and these palynological data have been instrumental in discussions of global correlations of Late Triassic non-marine strata (e.g., Litwin et al., 1991; Cornet, 1993; Lucas, 1997, 1998; Langer, 2005; Rayfield et al., 2005; Irmis et al., 2010, 2011; Lucas et al., 2007, 2012; Ogg, 2005, 2012). Traditionally, these palynomorph assemblages were interpreted to span the Carnian–Norian boundary (e.g., Litwin et al., 1991); however, recent revision of the Late Triassic timescale pushed the Carnian–Norian boundary back by 11 million years, from ~216 Ma to ~227 Ma (e.g., Muttoni et al., 2004; Furin et al., 2006; Olsen et al., 2011; Ogg, 2012). This, combined with new precise radioisotopic age constraints (e.g., Irmis et al., 2011; Ramezani et al., 2011; Atchley et al., 2013), suggests the Chinle Formation palynomorphs are likely Norian to Rhaetian in age (Parker, 2006; Parker and Martz, 2011; Olsen et al., 2011;

Irmis et al., 2010, 2011; Reichgelt et al., 2013), which has significant implications for global correlation of non-marine Late Triassic strata.

Even with these revisions, the ~35 my duration of the Late Triassic remains poorly constrained by absolute ages (Furin et al., 2006; Mundil, 2007; Mundil et al., 2010; Riggs et al., 2003; Rogers et al., 1993; Irmis et al., 2011; Ramezani et al., 2011). Thus, the timing, duration, and relation between major climatic and biotic events during this time interval are largely unknown. In an effort to improve correlations within the Upper Triassic, several papers published within the last decade have focused on magnetostratigraphic correlations (Muttoni et al., 2004; 2010; Gallet et al., 2007; Donohoo-Hurley et al., 2010; Zeigler and Geissman, 2011), but the lack of robust biostratigraphic correlations and radioisotopic ages still renders these correlations as largely heuristic hypotheses. Furthermore, many previous long distance correlations from continental to marine successions rely on the assumption that terrestrial biotic events are more or less synchronous across continents, which is not always the case (Irmis et al., 2010).

Here, we present new palynological data from the upper portion of the Chinle Formation at Ghost Ranch and vicinity in the Chama Basin of northern New Mexico, U.S.A. (Fig. 1). When complemented with published radioisotopic ages and an extensive and well-studied stratigraphic and faunal record, these palynological data provide insights into the biostratigraphy and terrestrial ecosystem changes during the Late Triassic of northern Pangaea. Furthermore, with the exception of a single study focused on a very short stratigraphic section (~10 m) (Reichgelt et al., 2013), we provide the most closely sampled palynomorph record so far published for Upper Triassic non-marine strata in the western United States.

2. Geological setting

During the Late Triassic, southwestern North America was located in the tropics and moved into the more arid subtropics as Pangaea drifted northward (Kent and Tauxe, 2005; Kent and Irving, 2010) (Fig. 1a). The Chinle Formation was deposited as fluvial, overbank, and minor lacustrine sediments in Arizona, New Mexico, Utah, and Colorado (Stewart et al., 1972; Blakey and Gubitosa, 1983; Dubiel, 1994). Paleocurrent and detrital zircon data indicate that these large river systems flowed from southeast to northwest, eventually emptying in the Panthalassic Ocean, in present-day Nevada (e.g., Stewart et al., 1972; Stewart et al., 1986; Riggs et al., 1996; Dickinson and Gehrels, 2008).

Depositional changes within the Chinle Formation are thought to be a result of a variety of causal mechanisms, including tectonic base level shift (Kraus and Middleton, 1987), changes in basin accommodation (Trendell et al., 2013), salt tectonism (e.g., Dubiel, 1994; Woody, 2006), arc magmatism (Atchley et al., 2013), and a progressive shift to a more arid climate (Dubiel et al., 1991; Dubiel, 1994; Dubiel and Hasiotis, 2011) resulting from the northward drift of North America out of the tropics (Kent and Tauxe, 2005; Kent and Irving, 2010; Whiteside et al., 2011).

Among the widespread Chinle Formation exposures on the Colorado Plateau, those in northern Arizona and northern New Mexico are best known for their paleontologic record, whereas those in Utah have been studied predominantly for their economic importance (i.e., uranium ore). The Chama Basin of northern New Mexico (Fig. 1b) is one area that is famous for its vertebrate fossil record (e.g., Colbert, 1989; Long and Murry, 1995; Zeigler et al., 2003; Irmis et al., 2007; Nesbitt et al., 2009a). Here, the Chinle Formation unconformably overlies the Lower Permian Cutler Group, and is divided into five lithologic members, in stratigraphic order: Agua Zarca Sandstone, Salitral Shale, Poleo Sandstone, Petrified Forest Member, and 'siltstone' member (Stewart et al., 1972; Dubiel, 1989; Irmis et al., 2007). The

Middle Jurassic Entrada Sandstone Formation unconformably overlies them. Plant macrofossils have been described from the Agua Zarca and Poleo sandstones (Daugherty, 1941; Ash, 1974b), but nearly all other paleontological records in the basin come from the Petrified Forest and 'siltstone' members (Irmis et al., 2007; Heckert et al., 2005; Lucas et al., 2003) in the upper part of the formation. These two lithologic units comprise fine to coarse-grained channel fill, and fine-grained levee and floodplain deposits (Stewart et al., 1972; Dubiel, 1989). In particular, the Petrified Forest Member contains numerous small channels (< 75 m wide) filled with reduced interbedded siltstones, sandstones, and intraformational conglomerates that often contain fossil charcoal, plant macrofossil fragments, and vertebrates (Dubiel, 1989; Zeigler, 2003; Irmis et al., 2007: supplemental information; Koeven et al., 2012). In both members, the overbank sediments are often well-oxidized, comprising red and orange hues.

The Chama Basin vertebrate fossil record is best known for its extensive record of early dinosaurs and their close relatives (Cope, 1889; Colbert, 1989; Heckert et al., 2003; Irmis et al., 2007; Nesbitt et al., 2009a; Sues et al., 2011), which was instrumental in demonstrating that dinosaurs did not replace early dinosauromorphs abruptly, but instead co-existed for ~20 million years (Irmis et al., 2007, 2011). Other vertebrate taxa include a diverse suite of actinopterygians, temnospondyl amphibians, sphenodontians, drepanosaurids, early archosauromorphs, the aquatic archosauriform *Vancleavea*, phytosaurs, and crocodile-line archosaurs (pseudosuchians) including aetosaurs, shuvosaurid poposaurids, rauisuchids, and crocodylomorphs (Berman and Reisz, 1992; Long and Murry, 1995; Clark et al., 2000; Zeigler et al., 2003; Heckert and Jenkins, 2005; Irmis et al., 2007; Nesbitt, 2007; Heckert et al., 2008; Nesbitt et al., 2009b; Pritchard et al., 2015). The dinosauromorph assemblage comprises the lagerpetid *Dromomeron romeri* (Irmis et al., 2007; Nesbitt et al., 2009c), silesaurids (Nesbitt et al., 2007; Irmis et al., 2007), basal theropod dinosaurs (*Chindesaurus*

151 *bryansmalli*, *Tawa hallae*, and *Daemonosaurus chauliodus*) (Irmis et al., 2007; Nesbitt et al.,
152 2009a; Sues et al., 2011), and coelophysoid theropods (Colbert, 1989; Heckert et al., 2003;
153 Irmis et al., 2007). Similar to other North American Triassic assemblages (Irmis, 2011), the
154 Chama Basin lacks any evidence of sauropodomorph and ornithischian dinosaurs. Because
155 sauropodomorph dinosaurs are abundant at coeval higher-paleolatitude localities in Europe
156 and Gondwana, they reinforce ideas about faunal provincialism across Pangaea, perhaps
157 controlled by climatic zones (Irmis et al., 2007; Nesbitt et al., 2009a; Ezcurra, 2010; Irmis,
158 2011; Whiteside et al., 2011; Kent et al., 2014). This hypothesis is supported by a recent high-
159 resolution paleoclimate proxy dataset, which indicates that the Chama Basin during this time
160 experienced an unpredictable arid climate that fluctuated between extremes within the context
161 of pervasive wildfires and elevated and rising atmospheric pCO₂ (Whiteside et al., 2012,
162 2015).

163 One of the main sites in the Chama Basin that documents this paleoclimate and fossil
164 record is the Hayden Quarry, which consists of three separate paleochannels in the lower part
165 of the Petrified Forest Member (for more information on the Hayden Quarry see Downs,
166 2005; Irmis et al., 2007, 2011; Whiteside et al., 2015). Together, these deposits preserve
167 abundant organic material suitable for isotopic analysis, fossil charcoal, and the single most
168 diverse vertebrate fossil assemblage in the basin (Irmis et al., 2007; Whiteside et al., 2012,
169 2015). The abundant organic record preserved in the reduced (i.e. deposited under low-
170 oxygen conditions) fine-grained sediments of these paleochannels makes them ideal for
171 palynological sampling, and they comprise a significant proportion of the palynomorph
172 samples presented here. Previous published palynological data from the Chama Basin are
173 limited to a few isolated samples from the ‘siltstone’ member (Scott, 1982; Litwin et al.,
174 1991).

Correlation of various units of the Chinle Formation between different areas of New Mexico, Arizona and Utah is difficult, because discontinuous outcrops and rapidly changing lithofacies cannot be easily compared. These challenges have led many workers to rely heavily on palynomorph and vertebrate biostratigraphy in correlating units (e.g., Camp, 1930; Colbert and Gregory, 1957; Gregory, 1957; Long and Padian, 1986; Murry and Long, 1989; Litwin et al., 1991; Cornet, 1993; Lucas, 1993, 1997, 1998; Long and Murry, 1995; Langer, 2005; Irmis, 2005; Parker, 2006; Parker and Martz, 2011; Irmis et al., 2010, 2011). However, new precise radioisotopic ages coupled with magnetostratigraphy are beginning to better constrain chronostratigraphic relationships, both among Chinle Formation units and in terms of correlation to the Late Triassic timescale (e.g., Irmis et al., 2011; Ramezani et al., 2011; Zeigler and Geissman, 2011). These new data suggest that the base of the Chinle Formation is likely to be earliest Norian in age, but the uppermost Chinle Formation units remain poorly constrained.

In the Chama Basin, the only available radioisotopic age is a U-Pb maximum age of 211.9 ± 0.7 Ma from the H2 paleochannel of the Hayden Quarry, indicating this part of the Petrified Forest Member is late Norian in age (Irmis et al., 2011) (Fig. 3). This age is consistent with new radioisotopic ages from the same member at Petrified Forest National Park, Arizona, where its lower part is dated to 213.1 ± 0.3 Ma, and its middle part (i.e. the Black Forest Bed) is dated to 209.9 ± 0.3 Ma (Ramezani et al., 2011). In addition, radioisotopic ages of 225.2 ± 0.3 Ma and 227.6 ± 0.1 Ma from the Mesa Redondo Member in and around Petrified Forest National Park, Arizona, constrain the age of the lowermost Chinle Formation, and a provisional age of 207.8 Ma for the top of the Petrified Forest Member, constrains most of the Chinle Formation to the Norian–early Rhaetian (Ramezani et al., 2011; Atchley et al., 2013), depending on the age of the Norian–Rhaetian boundary (compare Muttoni et al., 2010 with Wotzlaw et al., 2014). Uppermost Chinle units (e.g., Church Rock,

Rock Point, and ‘siltstone’ members) remain undated by precise radioisotopic ages, but these new data for the underlying Petrified Forest Member at Petrified Forest National Park and in the Chama Basin suggest the overlying units may be of latest Norian–Rhaetian age, which would be consistent with recently published magnetostratigraphy (Zeigler et al., 2008; Zeigler and Geissman, 2011).

Previous workers have suggested that the Poleo Sandstone in the Chama Basin corresponds to some part of the Sonsela Member in northern Arizona (Martz and Parker, 2010). The latter is dated to ~219–213 Ma based on multiple U-Pb ages coupled with magnetostratigraphy (Ramezani et al., 2011; Irmis et al., 2011), but there are no direct stratigraphic or absolute age tie points with the Poleo Sandstone at this time. The Poleo and Agua Zarca sandstones do not preserve any age-diagnostic floras (cf., Daugherty, 1941; Ash, 1974b). Although the presence of *Pelourdia poleoensis* in the Poleo Sandstone is characteristic of upper Chinle Formation assemblages (e.g., Arnold, 1964; Ash, 1987b), it is also found in some lower Chinle sections (e.g., Ash, 1980).

3. Previous palynological studies

Chinle Formation palynology has previously been studied by Daugherty (1941), Peabody and Kemp in Roadifer et al. (1964), Gottesfeld (1972a,b; 1975, 1980), Stone (1978), Doherty (1982), Scott (1982), Fisher and Dunay (1984), Litwin (1985), Zavada (1990), Litwin et al. (1991), and most recently by Reichgelt et al. (2013), amongst others. Many of these studies focused on one or a few samples from restricted geographic and stratigraphic areas, thus limiting any conclusions about palynostratigraphic changes within the Chinle Formation. Gottesfeld (1975, 1980) and Scott (1982) were the first to more broadly sample Chinle Formation palynomorphs, but because most of their sites are located in the lower portion of the Chinle Formation they did not observe any major biostratigraphic changes in palynofloral

composition. Nonetheless, they noted that the Chinle Formation assemblages implied a somewhat drier environment compared to those from the Late Triassic of Europe, and that this aridity signal became stronger in the upper Chinle Formation (Gottesfeld, 1972a, 1980; Scott, 1982).

The most extensive investigation of Chinle Formation palynology was presented by Litwin et al. (1991), who sampled over 25 different localities, and divided the palynofloral assemblages into three zones, I – III. The putatively oldest assemblage, zone I, exclusively comprised samples from the Temple Mountain Member in Utah. This assemblage was characterized by the presence of *Lunatisporites* sp. cf. *L. noviaulensis*, and *Infernopollenites claustratus*, and common to abundant *Minutosaccus crenulatus* and *Samaropollenites speciosus* (Litwin et al., 1991). The rare presence of *Brodipora striata*, *Equisetosporites chinleanus*, and *Lagenella martinii* in zone I, which are typical constituents of the overlying zone II, made Litwin et al. (1991) suggest that the pollen zone I assemblages were of early late Carnian age.

Whether the Temple Mountain Member (and therefore palynomorph zone I) is actually older than other Chinle units is unclear; regional stratigraphic work suggests that the Temple Mountain is equivalent to the Shinarump Member in other parts of Utah (Stewart et al., 1972: fig. 2; Dubiel, 1994). Furthermore, the characteristic mottling of the Temple Mountain Member, once thought to be a distinct stratigraphic unit below the Shinarump Member, is now recognized to often be simply various diagenetic zones within and above the Shinarump Member (Dubiel, 1994; Zeigler et al., 2008; Irmis et al., 2011 and Supplementary Information therein). Palynologically, zone I is defined more by its lack of taxa than anything else; only one taxon is uniquely present in zone I (*Lunatisporites* sp. cf. *L. noviaulensis*), and the zone shares many taxa with Shinarump Member localities assigned to zone II (Litwin et al., 1991).

Assemblages from the Shinarump Member (Utah and Arizona), the Monitor Butte Member (Utah, Arizona, New Mexico), the Kane Springs beds (“Moss Back Member” of Litwin) (Utah), and the Blue Mesa Member and lower portion of the Sonsela Member (“lower Petrified Forest Member” of Litwin) (Arizona), were all assigned to zone II by Litwin et al. (1991). Defined by the presence of *Brodipora striata*, *Camerosporites secatus*, *Infernopollenites claustratus*, *Lagenella martini*, and *Samaropollenites speciosus*, the zone also contains the first occurrences of *Cycadopites stonei*, *Enzonelasporites vigens*, *Froelichsporites traversei*, *Heliosaccus dimorphus*, *Ovalipollis ovalis*, *Playfordiaspora cancellosa*, and *Trileites klausii* (Litwin et al., 1991). It further contains the last occurrences of *B. striata*, *C. secatus*, *E. chinleanus*, *L. martini*, and *Trileites klausii*, and was found by Litwin et al. (1991) to be most similar to European assemblages assigned to the youngest part of the Carnian, but new radioisotopic dates from many of these sampled areas indicate they are early to mid-Norian in age (Irmis et al., 2011; Ramezani et al., 2011; Atchley et al., 2013).

Litwin et al. (1991) considered a single sample from the lower portion of the Sonsela Member (“Sonsela Sandstone”) at Petrified Forest National Park to be transitional between pollen zones II and III (Litwin et al., 1991). Samples now assigned to the upper portion of the Sonsela Member (see Parker and Martz, 2011; Reichgelt et al., 2013) were the lowest samples Litwin et al. (1991) referred to zone III. Recently, Reichgelt et al. (2013) examined the transition from zone II to zone III within the Sonsela Member at Petrified Forest National Park in more detail, confirming that a palynofloral change occurs in the middle of the unit and is marked by an overall drop in diversity and significant decreases in the abundances of *Protodiploxypinus* and *Cordaitina minor*. Zone III is characterized by a dominance of *Klausipollenites gouldii* and *Patinasporites densus*, and the presence of *Froelichsporites traversei* (Reichgelt et al., 2013).

Assemblages assigned to palynomorph zone III were recovered from the Petrified Forest Member (“upper Petrified Forest Member” of Litwin) in Utah and Arizona, the ‘siltstone’ member in northern New Mexico, and the Church Rock Member (including the “black ledge”) in Utah (Litwin et al., 1991). The assemblages referred to this zone generally contain *Alisporites opii*, *Froelichsporites traversei*, *Klausipollenites gouldii*, and monosaccate pollen (e.g., *Cordaitina minor*). First occurrences within this zone include *Camerosporites verrucosus*, *Foveolatitriteles potonieii*, *Iraqispora speciosa*, and *I. laevigata* (Litwin et al., 1991). The lack of taxa more typical of the European late Norian–Rhaetian and comparison with the Newark Supergroup led Litwin et al. (1991) to suggest that the assemblages of pollen zone III were early Norian in age, but revised age models for the Newark sequence (e.g., Muttoni et al., 2004; Furin et al., 2006; Olsen et al., 2011) and high-resolution radioisotopic ages for the Chinle Formation indicate they are instead late Norian to Rhaetian in age (Irmis et al., 2011; Ramezani et al., 2011).

4. Material and methods

4.1. Field and laboratory methods

We collected twenty-three outcrop samples from the upper portion of the Chinle Formation in the Chama Basin in New Mexico, targeting reduced and organic-rich units of mudstone and siltstone; 100–200 g of fresh, unweathered rock was collected for each sample. These samples were processed for palynomorphs according to standard palynological methods (e.g. Vidal, 1988). Approximately 50 g of bulk rock was treated in alternating steps with hydrochloric (38%) and hydrofluoric acid (40%) to remove carbonate and silicate mineral phases. After washing to neutrality, residues were sieved with 11 µm mesh-size sieves and mounted on strewn slides. Up to 300 palynomorphs were counted per slide with a compound microscope (Leica DM 2000) at 650x magnification. Abundance data were

calculated as percentages of total palynomorph assemblage, and thus represent relative abundances within the assemblages. Slides are permanently repositied in the collections of the University of California Museum of Paleontology (UCMP), Berkeley, California, U.S.A., and Natural History Museum of Utah (UMNH), Salt Lake City, Utah, U.S.A.; see Appendix 1 for specimen numbers.

For biostratigraphic purposes the first occurrence (FO) and last occurrence (LO) of a taxon are only used when discussing the range of that specific taxon within a particular section. The oldest or youngest known appearances of a taxon in a regional biozonation are referred to as first or last appearance datums, FAD and LAD, respectively.

All samples were placed into a precise stratigraphic framework from previous work (Irmis et al., 2007, 2011) using the base of the Entrada Sandstone and top of the Poleo Sandstone as datums.

4.2. Identification of plant affinity and ecological preference

The known or probable parent plant affinity of the identified palynomorphs encountered in this study are listed in Table 1, and these are based primarily on documented *in situ* occurrences of spores and pollen (Litwin, 1985; Balme, 1995; van Konijnenburg-van Cittert, 2002). However, for many spore/pollen taxa the probable parent plant affinity is merely based on their general morphology, which may suggest a relationship with a certain plant group. Litwin's (1985) report of *in situ* spores in fertile fern organs from the Chinle Formation of Arizona and New Mexico include *Osmundacidites* from the osmundacean *Todites fragilis*, *Punctatisporites*-like spores from *Wingatea plumosa* (?Gleicheniaceae), *Dictyophyllidites harrisi/mortonii* from the matoniacean *Phlebopteris smithii*, and *Granulatisporites infirmus* from the dipterid *Clathropteris walkeri*. These four taxa, or very similar forms, have all been identified in the Chama Basin palynofloral assemblages. However, we consider spores

assigned to *Punctatisporites* to be of osmundaceous affinity, following the *in situ* occurrences listed in Balme (1995).

Fossil spores assigned to *Deltoidospora* can be attributed to several different fern groups including the Dipteridaceae, Matoniaceae, Dicksoniaceae, and the Cyatheaceae (Balme, 1995; van Konijnenburg-van Cittert, 2002). Most spore producing plants, i.e., bryophytes, equisetopsids, lycopsids and ferns, probably grew as ground cover or understory in forested areas. Some of these taxa, such as the equisetopsids that produced *Calamospora* (Balme, 1995), are known to have inhabited riverbanks and lake shores (Kelber and van Konijnenburg-van Cittert, 1998). Monosulcate pollen grains, like *Cycadopites* and *Monosulcites*, have been found *in situ* in ginkgoalean, cycadalean and bennettitalean reproductive organs, although these palynomorphs may also have been produced by peltasperms (Balme, 1995). *Monosulcites minimus* has so far only been identified in bennettitaleans (Balme, 1995). Sulcate pollen assigned to *Eucommiidites* was produced by the Erdmanithecales (Friis et al., 2011), and the morphologically similar genus *Pretricolpipoollenites* may have the same affinity. Ash (1972) showed that *in situ* pollen grains from the male cone *Masculostrobus clathratus* were identical to *Equisetosporites chinleanus*. Balme (1995) tentatively placed *Masculostrobus clathratus* under probable Gnetales, but noted that Zavada (1984) pointed out that the complex tectate-columellate wall structure of *E. chinleanus* more resembles angiosperms than gnetaleans. Seed ferns mainly include bisaccate pollen assigned to *Alisporites*, *Chordasporites*, and *Falcisporites*, which are all considered to be of corystosperm affinity. The corystosperms are included in the upper canopy category, and taxa within this group may have been adapted to either lowland or upland environments. Ash and Litwin (1996) described *in situ* occurrences of bisaccate pollen from *Pramelreuthia*, with several of the pollen being compared to dispersed pollen assigned to the form taxon *Pityosporites*; however, one species, *Pramelreuthia dubielii*, was found to be larger in size

than the other described species and its pollen where found to be most similar to *Protodiploxypinus americanus*. Balme (1995) place *Pramelreuthia* under Coniferales or probable coniferales.

Some bisaccate pollen, such as *Protodiploxypinus* and *Platysaccus*, have not been found *in situ* and are assumed to be of either seed fern or conifer affinity. Because bisaccate pollen are adapted to wind dispersal, it seems likely that the parent plants of these pollen taxa were canopy trees. The small-sized cosmopolitan bisaccate genus *Vitreisporites*, which is known from the Permian to Cretaceous, is generally considered to be of caytonialean (seed fern) affinity, as it has been found *in situ* in *Caytonanthus* from Jurassic strata (see Balme, 1995 for references). There are no known *in situ* occurrences of this taxon from the Triassic, but Permian records are from *Salpingocarpus*, a peltasperm (Balme, 1995). McElwain et al. (2007) classify *Sagenopteris*, a caytonialean leaf taxon, as thermophilous. In the latest Triassic to earliest Jurassic, caytonialean pollen are particularly abundant in wet lowland settings (Petersen and Lindström, 2012), where the parent plants most likely occupied more well-drained areas of the mires, forming part of the canopy. In contrast, conifer pollen assigned to the circumpollid group (e.g., *Classopollis*, *Camerosporites*, and *Duplicisporites*) belong to the Cheirolepidiaceae and are regarded to have had a preference for somewhat drier conditions under a subtropical to tropical climatic regime (Vakhrameev 1981, 1991), sometimes in coastal habitats (Batten 1974, Abbink 1998). Pollen grains assigned to *Patinasporites*, herein included in the *Enzonalasporites*-group which encompasses members of *Enzonalasporites*, *Patinasporites*, and *Vallasporites*, are currently associated with the Permian voltzialean clade Majonicaceae based on *in situ* occurrence of *Patinasporites* in cones of probable majonicacean affinity, suggesting that the Majonicaceae may have persisted into the Triassic (Axsmith and Taylor, 1997; Axsmith et al., 1998; Reichgelt et al., 2013). Cornet (1977b) described *in situ* pollen assigned to *Patinasporites densus* from a *Glyptolepis*

conifer cone from the Newark Supergroup. Other pollen taxa of known voltzialean affinity include the genus *Triadispora*, which is known from *in situ* from voltziacean reproductive structures in the Triassic of Europe (Balme, 1995). Reichgelt et al. (2013) suggest that the bisaccate pollen *Klausipollenites gouldii* is also of voltzialean affinity as it shares some morphological features with *Triadispora*, although *K. gouldii* appears to lack the characteristic trilete mark that occurs in *Triadispora*.

4.3. Rarefaction analysis

To control for sample size when evaluating changes in taxonomic diversity, we conducted a rarefaction analysis (e.g., Raup, 1975; Tipper, 1979), with samples binned by lithologic member. Specifically and generically indeterminate records were excluded unless they represented a distinct taxon not otherwise in the dataset. All rarefaction analyses were conducted using the software package Analytic Rarefaction v.1.3 (Holland, 2003), including calculation of 95% confidence intervals.

5. Results

Palynomorphs were successfully recovered from Poleo Sandstone, Petrified Forest, and ‘siltstone’ member samples; nearly all of the productive samples from these three members were collected from reduced organic-rich fine-grained channel-fill facies. All samples collected from the Agua Zarca Sandstone proved to be barren, and no potentially suitable facies for sampling were identified in the Salitral Shale. Additionally, four samples from the Petrified Forest Member, and five from the ‘siltstone’ member were either barren of palynomorphs or contained only very few specimens. The stratigraphic distribution of productive samples in our dataset is controlled largely by lithology rather than sampling

strategy. For example, the low sampling density of the Poleo Sandstone is a result of the rarity of fine-grained channel fill facies in this coarse-grained unit, and the absence of productive samples from the lower portion of the 'siltstone' member is a consequence of a lack of organic-rich horizons in this interval. In all, over ninety spore/pollen form taxa were identified (Fig. 2) and these have been grouped by their known or probable parent plant affinities (Table 1; Fig. 3).

5.1. Poleo Sandstone

Five samples were studied from the Poleo Sandstone, but the uppermost sample (UMNH PB 70) contains only twenty-three specimens and is therefore not statistically significant (Fig. 2). The two lowest samples from this unit are from approximately 10 m above the base of the Poleo Sandstone, but because of limitations in outcrop exposure and correlation, it is unclear exactly how far stratigraphically below they are in relation to the next highest sample. The lowest sample (UMNH PB 71A) contains few palynomorphs and the majority of these (56%) are marine acritarchs, including sphaeromorphs, *Leiosphaeridia* sp., *Cymatiosphaera* sp., *Micrhystridium* sp., which we interpret as being reworked. The *in situ* palynoflora is sparse and only fifteen spore/pollen taxa have been identified, but the presence of *Praecirculina granifer* is noteworthy (Fig. 2). The overlying sample (UMNH PB 71B), from slightly higher in the section, contains abundant and well-preserved palynomorphs. The palynoflora is fairly diverse, containing 43 spore-pollen taxa (Fig. 2). Bisaccate pollen dominate, with high abundances of *Alisporites opii* and *Klausipollenites gouldii*, together with *Patinasporites densus*. Single specimens of *Infernopollenites claustratus* and *Equisetosporites chinleanus* are also present in the sample. The next two samples (UCMP PA1178 and UCMP PA1177) from the Poleo Sandstone contain abundant palynomorphs, and they are characterized by moderately high diversity spore-pollen assemblages, containing 54 and 55 taxa respectively.

The samples are dominated by various species of *Alisporites* bisaccate pollen grains, primarily *A. opii*. Other bisaccate taxa that are common in the Poleo Sandstone include *Colpectopollis ellipsoideus*, *Enzonalasporites*-group, *Klausipollenites gouldii*, and *Protodiploxypinus* spp. In the lower of these two samples, there is a single occurrence of *Classopollis* cf. *C. torosus*, the first reported record of this taxon from the Chinle Formation (Fig. 3). Cheirolepidiacean conifers are otherwise mainly represented by *Camerosporites* and comprise 3–6% of the palynoflora in the two middle samples (UCMP PA1178 and UCMP PA1177). These Poleo Sandstone assemblages also contain rare occurrences of *Cycadopites stonei*.

The two middle samples (UCMP PA1178 and UCMP PA1177) from the Poleo Sandstone contain rare spores, 2% and 4% respectively. In the lower sample of the two, spores are primarily represented by osmundacean (*Punctatisporites*) and dipteridacean/matoniacean ground ferns (*Deltoidospora*, *Dictyophyllidites*). In the higher sample, rare occurrences of *Gordonispora fossulata*, *Nevesisporites* sp., and *Retusotriletes* sp. may signal a presence of bryophytes during the time of deposition, but otherwise, the osmundacean ground fern spore *Punctatisporites* is still the most common spore taxon, whereas dipteridacean/matoniacean spores are almost absent (Fig. 2). Rare occurrences of *Iraqispora laevigata* and *I. speciosa* are also registered in these assemblages (Fig. 2).

There is a marked drop in diversity between the Poleo Sandstone and the overlying Petrified Forest Member, with a >30% loss of species richness (Fig. 2). Among the taxa that have not been found in samples above the Poleo Sandstone are *Cycadopites stonei*, *Lagenella martini*, and *Retisulcites perforatus* (Fig. 2).

5.2. Petrified Forest Member

The six productive samples from the Petrified Forest Member are all from the lower half of the unit (Fig. 2). The taxonomic richness of individual samples in the Petrified Forest Member ranges between 20 to 36 taxa, significantly less than the samples from the underlying Poleo Sandstone (Fig. 4a).

In the lowest part of the Petrified Forest Member, monosaccate conifer pollen assigned to the *Enzonalasporites*-group becomes superabundant (Fig. 3). These types of pollen grains are currently associated with the Permian voltzialean clade Majonicaceae (Axsmith and Taylor, 1997; Axsmith et al., 1998; Reichgelt et al., 2013), but are common components of Late Triassic palynomorph assemblages (Litwin et al., 1991; Reichgelt et al., 2013). Higher in section, the enigmatic palynomorph *Froelichsporites traversei* (Litwin et al., 1993) is also abundant (Fig. 3). Bisaccate pollen assigned to *Protodiploxypinus* are occasionally common in some samples (but never exceeding 9%), and increase in abundance inversely to that of the *Enzonalasporites*-group. Presumed cheirolepidiacean conifer pollen, mainly assigned to *Camerosporites*, decreases in abundance and becomes rare (Fig. 3). Spores are extremely rare in the lower part of the Petrified Forest Member, never constituting more than 1% of the assemblage.

Twenty-five of the sixty-one (41%) spore-pollen taxa observed in the Petrified Forest Member are not present in samples from the overlying 'siltstone' member, suggesting an on-going disappearance of taxa during the Petrified Forest Member-'siltstone' member transition (Fig. 2). Among the taxa absent above the Petrified Forest Member are: *Camerosporites secatus*, *C. verrucosus*, *Cordaitina minor*, *Equisetosporites chinleanus*, *Froelichsporites traversei*, *Heliosaccus dimorphus*, and *Playfordiaspora cancellosa*, many of which are considered typical of the Chinle Formation palynoflora (cf. Litwin et al., 1991). There is also a slight drop in average diversity per sample from the Petrified Forest Member to the

'siltstone' member, the latter displaying 17–35 in taxa richness/sample for the most productive samples (Fig. 4).

5.3. 'siltstone' member

Three productive samples were recovered from the upper part of the 'siltstone' member; these are from the same approximate stratigraphic horizon as those of Litwin et al. (1991; R4349 samples) (Fig. 2). Five taxa appear for the first time in the 'siltstone' member: , *Anapiculatisporites* sp., *Callialasporites* sp. cf. *C. dampieri*, a granulate form of *Iraqispora*, *Pinuspollenites* sp., and *Protodiploxypinus doubingerii* (Fig. 2). The 'siltstone' member assemblages are dominated by corystosperm pollen, mainly *Alisporites* spp. and the *Enzonalasporites*-group, although the latter has decreased significantly in relative abundance compared to the underlying Petrified Forest Member (Fig. 3). There is also an additional decrease in *Protodiploxypinus*, whereas there is a slight increase in fern spores, predominantly laevigate triangular trilete spores assigned to *Deltoidospora*, *Dictyophyllidites mortoni*, and *Gleicheniidites nilssoni* (Fig. 3).

5.4. Diversity Dynamics

There is a marked loss in diversity from the Poleo Sandstone Member to the 'siltstone' member, as indicated both by the taxonomic richness (number of taxa per sample) and the range-through diversity (Fig. 4). Range-through diversity considers the diversity of a sample based on the total range of species, i.e. all samples between the first (FO) and last (LO) occurrence of a species are considered to contain that species, though the species may in fact be absent in certain samples. The number of FOs is highest in the lower part of the Poleo Sandstone Member (lowest sample not included as the composition of older assemblages in unknown), and decreases gradually upwards within the unit. The number of FOs remains low through the Petrified Forest Member and the 'siltstone' member, with minor peaks in first

occurrences within the most diverse assemblages. Even though several of the FOs within the upper portion of the Poleo Sandstone and the Petrified Forest Member consist of taxa occurring only in one sample, the first occurrence rates are higher in the Poleo Sandstone Member than in overlying strata. LOs show a three-fold stepwise pattern, with increased numbers of disappearances in the upper portion of the Poleo Sandstone Member (UCMP PA1177), in the lower portion of the Petrified Forest Member (UCMP PA1092 to UCMP PA1095a), and within the ‘siltstone’ member (UCMP PA1088b). In all, there is a 50% loss in diversity from the maximum range-through diversity in the Poleo Sandstone Member (70 taxa) to the topmost assemblage (35 taxa) in the ‘siltstone’ member. However, a rarefaction analysis of the Chama Basin palynomorph assemblages (Fig. 5) indicates that when accounting for the number of palynomorphs counted in each sample, the ‘siltstone’ member is just as diverse as the Poleo Sandstone, but the Petrified Forest Member is clearly lower in diversity. This does not necessarily mean that the drop in diversity between the Petrified Forest and siltstone members is purely a sampling artifact, but is certainly influenced on some level by the lower number of palynomorph grains in the ‘siltstone’ member samples.

6. Discussion

6.1. Ecosystem and palaeoclimatic interpretations

Except for the lowermost sample, assemblages from the Poleo Sandstone are remarkably diverse, indicating vegetation dominated by corystospermous seed ferns, with abundant majonicacean and voltziacean conifers (Fig. 3). The corystosperms most likely inhabited lowland areas, as suggested by macrofloral taphonomic evidence from the lower portion of the Chinle Formation (Demko et al., 1998) and later during the Jurassic Period (Abbink, 1998). Ash (1999) described an upland macroflora from Petrified Forest Member-equivalent strata (Garita Creek Formation – this was incorrectly reported by Ash as the “Carita Creek

Fm'') of north-central New Mexico, that contained predominantly various types of conifers, an enigmatic gymnosperm (*Dinophyton spinosus*), small leaves of *Pelourdia poleoensis*, and the horsetail *Neocalamites*, confirming that conifers may primarily have inhabited more upland areas. However, in the Blue Mesa Member at Petrified Forest National Park, *in situ* conifer stumps demonstrate that at least some members grew on floodplains (Walker and Felton, 1935; Goebel, 1936; Seff, 1966; Gottesfeld, 1972a; Ash and Creber, 1992). Also common in the Poleo Sandstone assemblages are cheirolepidiacean conifer pollen and monosulcate pollen that can be assigned to one of the following: ginkgos, cycads, or Bennettitales. The cheirolepidiaceans may also have inhabited more upland areas, but in the Chama Basin they were definitely present in the lowland areas as indicated by macroplant fossils (Ash, 1974b). The ginkgo/cycads and Bennettitales are generally considered to have been more hygrophytic lowland elements that may have thrived in riparian environments (Abbink, 1998). The common presence of the latter group, together with hygrophytic bryophytes, lycophytes, and ferns, indicates at least seasonally humid conditions during the deposition of the Poleo Sandstone.

In the lower portion of the Petrified Forest Member there is a marked increase in abundance of probable majonicacean conifer pollen (*Enzonalasporites*-group) that are generally regarded as xerophytic elements. These pollen taxa are abundant in Carnian–Norian successions in the Tethys region, where they are associated with evaporate deposition (Visscher and van der Zwan, 1981; Visscher et al., 1994).

The abundance of the *Enzonalasporites*-group together with the on-going loss of taxa not matched by introduction of new species during this interval may reflect increasing aridity, and is consistent with a variety of palaeoclimatic proxies (Cleveland et al., 2008a,b; Whiteside et al., 2012, 2015). The succeeding palynologically barren or almost barren interval in the upper portion of the Petrified Forest and the lower portion of the 'siltstone' members may be a

further expression of an increasingly more arid climate less suitable for palynomorph preservation, as fine-grained channel fills are still present in this part of the section (Figs. 2–3). A return to at least seasonally slightly wetter conditions in the upper portion of the ‘siltstone’ member is suggested by the presence of a fairly diverse palynoflora with a decrease in abundance of majonicaean conifers, and more common hygrophytic ferns, though these assemblages are still less diverse than those of the underlying Petrified Forest Member (Figs. 2–3). The high amount of single sample occurrences in the Poleo Sandstone and lower portion of the Petrified Forest members may be a reflection of a high stress environment. The marked 50% drop in range-through diversity from the Poleo Sandstone member to the ‘siltstone’ member suggests increasingly harsh conditions within this part of the Chinle Formation (Fig. 2).

New palaeoclimate evidence from organic carbon isotopes, $p\text{CO}_2$ estimates from pedogenic carbonates, and fossil charcoal indicate that the Petrified Forest and ‘siltstone’ members experienced arid and warm conditions, fluctuating between extremes (Whiteside et al., 2012, 2015). In particular, the isotopic values of bulk organic carbon correlate with the relative abundance of several common palynomorphs (*Alisporites*, *Camerosporites*, and *Enzonalasporites*-group). These data are consistent with estimated mean annual precipitation (MAP) based on paleosols and estimated mean annual palaeotemperature (MAT) from pedogenic carbonates (Cleveland et al., 2008a,b), which indicate that MAT increased substantially and MAP decreased through time in the Petrified Forest and ‘siltstone’ members (Cleveland et al., 2008b). There is also evidence for rising $p\text{CO}_2$ during this interval (Cleveland et al., 2008b). Together, these data fit well with our palynological evidence for progressive aridification during deposition of the upper Chinle Formation in the Chama Basin of northern New Mexico. This climate change makes sense in the context of a northward-moving Pangaea, as the Chama Basin would have moved from approximately 10°N to 15°N

during the last 15 million years of the Triassic (Kent and Irving, 2010), which would have shifted the basin into progressively more arid climate zones (Kent and Tauxe, 2005; Whiteside et al., 2011).

Ferns, fern allies, and most gymnosperms are plant groups that are generally considered to be of exceptionally low nutritional quality (Hummel et al., 2008). Together with seed ferns, ginkgos, and cycads, these plants would have been the main food source available to herbivorous tetrapods during the Late Triassic of southwestern North America. *In vitro* studies of the degradability of some of the nearest living relatives of Mesozoic plants, suggest that the horsetail *Equisetum* is one of the most nutritional plants and its predecessors may have been a preferred food plant for many herbivorous dinosaurs (Hummel et al., 2008). However, they are generally most abundant in moist and open habitats during the Mesozoic, and likely grew along watercourses. Nonetheless, in the Chinle palynoflora generally, and the Chama Basin record specifically, spores of equisetaleans (i.e., members of *Calamospora*) are generally rare, suggesting that these plants were never abundant during the time of deposition, though equisetalean macrofossils can be locally common throughout the Chinle Formation (Daugherty, 1941; Seff, 1966; Ash, 1967, 1974a, 1975, 1980, 1987a,b, 2005a,b, 2009). Besides Equisetales, ginkgos, araucariacean (*Araucariacites*) and cupressacean/taxodiacean (e.g., *Perinopollenites*, *Callialasporites*) conifers, as well as osmundacean ferns (e.g., *Osmundacidites*, *Baculatisporites*, *Punctatisporites*), also have relatively high nutritional value and could have fulfilled the nutritional needs of herbivores if the plants were abundant enough and consistently present throughout the year (Hummel et al., 2008; Gee, 2011). With the exception of osmundaceans, these taxa were generally rare, and repeated periods of pronounced droughts during the deposition of the upper portion of the Chinle Formation likely limited nutritional vegetation available to herbivores throughout the year. These

resource limitations may explain the complete lack of large herbivorous sauropodomorph dinosaurs in the Triassic Pangaeon low paleolatitudes (c.f., Whiteside et al., 2015).

6.2. Biostratigraphic correlation

The overall composition of the spore/pollen assemblages from the Poleo Sandstone and the Petrified Forest Member, with abundant members of the *Enzonasporites*-group, *Froelichsporites traversei*, and *Klausipollenites gouldii*, suggests correlation with zone III of Litwin et al. (1991). However, there are a few elements that are typical of zone II, namely *Cycadopites stonei*, *Equisetosporites chinleanus* and *Lagenella martini* (Litwin et al., 1991). In the Chama Basin, *C. stonei* and *L. martini* are last observed within the upper portion of the Poleo Sandstone, whereas *E. chinleanus* is present in both the Poleo Sandstone and the lower part of the Petrified Forest Member (Fig. 6). The upper occurrence of *E. chinleanus* consists of a single poorly preserved specimen. Similarly, *Infernopollenites claustratus* is present in a single sample in the lower part of the Poleo Sandstone. Reworking of specimens of all four taxa from older strata within the lower part of the investigated succession is a real possibility given their rarity in the samples (1–2 grains) and the presence in these samples of various reworked marine acritarchs (Plate 6), especially in the Poleo Sandstone. Rare occurrences of pollen specimens assigned to *Lueckisporites* sp. and *Potonieisporites* sp. may be reworked from marine strata of the Pennsylvanian Madera Group, which are exposed below the Chinle Formation in this area (NMBGMR, 2003). Alternatively, detrital zircon data from the Poleo Sandstone suggest some input of late Paleozoic age source sediments from the Ouachita orogen to the southeast (Dickinson and Gehrels, 2008, 2010).

The LO of *L. martinii* in the Chinle Formation is otherwise in the lowermost Bluewater Creek Member of the Chinle Formation near Fort Wingate, New Mexico (Litwin, 1985; Litwin et al., 1991), which is older than the Poleo Sandstone (e.g., Irmis et al., 2011) (Fig. 6).

The LO of *C. stonei* in other outcrops of the Chinle Formation is slightly higher, in the lower part of the Sonsela Member in Petrified Forest National Park, Arizona (sample R4341 of Litwin et al., 1991; see Parker and Martz, 2011 for stratigraphic position). Outside the Colorado Plateau, *L. martinii* and *C. stonei* are absent from published Dockum Group samples (e.g., Dunay, 1972; Gottesfeld, 1975; Dunay and Fisher, 1979; Cornet, 1993). These two taxa are present in late Carnian strata of Richmond Basin in the Newark Supergroup of eastern North America (Cornet, 1993), and Litwin and Ash (1993) recorded the LOs of *Lagenella martinii* and *Cycadopites stonei* in the late Carnian–early Norian Pekin and Cumnock formations of the Deep River Basin in North Carolina (Whiteside et al., 2011; Olsen et al., 2014), together with *Camerosporites secatus* (Fig. 7). The LO of these two taxa in early Norian strata of the Newark Supergroup is consistent with the LO of *L. martinii* in the lowermost Bluewater Creek Member of the Chinle Formation in New Mexico, which is also early Norian in age (Irmis et al., 2011). However, the LO of *C. stonei* in the lower portion of the Sonsela Member, which is middle Norian in age (Ramezani et al., 2011), appears to post-date the LO of this taxon in eastern North America (Fig. 7). *Cycadopites stonei* is also reported from the Norian of Australia, where it occurs together with *Enzonalasporites* spp. and is a key taxon in the lower to middle *Minutosaccus crenulatus* Zone (Helby et al., 1987; Backhouse et al., 2002).

Outside of the Chama Basin, the youngest occurrences of *Infernopollenites claustratus* are in the upper part of the Blue Mesa Member of Petrified Forest National Park, Arizona (Fisher and Dunay, 1984), and the lowermost Chinle Formation (Temple Mountain Member) of Utah (Litwin et al., 1991) (Fig. 6). Elsewhere, *I. claustratus* is present in the Tecovas Formation of the lower portion of the Dockum Group in west Texas, but absent in the Newark Supergroup of eastern North America (Cornet, 1993).

An alternative to the reworking hypothesis for the late occurrences of *C. stonei*, *I. claustratus*, and *L. martini* in the Chama Basin is that these taxa have diachronous LOs across the Chinle depositional basin. There is definitely a discrepancy in correlating with northwestern Europe, where *L. martini* has its LAD at the top of the lower Carnian, the LAD of *I. claustratus* is in the upper Carnian, and *Cycadopites stonei* and *Equisetosporites chinleanus* have not been recorded in any Upper Triassic strata (Kürschner and Herngreen, 2010) (Fig. 7). In northwestern Europe, the boundary between the Carnian and the Norian is marked by the LADs of *Camerosporites secatus*, *Duplicisporites granulatus*, and *Triadispora verrucata* (Kürschner and Herngreen 2010) (Fig. 7).

Lucas et al. (2012) used the LAD of *Camerosporites secatus* and FAD of *Camerosporites verrucosus* to argue for the presence of the Carnian–Norian boundary in the Chinle Formation, the Newark Supergroup, and the German Keuper, by referencing Litwin and Skog (1991); in their statement the former taxon is known only from Ladinian to Carnian strata and the latter is only known from the Norian. However, Litwin and Skog (1991) was published well before the age revisions of the Chinle Formation and Newark Supergroup using biostratigraphically-independent age constraints, which provide clear evidence these occurrences do not correlate with the Carnian–Norian boundary in the Chinle Formation or Newark Supergroup (e.g., Muttoni et al., 2004; Furin et al., 2006; Olsen et al., 2011; Irmis et al., 2011; Ramezani et al., 2011). In any case, the two taxa clearly co-occur in the Chama Basin, where *C. secatus* and *C. verrucosus* are both present in the Poleo Sandstone and the lower part of the Petrified Forest Member, strata well-dated to the middle Norian based on a precise radioisotopic date (Irmis et al., 2011). The ranges of the two species also possibly overlap in a sample from the Petrified Forest Member in White Canyon, southeastern Utah (Litwin et al., 1991; Litwin and Skog, 1991) (Fig. 6). Reichgelt et al. (2013) did report the presence of *Camerosporites* in the Sonsela Member in Arizona, but did not refer their

specimens to the species level. Radioisotopic ages of detrital zircons from the Chinle Formation (Irmis et al., 2011; Ramezani et al., 2011) help to constrain the stratigraphic range of *Camerosporites secatus* in the Chinle Formation. In the Chama Basin, the LO of *C. secatus* occurs in the middle part of the Petrified Forest Member, post-dating the 211.9 ± 0.7 Ma age for the H2 paleochannel at Hayden Quarry, which is in the lower part of the same member. In Arizona, the LO of *C. secatus* is in the lower part of the Sonsela Member, and the base of this unit has been dated to 219.3 ± 0.27 Ma by Ramezani et al. (2011) (Fig. 6).

Compilations of Newark Supergroup records show that *C. verrucosus* first appears in the succeeding Lower Passaic-Heidlersburg assemblage (Cornet, 1977a, 1993; Cornet and Olsen, 1985); however, Cornet (1993) documented the presence of *C. verrucosus* in New Oxford-Lockatong correlative strata of the Taylorsville Basin, and also reported it in a sample from the Lockatong Formation of the Newark Basin (Olsen and Flynn, 1989; Olsen et al., 2011). Additionally, a careful reading of the underlying data Cornet used for his compilations (Cornet, 1977a) demonstrates that he only observed *C. secatus* in samples from the Richmond Basin of Virginia, with the highest stratigraphic occurrence in the Vinita Formation. This stratigraphic interval is late Carnian in age (Olsen et al., 2011, 2014; Whiteside et al., 2011), not early Norian as the rest of the New Oxford-Lockatong palynofloral samples (Muttoni et al., 2004; Olsen et al., 2011). Litwin and Ash (1993) did report *C. secatus* from the lower Cumnock Formation in the Deep River Basin of North Carolina, which is early Norian in age (Olsen et al., 2014). They further reported *C. secatus* from the lower Cow Branch Formation in the Danville Basin (Litwin and Ash, 1993), which is considered late–early to middle Norian in age (Olsen et al., 2014). Thus, *C. secatus* and *C. verrucosus* probably do have overlapping ranges in the Newark Supergroup (Fig. 7).

If the LAD of *C. secatus* was used as a marker for the Carnian–Norian boundary, the division would be placed in the middle of the Sonsela Member in Arizona (Parker and Martz,

2011; Reichgelt et al., 2013) and the lower part of the Petrified Forest Member in the Chama Basin (Fig. 5). Such a correlation to the Triassic timescale is not supported by any available independent age constraints (Muttoni et al., 2004; Furin et al., 2006; Olsen et al., 2011; Irmis et al., 2010, 2011; Ramezani et al., 2011; Ogg, 2012). Instead, a correlation of zone II palynomorphs in the lower portion of the Chinle Formation to the New Oxford-Locketong palynozone in the Newark Supergroup is consistent with the proposed early to mid-Norian age for both of these units (Muttoni et al., 2004; Olsen et al., 2011; Irmis et al., 2011; Ramezani et al., 2011). Similarly a correlation between zone III of the Chinle Formation and the lower Passaic-Heidlersburg palynozone of the Newark, as first hypothesized by Litwin et al. (1991), is also completely consistent with both the late Norian age recently proposed for these units and available independent geochronologic constraints (Muttoni et al., 2004; Olsen et al., 2011; Irmis et al., 2011; Ramezani et al., 2011) (Figs. 6–7).

Rather than being a global biostratigraphic datum, we suggest that the LO of *C. secatus* is better interpreted as tracking palaeoclimate. Previous authors have already recognized that the occurrence of this taxon has a latitudinal signal in the Tethys region that is climatically related (Visscher and van der Zwan, 1981). The LO of *C. secatus* across northwestern Europe, eastern North America (Newark Supergroup), and southwestern North America (Chinle Formation) (see Figure 6) is consistent with a change towards more arid conditions as Pangaea drifted northward during the Late Triassic (Kent and Tauxe, 2005; Kent and Irving, 2010). In all three areas, *C. secatus* is only found in strata that were relatively more humid, and it disappears as aridity becomes more pronounced. More generally, the hypothesis that climate in large part controls the presence, absence, and range of palynomorphs during the Late Triassic is not only consistent with what we know about Late Triassic climate variation across Pangaea (Kent and Tauxe, 2005; Sellwood and Valdes, 2006; Whiteside et al., 2011), but also supported by Carnian records from the Tethys, where there are distinct regional

variations in palynomorph assemblages that correlate with inferred palaeoclimate differences (Visscher and van der Zwan, 1981).

Locally, the geographically closest Late Triassic palynomorph sample to the Chama Basin (besides those from Ghost Ranch published by Litwin et al., 1991) is from the Lamy Amphibian Quarry of north-central New Mexico. This sample was described by Litwin (1986, sample number/name A1/MAD1; see discussion in Ash, 1999), but was not included in the published dataset of Litwin et al. (1991). This vertebrate site is located in the lower portion of the Garita Creek Formation (Zeigler et al., 2002), and its exact age is controversial. Authors have referred the locality to either the Adamanian or Revueltian vertebrate biozone (Hunt et al., 2005; Heckert, 2006; Parker, 2006; Parker and Martz, 2011), and the boundary between these two vertebrate zones corresponds to the Chinle palynomorph zone II/III boundary, at least in Petrified Forest National Park, Arizona (Parker and Martz, 2011; Reichgelt et al., 2013). Although the Lamy palynomorph sample includes some species that are only found in the Poleo Sandstone and lowermost Petrified Forest Member samples from the Chama Basin (*Cordaitina minor*, *Equisetosporites chinleanus*, and *Infernopollenites claustratus*), it lacks any taxa diagnostic of zone III assemblages, and contains several diagnostic zone II taxa, e.g. *Brodipora striata* and *Protodiploxypinus (Microcachrydites) doubingeri* (Litwin, 1986). These data suggest the Lamy sample is older than any of our samples from the Chama Basin, and indirectly support assignment of the Lamy Amphibian Quarry to the Adamanian vertebrate biozone.

6.3. Palynofloral diversity trends and extinction patterns

One difficulty with further development of Late Triassic palynofloral studies is that there appears to be few clear global or regional trends, likely in part because of the lack of independent age constraints (Mundil, 2007; Mundil et al., 2010; Ogg, 2012) and uneven

sampling across paleolatitudes (and therefore climate zones). Even within the Chinle Formation, variations in composition of age-equivalent assemblages show no clear patterns (cf. Fig. 6). Although several authors (Litwin et al., 1991; Litwin and Ash, 1993; Reichgelt et al., 2013) have noted major decreases in diversity through time within particular sections of the Chinle Formation, there are few consistent patterns of extinction between local areas (Fig. 6). In the Chama Basin, there is a 50% range-through diversity drop between the palynoflora of the Poleo Sandstone Member and the upper 'siltstone' member, marked by the LOs of *Camerosporites secatus*, *C. verrucosus*, *Cordaitina minor*, *Equisetosporites chinleanus*, *Froelichsporites traversei*, *Heliosaccus dimorphus*, and *Playfordiaspora cancellosa*. A similar drop in diversity is observed between the Petrified Forest Member and the overlying Church Rock Member in Utah, with the disappearance of *Alisporites gottesfeldii*, *Enzonalasporites vicens*, *Foveolatitriteles potoniei*, *Minutosaccus crenulatus*, *Ovalipollis ovalis*, and possibly *Camerosporites secatus* (Litwin et al., 1991), but the LO of *C. secatus* is the only event potentially shared between the two regions (Fig. 6). As mentioned above, independent age constraints show that the LO of *C. secatus* in these two areas are not synchronous (Fig. 6). Although floras of the Chinle Formation can be expected to have been adapted to seasonally harsh conditions, the increased aridity as Pangaea drifted northward during the Late Triassic (Kent and Tauxe, 2005; Kent and Irving, 2010; Cleveland et al., 2008a,b; Whiteside et al., 2011, 2012, 2015) must have caused long-term on-going environmental stress to the ecosystem. The variations in extirpation patterns among penecontemporaneous strata of the Chinle Formation are most likely the result of the local/regional floras reacting differently depending on variations in local conditions, such as groundwater availability, precipitation, nutrients, and temperature. A similar on-going aridification also took place in northwestern Europe during the Late Triassic which, albeit being punctuated by a widespread late Carnian humid phase (the Carnian Pluvial Event; Dal

Corso et al., 2012), led to a 50% drop in spore-pollen diversity between the early Carnian and the early Norian (Kürschner and Herengreen, 2010), earlier than the recorded palynofloral diversity drop in the Chinle Formation. Unfortunately, northwest European Norian palynological records are rare and discontinuous, so direct comparison of coeval strata with the diversity loss observed in the Chama Basin is difficult. In contrast, palynofloral assemblages from New Zealand show the opposite pattern, with progressive first appearances throughout the Norian–Rhaetian (de Jersey and Raine, 1990; Zhang and Grant-Mackie, 2001).

The 75–100 km-wide Manicouagan impact crater in Quebec, Canada, has been dated to 215.5 Ma (Hodych and Dunning, 1992; Ramezani et al., 2005), and middle Norian impact ejecta layers from deep-sea sediments in Japan (Onoué et al., 2012) and Britain (214.7 ± 2.5 Ma $^{40}\text{Ar}/^{39}\text{Ar}$ age from authigenic K-feldspar [Walkden et al., 2002], recalculated to 216.7 ± 2.5 Ma [Renne et al., 2010]), have both been attributed to this impact. Onoué et al. (2012) could find no evidence of mass extinction among radiolarians, calcareous nannoplankton, or dinoflagellate cysts in the deep sea, although the largest set of nearly synchronous last occurrences is in very close proximity to the impact layer (i.e., Onoué et al., 2012, fig. 5). The ages of the palynomorph zone II–III transition and vertebrate faunal turnover in the middle Chinle Formation are consistent with the age of the Manicouagan impact (Parker and Martz, 2011; Reichgelt et al., 2013). It is tempting to speculate that the environmental and biotic after-effects of this impact are preserved in the Poleo Sandstone–Petrified Forest Member transition of the Chama Basin, but as Onoué et al. (2012) caution, extremely precise absolute age constraints for marine and terrestrial sections with biotic turnover, impact ejecta layers, and the impact structures themselves are necessary in order to evaluate a possible connection (cf. Renne et al., 2013).

The high abundance of the enigmatic fused tetrad *Froelichsporites traversei* (Litwin et al., 1993) in the Petrified Forest Member of the Chama Basin is intriguing (Figs. 2–3) when

797 compared with its low abundance in other studies of Chinle Formation palynofloral
798 assemblages. In the present study it was not recovered from strata higher than the Petrified
799 Forest Member, but Litwin et al. (1991, 1993) listed an occurrence within the 'siltstone'
800 member (sample R4349C). Litwin et al. (1991) observed this taxon in both zone II and zone
801 III samples, but did not mention any abundance changes. Reichgelt et al. (2013) reported *F.*
802 *traversei* in low numbers in the upper part of the Sonsela Member of Arizona.
803 *Froelichsporites traversei* has never been found associated with the reproductive parts of a
804 parent plant; hence, its affinity is unclear. Fused tetrads occur amongst Palaeozoic
805 cryptospores (e.g. *Tetrahedraletes*), but are seldom present in Paleozoic–Mesozoic
806 embryophytic plants (Traverse, 2007). In extant plants, unseparated tetrads occur only
807 immediately after male meiosis, during the early stages of spore/pollen ontogeny (Visscher et
808 al., 2004). Today, reproductively functional permanent tetrads are produced only by a limited
809 number of bryophyte taxa, and by representatives of a wide variety of angiosperm families,
810 with the retention of mature spores/pollen in a permanent tetrad being the result of a mutation
811 in two genes (Visscher et al., 2004). Usually, when encountered in the fossil record, the fused
812 tetrads are in low abundance, and represent immature specimens of dispersed single
813 spores/pollen. Exceptions include the enigmatic *Ricciisporites tuberculatus*, a fused probable
814 gymnospermous pollen tetrad typical that often occurs in high abundance in Rhaetian strata of
815 NW Europe (Mander et al., 2012). The increased abundance of fused lycophyte spore tetrads
816 in the latest Permian is interpreted as a result of mutagenesis during the end-Permian event
817 due to destruction of the ozone layer (Looy et al., 1999, 2001; Visscher et al., 2004). Thus, it
818 could be that *Froelichsporites* is a form that responded to the increased environmental stress,
819 either as a 'disaster taxon' that colonized disturbed areas, or through mutagenesis.

821 7. Conclusions

The new palynological data reported here from the upper portion of the Chinle Formation in the Chama Basin, northern New Mexico, provide evidence of continuing ecosystem change during the deposition of the Poleo Sandstone, Petrified Forest, and 'siltstone' members. The spore-pollen assemblages are dominated by corystospermous seed fern and voltziacean conifer pollen, and are correlated with Chinle palynomorph zone III of Litwin et al. (1991). Major changes in palynological plant group abundances from the Poleo Sandstone to the Petrified Forest Member, with marked increases in the latter in the abundances of the *Enzonasporites*-group (*Enzonasporites*, *Patinasporites*, *Pseudoenzonasporites*, *Vallasporites*) and the enigmatic fused tetrad *Froelichsporites traversei*, indicate restructuring of the terrestrial ecosystem during deposition of the lower part of the Petrified Forest Member. A detrital zircon U-Pb radioisotopic date from this part of the succession has provided a maximal depositional age of 211.9 ± 0.7 Ma, i.e. a late Norian age (Irmis et al., 2011), demonstrating that the entire investigated Chama Basin succession is Norian–Rhaetian in age. A total 50% range-through drop in diversity is registered through the sampled sequence of the Chama Basin. Marked step-wise losses of species richness, along with only minor appearances of new taxa, are interpreted as a possible consequence of increased aridity as Pangaea drifted northward (Kent and Tauxe, 2005; Kent and Irving, 2010; Cleveland et al., 2008a,b; Whiteside et al., 2011, 2012, 2015). However, it is interesting to note that some major biotic changes might be synchronous to the middle Norian Manicouagan impact (Hodych and Dunning, 1992; Ramezani et al., 2005; Onoue et al., 2012). Comparison with other penecontemporaneous palynofloras from the Chinle Formation in Utah and Arizona show discrepancies in the last occurrences of specific taxa between these areas, and this probably reflects local environmental variations within the western United States. Similarly, differences in the stratigraphic ranges of some spore-pollen taxa between the western and

eastern United States and northwestern Europe can probably be attributed to regional differences in palaeoenvironment.

Acknowledgments

This work was funded by the Society of Vertebrate Paleontology Bryan Patterson Award (RBI), University of California Department of Integrative Biology Robert and Nancy Beim Graduate Field Research Fund (RBI), University of California Museum of Paleontology Graduate Student Research Award (RBI), University of Utah (RBI), the National Geographic Society (#8014-06 to K. Padian), and the National Science Foundation (EAR 1349650, 1349554, 1349667, and 1349654 to RBI, JHW, NDS, SJN, and AHT). We thank the Ghost Ranch Conference Center for permission to work there, and Alex Downs for facilitating our research at Ghost Ranch in countless ways. SL publishes with the permission of the director of the Geological Survey of Denmark and Greenland. The authors are grateful for constructive commentary from the editor and two anonymous reviewers.

References

- Abbink, O. 1998. Palynological investigations in the Jurassic of the North Sea Region. LPP Contributions Series 8. Ph.D. thesis. Universiteit Utrecht, Utrecht.
- Arnold, C.A., 1964. *Cordaites*-type foliage associated with palm-like plants from the Upper Triassic of south-western Colorado. Journal of the Indian Botanical Society 42A, 4–9.
- Ash, S.R., 1967. The Chinle (Upper Triassic) megaf flora of the Zuni Mountains, New Mexico. New Mexico Geological Society Guidebook 18, 125–131.
- Ash, S.R., 1972. Late Triassic plants from the Chinle Formation in north-eastern Arizona. Palaeontology 15, 598–618.
- Ash, S.R., 1974a. The Upper Triassic Chinle flora of Petrified Forest National Park, Arizona. In: S.R. Ash (Editor), Guidebook to Devonian, Permian and Triassic Plant Localities, East-Central Arizona. Paleobotanical Section of the Botanical Society of America, Tempe, pp. 43–50.
- Ash, S.R., 1974b. Upper Triassic plants of Cañon del Cobre, New Mexico. New Mexico Geological Society Guidebook 25, 179–184.
- Ash, S.R., 1975. The Chinle (Upper Triassic) flora of southeastern Utah. Four Corners Geological Society Guidebook 8, 143–147.
- Ash, S.R., 1980. Upper Triassic floral zones of North America. In: D.L. Dilcher and T.M. Taylor (Editors), Biostratigraphy of Fossil Plants. Dowden, Hutchinson & Ross, Inc., Stroudsburg, pp. 153–170.
- Ash, S.R., 1987a. The Upper Triassic red bed flora of the Colorado Plateau, western United States. Journal of the Arizona-Nevada Academy of Science 22, 95–105.
- Ash, S.R., 1987b. Growth habit and systematics of the Upper Triassic plant *Pelourdea poleoensis*, southwestern U.S.A. Review of Palaeobotany and Palynology 51, 37–49.

- 885 Ash, S.R., 1999. An Upper Triassic upland flora from north-central New Mexico, U.S.A.
886 Review of Palaeobotany and Palynology 105, 183–199.
- 887 Ash, S.R., 2005a. Synopsis of the Upper Triassic flora of Petrified Forest National Park and
888 vicinity. Mesa Southwest Museum Bulletin 9, 53–61.
- 889 Ash, S., 2005b. A new Upper Triassic flora and associated invertebrate fossils from the basal
890 beds of the Chinle Formation, near Cameron, Arizona. PaleoBios 25, 17–34
- 891 Ash, S., 2009. A Late Triassic flora and associated invertebrate fossils from the basal beds of
892 the Chinle Formation in Dinnebito Wash, east-central Arizona, USA. Palaeontographica
893 Abteilung B 282, 1–37.
- 894 Ash, S.R., Creber, G.T., 1992. Palaeoclimatic interpretation of the wood structures of the trees
895 in the Chinle Formation (Upper Triassic), Petrified Forest National Park, Arizona, USA.
896 Palaeogeography, Palaeoclimatology, Palaeoecology 96, 299–317.
- 897 Ash, S.R., Litwin, R.J., 1996. Two new species of the pinnate microsporophyll *Pramelreuthia*
898 from the Upper Triassic of the southwestern United States. American Journal of Botany
899 83, 1091–1099.
- 900 Atchley, S.C., Nordt, L.C., Dworkin, S.I., Ramezani, J., Parker, W.G., Ash, S.R., Bowring,
901 S.A., 2013. A linkage among Pangean tectonism, cyclic alluviation, climate change, and
902 biologic turnover in the Late Triassic: the record from the Chinle Formation,
903 southwestern United States. Journal of Sedimentary Research 83, 1147–1161.
- 904 Axsmith, B.J., Taylor, T.N., 1997. The Triassic conifer seed cone *Glyptolepis*. Review of
905 Palaeobotany and Palynology 96, 71–79
- 906 Axsmith, B.J., Taylor, T.N., Taylor, E.L., 1998. A new fossil Conifer from the Triassic of
907 North America: implications for models of ovulate cone scale evolution. International
908 Journal of Plant Sciences 159, 358–366.

- 909 Backhouse, J., Balme, B.E., Helby, R., Marshall, N.G., Morgan, R., 2002. Palynological
910 zonation and correlation of the latest Triassic, Northern Carnarvon Basin. In: Keep, M.,
911 Moss, S.J. (eds.), The sedimentary basins of Western Australia 3: Proceedings of the
912 Petroleum Exploration Society of Australia Symposium, Perth, WA, 179–201.
- 913 Balme, B.E., 1995. Fossil in situ spores and pollen grains: an annotated catalogue. Review of
914 Palaeobotany and Palynology 87, 81–323.
- 915 Batten, D.J. 1974. Wealden palaeoecology from the distribution of plant fossils. Proceedings
916 of the Geologists' Association 85, 433–458.
- 917 Berman, D.S., Reisz, R.R., 1992. *Dolabrosaurus aquatilis*, a small lepidosauromorph reptile
918 from the Upper Triassic Chinle Formation of north-central New Mexico. Journal of
919 Paleontology 66, 1001–1009.
- 920 Blakey, R., 2011. Colorado Plateau Geosystems. HYPERLINK
921 "<http://cpgeosystems.com/paleomaps.html>". January 2015
- 922 Blakey, R.C., Gubitosa, R., 1983. Late Triassic paleogeography and depositional history of
923 the Chinle Formation, southern Utah and northern Arizona. In: M.W. Reynolds and E.D.
924 Dolly (Editors), Mesozoic Paleogeography of West–Central United States. Society of
925 Economic Paleontologists and Mineralogists, Rocky Mountain Section, Denver, CO, pp.
926 57–76.
- 927 Camp, C.L., 1930. A study of the phytosaurs with description of new material from western
928 North America. Memoirs of the University of California 10, 1–160.
- 929 Clark, J.M., Sues, H.-D., Berman, D.S., 2000. A new specimen of *Hesperosuchus agilis* from
930 the Upper Triassic of New Mexico and the interrelationships of basal crocodylomorph
931 archosaurs. Journal of Vertebrate Paleontology 20, 683–704.

- 932 Cleveland, D.M., Nordt, L.C., Atchley, S.C., 2008a. Paleosols, trace fossils, and precipitation
933 estimates of the uppermost Triassic strata in northern New Mexico. *Palaeogeography,*
934 *Palaeoclimatology, Palaeoecology* 257, 421–444.
- 935 Cleveland, D.M., Nordt, L.C., Dworkin, S.I., Atchley, S.C., 2008b. Pedogenic carbonate
936 isotopes as evidence for extreme climatic events preceding the Triassic–Jurassic
937 boundary: implications for the biotic crisis? *Geological Society of America Bulletin* 120,
938 1408–1415.
- 939 Colbert, E.H., 1989. The Triassic dinosaur *Coelophysis*. Museum of Northern Arizona
940 Bulletin 57, 1–160.
- 941 Colbert, E.H., Gregory, J.T., 1957. Correlation of continental Triassic sediments by vertebrate
942 fossils. *Geological Society of America Bulletin* 68, 1456–1467.
- 943 Cope, E.D., 1889. On a new genus of Triassic Dinosauria. *American Naturalist* 23, 626.
- 944 Cornet, B., 1977a. The palynostratigraphy and age of the Newark Supergroup. PhD
945 dissertation, Pennsylvania State University, State College, 506 pp.
- 946 Cornet, B., 1977b. Preliminary investigation of two Late Triassic conifers from York County,
947 Pennsylvania. IN: Romans, R.C. (Ed.), *Geobotany*. Plenum Publishing, New York, 165–
948 172.
- 949 Cornet, B., 1993. Applications and limitations of palynology in age, climatic, and
950 paleoenvironmental analyses of Triassic sequences in North America. *New Mexico*
951 *Museum of Natural History and Science Bulletin* 3, 75–93.
- 952 Cornet, B., Olsen, P.E., 1985. A summary of the biostratigraphy of the Newark Supergroup of
953 eastern North America with comments on early Mesozoic provinciality. In: R. Weber
954 (Editor), *III Congreso Latino Americano de Paleontología, Memoria*. Instituto de
955 Geología Universidad Nacional Autónoma de México, México, pp. 67–81.

- 956 Dal Corso, J., Mietto, P., Newton, R.J., Pancost, R.D., Preto, N., Roghi, G., Wignall, P.B.,
957 2012. Discovery of a major negative $\delta^{13}\text{C}$ spike in the Carnian (Late Triassic) linked to
958 the eruption of Wrangellia flood basalts. *Geology* 40, 79–82.
- 959 Daugherty, L.H., 1941. The Upper Triassic flora of Arizona. Carnegie Institute of Washington
960 Publication 526, 1–108.
- 961 de Jersey, N.J., Raine, J.I., 1990. Triassic and earliest Jurassic miospores from the Murihiku
962 Supergroup, New Zealand. *New Zealand Geological Survey Paleontological Bulletin* 62,
963 1–164.
- 964 Dickinson, W.R., Gehrels, G.E., 2008. U-Pb ages of detrital zircons in relation to
965 paleogeography: Triassic paleodrainage networks and sediment dispersal across
966 southwestern Laurentia. *Journal of Sedimentary Research* 78, 745–764.
- 967 Dickinson, W.R., Gehrels, G.E., 2010. Insights into North American paleogeography and
968 paleotectonics from U-Pb ages of detrital zircons in Mesozoic strata of the Colorado
969 Plateau, USA. *International Journal of Earth Sciences* 99, 1247–1265.
- 970 Doherty, L.I., 1982. Illustrations of plant microfossils from the Chinle Formation, Garfield
971 County, Utah. U.S. Geological Survey Open-File Report 82-1092, 1–35.
- 972 Donohoo-Hurley, L.L., Geissman, J.W., Lucas, S.G., 2010. Magnetostratigraphy of the
973 uppermost Triassic and lowermost Jurassic Moenave Formation, western United States:
974 Correlation with strata in the United Kingdom, Morocco, Turkey, Italy, and eastern
975 United States. *Geological Society of America Bulletin* 122, 2005–2019.
- 976 Downs, A., 2005. The Hayden Quarry, a new Upper Triassic fossil locality at Ghost Ranch,
977 New Mexico. *New Mexico Geological Society Guidebook* 56, 355–356.
- 978 Dubiel, R.F., 1989. Depositional and climatic setting of the Upper Triassic Chinle Formation,
979 Colorado Plateau. In: S.G. Lucas and A.P. Hunt (Editors), *Dawn of the Age of Dinosaurs*

- 980 in the American Southwest. New Mexico Museum of Natural History, Albuquerque, pp.
981 177–187.
- 982 Dubiel, R.F., 1994. Triassic deposystems, paleogeography, and paleoclimate of the Western
983 Interior. In: M.V. Caputo, J.A. Peterson and K.J. Franczyk (Editors), Mesozoic systems
984 of the Rocky Mountain region, USA. Society of Economic Paleontologists and
985 Mineralogists Rocky Mountain Section, Denver, pp. 133–168.
- 986 Dubiel, R.F., Hasiotis, S.T., 2011. Deposystems, paleosols, and climatic variability in a
987 continental system: the Upper Triassic Chinle Formation, Colorado Plateau, U.S.A.
988 SEPM Special Publication 97, 393–422.
- 989 Dubiel, R.F., Parrish, J.T., Parrish, J.M., Good, S.C., 1991. The Pangaeian megamonsoon -
990 evidence from the Upper Triassic Chinle Formation, Colorado Plateau. *Palaios* 6, 347–
991 370.
- 992 Dunay, R.E., Fisher, M.J., 1979. Palynology of the Dockum Group (Upper Triassic), Texas,
993 U.S.A. *Review of Palaeobotany and Palynology* 28, 61–92.
- 994 Ezcurra, M.D., 2010. Biogeography of Triassic tetrapods: evidence for provincialism and
995 driven sympatric cladogenesis in the early evolution of modern tetrapod lineages.
996 *Proceedings of the Royal Society of London, Biological Sciences* 277, 2547–2552.
- 997 Fisher, M.J., Dunay, R.E., 1984. Palynology of the Petrified Forest Member of the Chinle
998 Formation (Upper Triassic), Arizona, U.S.A. *Pollen et Spores* 26, 241–284.
- 999 Friis, E.M, Crane, P.R., Pedersen, K.R., 2011. Early flowers and angiosperm evolution.
1000 Cambridge University Press. 596 pp.
- 1001 Furin, S., Preto, N., Rigo, M., Roghi, G., Gianolla, P., Crowley, J.L., 2006. High precision
1002 U/Pb zircon age from the Triassic of Italy: implications for the Triassic time scale and the
1003 Carnian origin of calcareous nannoplankton and dinosaurs. *Geology* 34, 1009–1012.

- 1004 Gallet, Y., Krystyn, L., Marcoux, J., Besse, J., 2007. New constraints on the End-Triassic
1005 (Upper Norian – Rhaetian) magnetostratigraphy. *Earth and Planetary Science Letters* 255,
1006 458–470.
- 1007 Gee, C.T., 2011. Dietary options for the sauropod dinosaurs from an integrated botanical and
1008 paleobotanical perspective. In: N. Klein, K. Remes, C. T. Gee, and P. M. Sander
1009 (Editors), *Biology of the Sauropod Dinosaurs: Understanding the Life of Giants*. Indiana
1010 University Press, Bloomington, 34–56.
- 1011 Goebel, L.A., 1936. A correlation of the "forests" in the Petrified Forest National Monument.
1012 Unpublished National Park Service Report, 1–13.
- 1013 Good, S.C., 1998. Freshwater bivalve fauna of the Late Triassic (Carnian–Norian) Chinle,
1014 Dockum, and Dolores formations of the southwest United States. In: P.A. Johnson and
1015 J.W. Haggart (Editors), *Bivalves: an Eon of Evolution - Paleobiological Studies*
1016 Honoring Norman D. Newell. University of Calgary Press, Calgary, pp. 223–249.
- 1017 Gottesfeld, A.S., 1972a. Paleoecology of the lower part of the Chinle Formation. *Museum of*
1018 *Northern Arizona Bulletin* 47, 59–73.
- 1019 Gottesfeld, A.S., 1972b. Palynology of the Chinle Formation. *Museum of Northern Arizona*
1020 *Bulletin* 47 (Supplement), 13–18.
- 1021 Gottesfeld, A.S., 1975. Upper Triassic palynology of the southwestern United States. PhD
1022 Thesis, University of California, Berkeley, Berkeley, CA, 219 pp.
- 1023 Gottesfeld, A.S., 1980. Upper Triassic palynofloras of the western United States. *Proceedings*
1024 *of the IV International Palynological Conference, Lucknow, 2*, 295–308.
- 1025 Gregory, J.T., 1957. Significance of fossil vertebrates for correlation of Late Triassic
1026 continental deposits of North America, XX Congreso Geológico Internacional, Sección II
1027 - El Mesozoico del Hemisferio Occidental y sus Correlaciones Mundiales. *International*
1028 *Geological Congress, Mexico City*, pp. 7–25.

- 1029 Heckert, A.B., 2006. Geographic and stratigraphic distribution of the enigmatic Upper
1030 Triassic (Adamanian: Carnian) vertebrate fossil *Colognathus obscurus* Case. Museum of
1031 Northern Arizona Bulletin 62, 155–156.
- 1032 Heckert, A.B., Jenkins, H.S., 2005. The microvertebrate fauna of the Upper Triassic
1033 (Revueltian) Snyder Quarry, north-central New Mexico. New Mexico Geological Society
1034 Guidebook 56, 319–334.
- 1035 Heckert, A.B., Zeigler, K.E., Lucas, S.G., Rinehart, L.F., 2003. Coelophysids
1036 (Dinosauria: Theropoda) from the Upper Triassic (Revueltian) Snyder Quarry. New
1037 Mexico Museum of Natural History and Science Bulletin 24, 127–132.
- 1038 Heckert, A.B., Lucas, S.G., Sullivan, R.M., Hunt, A.P., Spielmann, J.A., 2005. The vertebrate
1039 fauna of the Upper Triassic (Revueltian: early–mid Norian) Painted Desert Member
1040 (Petrified Forest Formation: Chinle Group) in the Chama Basin, northern New Mexico.
1041 New Mexico Geological Society Guidebook 56, 302–318.
- 1042 Heckert, A.B., Lucas, S.G., Rinehart, L.F., Hunt, A.P., 2008. A new genus and species of
1043 sphenodontian from the Ghost Ranch *Coelophysis* Quarry (Upper Triassic: Apachean),
1044 Rock Point Formation, New Mexico, USA. Palaeontology 51, 827–845.
- 1045 Helby, R., Morgan, R., Partridge, A.D., 1987. A palynological zonation of the Australian
1046 Mesozoic. Memoirs of the Association of Australasian Palaeontologists 4, 1–94.
- 1047 Hodych, J.P., Dunning, G.R., 1992. Did the Manicouagan impact trigger end-of-Triassic mass
1048 extinction? Geology 20, 51–54.
- 1049 Holland, S.M., 2003. Analytic Rarefaction. <http://www.uga.edu/strata/software/>.
- 1050 Hummel, J., Gee, C.T., Südekum, K.-H., Sander, P.M., Nogge, G., Clauss, M., 2008. *In vitro*
1051 digestibility of fern and gymnosperm foliage: implication for sauropod feeding ecology
1052 and diet selection. Proceedings of the Royal Society B 275, 1015–1021.

- Hunt, A.P., Lucas, S.G., Heckert, A.B., 2005. Definition and correlation of the Lamayan: a new biochronological unit for the nonmarine late Carnian (Late Triassic). New Mexico Geological Society Guidebook 56, 357–366.
- Irmis, R.B., 2005. The vertebrate fauna of the Upper Triassic Chinle Formation in northern Arizona. Mesa Southwest Museum Bulletin 9, 63–88.
- Irmis, R.B., 2011. Evaluating hypotheses for the early diversification of dinosaurs. Earth and Environmental Science Transactions of the Royal Society of Edinburgh 101, 397–426.
- Irmis, R.B., Nesbitt, S.J., Padian, K., Smith, N.D., Turner, A.H., Woody, D., Downs, A., 2007. A Late Triassic dinosauromorph assemblage from New Mexico and the rise of dinosaurs. Science 317, 358–361.
- Irmis, R.B., Martz, J.W., Parker, W.G., Nesbitt, S.J., 2010. Re-evaluating the correlation between Late Triassic terrestrial vertebrate biostratigraphy and the GSSP-defined marine stages. Albertiana 38, 40–52.
- Irmis, R.I., Mundil, R., Martz, J.W., Parker, W.G., 2011. High-resolution U-Pb ages from the Upper Triassic Chinle Formation (New Mexico, USA) support a diachronous rise of dinosaurs. Earth and Planetary Science Letters 309, 258–267.
- Kelber, K.-P., van Konijnenburg-van Cittert, J.H.A., 1998. *Equisetites arenaceus* from the Upper Triassic of Germany with evidence for reproductive strategies. Review of Palaeobotany and Palynology 100, 1–26.
- Kent, D.V., Tauxe, L., 2005. Corrected Late Triassic latitudes for continents adjacent to the North Atlantic. Science 307, 240–244.
- Kent, D.V., Irving, E., 2010. Influence of inclination error in sedimentary rocks on the Triassic and Jurassic apparent pole wander path for North America and implications for Cordilleran tectonics. Journal of Geophysical Research 115, B10103, 1–25.

- 1077 Kent, D.V., Santi Malnis, P., Colombi, C.E., Alcober, O.A., Martínez, R.N., 2014. Age
1078 constraints on the dispersal of dinosaurs in the Late Triassic from magnetostratigraphy of
1079 the Los Colorados Formation (Argentina). *Proceedings of the National Academy of*
1080 *Sciences* 111, 7958–7963.
- 1081 Koeven, K., Irmis, R.B., Chan, M., 2012. Diagenetic iron oxide concretions associated with
1082 vertebrate fossils in the Upper Triassic Chinle Formation of northern New Mexico:
1083 implications for paleoenvironmental and diagenetic history. *Geological Society of*
1084 *America Abstracts with Programs* 44, 604.
- 1085 Krassilov, V.A., Ash, S.R., 1988. On *Dinophyton*-protognetalean Mesozoic plant.
1086 *Palaeontographica B* 208, 33–38.
- 1087 Kraus, M.J., Middleton, L.T., 1987. Dissected paleotopography and base-level changes in a
1088 Triassic fluvial sequence. *Geology* 15, 18–21.
- 1089 Kürschner, W.M., Herengreen, G.F.W., 2010. Triassic palynology of central and northwestern
1090 Europe: a review of palynofloral diversity patterns and biostratigraphic subdivisions.
1091 *Geological Society of London Special Publication* 334, 263–283.
- 1092 Langer, M.C., 2005. Studies on continental Late Triassic tetrapod biochronology. II. The
1093 Ischigualastian and a Carnian global correlation. *Journal of South American Earth*
1094 *Sciences* 19, 219–239.
- 1095 Litwin, R.J., 1985. Fertile organs and in situ spores of ferns from the Late Triassic Chinle
1096 Formation of Arizona and New Mexico, with discussion of the associated dispersed
1097 spores. *Review of Palaeobotany and Palynology* 44, 101–146.
- 1098 Litwin, R.J., 1986. The palynostratigraphy and age of the Chinle and Moenave formations,
1099 southwestern U.S.A. PhD dissertation, Pennsylvania State University, State College, PA,
1100 266 pp.

- 1101 Litwin, R.J., Ash, S.R., 1993. Revision of the biostratigraphy of the Chatham Group (Upper
1102 Triassic), Deep River Basin, North Carolina, USA. Review of Palaeobotany and
1103 Palynology 77, 75–95.
- 1104 Litwin, R.J., Skog, J.E., 1991. Morphology and palynostratigraphy of the Genus
1105 *Camerosporites* Leschik 1956. Palynology 15, 5–28.
- 1106 Litwin, R.J., Traverse, A., Ash, S.R., 1991. Preliminary palynological zonation of the Chinle
1107 Formation, southwestern U.S.A., and its correlation to the Newark Supergroup (eastern
1108 U.S.A.). Review of Palaeobotany and Palynology 68, 269–287.
- 1109 Litwin, R.J., Smoot, J.P., Weems, R.E., 1993. *Froelichsporites* gen. nov. - a biostratigraphic
1110 marker palynomorph of Upper Triassic continental strata in the conterminous U.S.
1111 Palynology 17, 157–168.
- 1112 Long, R.A., Murry, P.A., 1995. Late Triassic (Carnian and Norian) tetrapods from the
1113 southwestern United States. New Mexico Museum of Natural History & Science Bulletin
1114 4, 1–254.
- 1115 Long, R.A., Padian, K., 1986. Vertebrate biostratigraphy of the Late Triassic Chinle
1116 Formation, Petrified Forest National Park, Arizona: preliminary results. In: K. Padian
1117 (Editor), The Beginning of the Age of Dinosaurs: Faunal Changes Across the Triassic–
1118 Jurassic Boundary. Cambridge University Press, Cambridge, pp. 161–169.
- 1119 Looy, C.V., Brugman, W.A., Dilcher, D.L., Visscher, H., 1999. The delayed resurgence of
1120 equatorial forest after the Permian–Triassic ecologic crisis. Proceedings of the National
1121 Academy of Sciences 96, 13857–13862.
- 1122 Looy, C.V., Twitchett, R.J., Dilcher, D.L., Van Konijnenburg-Van Cittert, J.H.A., Visscher,
1123 H., 2001. Life in the end-Permian dead zone. Proceedings of the National Academy of
1124 Sciences 98, 7879–7883.

- 1125 Lucas, S.G., 1993. The Chinle Group: revised stratigraphy and biochronology of Upper
1126 Triassic nonmarine strata in the western United States. Museum of Northern Arizona
1127 Bulletin 59, 27–50.
- 1128 Lucas, S.G., 1997. Upper Triassic Chinle Group, western United States: a nonmarine standard
1129 for Late Triassic time. In: J.M. Dickins (Editor), Late Palaeozoic and Early Mesozoic
1130 Circum-Pacific Events and Their Global Correlation. Cambridge University Press,
1131 Cambridge, pp. 209–228.
- 1132 Lucas, S.G., 1998. Global Triassic tetrapod biostratigraphy and biochronology.
1133 Palaeogeography, Palaeoclimatology, Palaeoecology 143, 347–384.
- 1134 Lucas, S.G., Zeigler, K.E., Heckert, A.B., Hunt, A.P., 2003. Upper Triassic stratigraphy and
1135 biostratigraphy, Chama Basin, north-central New Mexico. New Mexico Museum of
1136 Natural History and Science Bulletin 24, 15–39.
- 1137 Lucas, S.G., Hunt, A.P., Heckert, A.B., Spielmann, J.A., 2007. Global Triassic tetrapod
1138 biostratigraphy and biochronology: 2007 status. New Mexico Museum of Natural History
1139 and Science Bulletin 41, 229–240.
- 1140 Lucas, S.G., Tanner, L.H., Kozur, H.W., Weems, R.E., Heckert, A.B., 2012. The Late
1141 Triassic timescale: age and correlation of the Carnian–Norian boundary. Earth-Science
1142 Reviews 114, 1–18.
- 1143 Martz, J.W., Parker, W.G., 2010. Revised lithostratigraphy of the Sonsela Member (Chinle
1144 Formation, Upper Triassic) in the southern part of Petrified Forest National Park,
1145 Arizona. PLoS One 5, e9329, 1–26.
- 1146 McElwain, J.C., Popa, M.E., Hesselbo, S.P., Haworth, M., Suryk, F., 2007. Macroecological
1147 responses of terrestrial vegetation to climatic and atmospheric change across the
1148 Triassic/Jurassic boundary in East Greenland. Paleobiology 33, 547–573.

- 1149 Mundil, R., 2007. Critical view of the calibration of the Triassic time scale. New Mexico
1150 Museum of Natural History and Science Bulletin 41, 314–315.
- 1151 Mundil, R., Pálffy, J., Renne, P.R., Brack, P., 2010. The Triassic time scale: new constraints
1152 and a review of geochronological data. Geological Society of London Special Publication
1153 334, 41–60.
- 1154 Murry, P.A., Long, R.A., 1989. Geology and paleontology of the Chinle Formation, Petrified
1155 Forest National Park and vicinity, Arizona and a discussion of vertebrate fossils of the
1156 southwestern Upper Triassic. In: S.G. Lucas and A.P. Hunt (Editors), Dawn of the Age of
1157 Dinosaurs in the American Southwest. New Mexico Museum of Natural History,
1158 Albuquerque, pp. 29–64.
- 1159 Muttoni, G., Kent, D.V., Olsen, P.E., Di Stefano, P., Lowrie, W., Bernasconi, S.M.,
1160 Hernández, F.M., 2004. Tethyan magnetostratigraphy from Pizzo Mondello (Sicily) and
1161 correlation to the Late Triassic Newark astrochronological polarity time scale. Geological
1162 Society of America Bulletin 116, 1043–1058.
- 1163 Muttoni, G., Kent, D.V., Jadoul, F., Olsen, P.E., Rigo, M., Galli, M.T., Nicora, A., 2010.
1164 Rhaetian magneto-biostratigraphy from the southern Alps (Italy): constraints on Triassic
1165 chronology. Palaeogeography, Palaeoclimatology, Palaeoecology 285, 1–16.
- 1166 Nesbitt, S.J., 2007. The anatomy of *Effigia okeeffeae* (Archosauria, Suchia), theropod-like
1167 convergence, and the distribution of related taxa. Bulletin of the American Museum of
1168 Natural History 302, 1–84.
- 1169 Nesbitt, S.J., Irmis, R.B., Parker, W.G., 2007. A critical re-evaluation of the Late Triassic
1170 dinosaur taxa of North America. Journal of Systematic Palaeontology 5, 209–243.
- 1171 Nesbitt, S.J., Smith, N.D., Irmis, R.B., Turner, A.H., Downs, A., Norell, M.A., 2009a. A
1172 complete skeleton of a Late Triassic saurichian and the early evolution of dinosaurs.
1173 Science 326, 1530–1533.

- 1174 Nesbitt, S.J., Stocker, M.R., Small, B.J., Downs, A., 2009b. The osteology and relationships
1175 of *Vancleavea campi* (Reptilia: Archosauriformes). *Zoological Journal of the Linnean*
1176 *Society* 157, 814–864.
- 1177 Nesbitt, S.J., Irmis, R.B., Parker, W.G., Smith, N.D., Turner, A.H., Rowe, T., 2009c.
1178 Hindlimb osteology and distribution of basal dinosauiromorphs from the Late Triassic of
1179 North America. *Journal of Vertebrate Paleontology* 29, 498–516.
- 1180 NMBGMR, 2003. *Geologic Map of New Mexico*, 1:500,000. New Mexico Bureau of
1181 *Geology and Mineral Resources*, Socorro.
- 1182 Ogg, J.G., 2005. The Triassic Period. In: F.M. Gradstein, J.G. Ogg and A.G. Smith (Editors),
1183 *A Geologic Time Scale 2004*. Cambridge University Press, Cambridge, pp. 271–306.
- 1184 Ogg, J.G., 2012. Triassic. In: F.M. Gradstein, J.G. Ogg, M.D. Schmitz and G.M. Ogg
1185 (Editors), *The Geologic Time Scale 2012*. Elsevier, Amsterdam, pp. 681–730.
- 1186 Olsen, P.E., Flynn, J.J., 1989. Field guide to the vertebrate paleontology of Late Triassic age
1187 rocks in the southwestern Newark Basin (Newark Supergroup, New Jersey and
1188 Pennsylvania). *The Mosasaur* 4, 1–44.
- 1189 Olsen, P.E., Kent, D.V., Whiteside, J.H., 2011. Implications of the Newark Supergroup-based
1190 astrochronology and geomagnetic polarity time scale (Newark-APTS) for the tempo and
1191 mode of the early diversification of the Dinosauria. *Earth and Environmental Science*
1192 *Transactions of the Royal Society of Edinburgh* 101, 201–229.
- 1193 Olsen, P., Kent, D.V., Whiteside, J.H., Reid, J.C., Taylor, K.B., 2014. Chronostratigraphic
1194 context of the biotic assemblages of the Dan River-Danville and Deep River basins
1195 (Newark Supergroup, Virginia and North Carolina, USA). *Geological Society of America*
1196 *Abstracts with Programs* 46, 20.
- 1197 Onoue, T. et al., Sato, H., Nakamura, T., Noguchi, T., Hidaka, Y., Shirai, N., Ebihara, M.,
1198 Osawa, T., Hatsukawa, Y., Toh, Y., Koizumi, M., Harada, H., Orchard, M.J., Nedachi,

- 1199 M., 2012. Deep-sea record of impact apparently unrelated to mass extinction in the Late
1200 Triassic. *Proceedings of the National Academy of Sciences* 109, 19134–19139.
- 1201 Parker, W.G., 2006. The stratigraphic distribution of major fossil localities in Petrified Forest
1202 National Park, Arizona. *Museum of Northern Arizona Bulletin* 62, 46–61.
- 1203 Parker, W.G., Martz, J.W., 2011. The Late Triassic (Norian) Adamanian–Revueltian tetrapod
1204 faunal transition in the Chinle Formation of Petrified Forest National Park, Arizona.
1205 *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 101,
1206 231–260.
- 1207 Parker, W.G., Irmis, R.B., Nesbitt, S.J., Martz, J.W., Browne, L.S., 2005. The Late Triassic
1208 pseudosuchian *Revueltasaurus callenderi* and its implications for the diversity of early
1209 ornithischian dinosaurs. *Proceedings of the Royal Society of London, Biological Sciences*
1210 272, 963–969.
- 1211 Pedersen, K.R., Crane, P.R., Friis, E.M., 1989. Pollen organs and seeds with *Eucommiidites*
1212 pollen. *Grana* 28, 279–294.
- 1213 Petersen, H.I., Lindström, S., 2012. Synchronous wildfire activity rise and mire deforestation
1214 at the Triassic–Jurassic boundary. *PLoS ONE* 7, e47236.
- 1215 Pritchard, A.C., Turner, A.H., Nesbitt, S.J., Irmis, R.B., Smith, N.D., 2012. A new
1216 drepanosaurid from the Late Triassic of New Mexico: insights into the forelimb evolution
1217 and biogeography of drepanosaurs. *Journal of Vertebrate Paleontology* 32 (Online
1218 Supplement), 158.
- 1219 Pritchard, A.C., Turner, A.H., Nesbitt, S.J., Irmis, R.B., Smith, N.D., 2015. Late Triassic
1220 tanystropheids (Reptilia, Archosauromorpha) from northern New Mexico (Petrified
1221 Forest Member, Chinle Formation) and the biogeography, functional morphology, and
1222 evolution of Tanystropheidae. *Journal of Vertebrate Paleontology* 35(2), e911186.

- Ramezani, J., Bowring, S.A., Pringle, M.S., Winslow, F.D., III, Rasbury, E.T., 2005. The Manicouagan impact melt rock: a proposed standard for intercalibration of U-Pb and $^{40}\text{Ar}/^{39}\text{Ar}$ isotopic systems, 15th V.M. Goldschmidt Conference Abstract Volume, Moscow, ID, pp. A321.
- Ramezani, J., Hoke, G.D., Fastovsky, D.E., Bowring, S.A., Therrien, F., Dworkin, S.I., Atchley, S.C., Nordt, L.C., 2011. High-precision U-Pb zircon geochronology of the Late Triassic Chinle Formation, Petrified Forest National Park (Arizona, USA): Temporal constraints on the early evolution of dinosaurs. *Geological Society of America Bulletin* 123, 2142–2159.
- Raup, D.M., 1975. Taxonomic diversity estimation using rarefaction. *Paleobiology* 1, 333–342.
- Rayfield, E.J., Barrett, P.M., McDonnell, R.A., Willis, K.J., 2005. A Geographical Information System (GIS) study of Triassic vertebrate biochronology. *Geological Magazine* 142, 327–354.
- Reichgelt, T., Parker, W.G., Martz, J.W., Conran, J.G., van Konijnenburg-van Cittert, J.H.A., Kürschner, W., 2013. The palynology of the Sonsela Member (Late Triassic, Norian) at Petrified Forest National Park, Arizona, USA. *Review of Palaeobotany and Palynology* 189, 18–23.
- Renne, P.R., Mundil, R., Balco, G., Min, K., Ludwig, K.R., 2010. Joint determination of ^{40}K decay constants and $^{40}\text{Ar}/^{39}\text{Ar}$ geochronology. *Geochimica et Cosmochimica Acta* 74, 5349–5367.
- Renne, P.R., Deino, A.L., Hilgin, F.J., Kuiper, K.F., Mark, D.F., Mitchell, W.S., III, Morgan, L.E., Mundil, R., Smit, J., 2013. Time scales of critical events around the Cretaceous–Paleogene boundary. *Science* 339, 684–687.

- Riggs, N.R., Lehman, T.M., Gehrels, G.E., Dickinson, W.R., 1996. Detrital zircon link between headwaters and terminus of the Upper Triassic Chinle-Dockum paleoriver system. *Science* 273, 97–100.
- Riggs, N.R., Ash, S.R., Barth, A.P., Gehrels, G.E., Wooden, J.L., 2003. Isotopic age of the Black Forest Bed, Petrified Forest Member, Chinle Formation, Arizona: an example of dating a continental sandstone. *Geological Society of America Bulletin* 115, 1315–1323.
- Roadifer, J.E., Joseph F. Schreiber, J., Peabody, D.M., Kremp, G.O.W., Smiley, T.L., 1964. Preliminary investigations of the microenvironment of the Chinle Formation, Petrified Forest National Park, Arizona. University of Arizona Geochronology Laboratories Interim Research Report 3, 1–26.
- Rogers, R.R., Swisher, C.C., III, Sereno, P.C., Monetta, A.M, Forster, C.A., Martínez, R.N., 1993. The Ischigualasto tetrapod assemblage (Late Triassic, Argentina) and $^{40}\text{Ar}/^{39}\text{Ar}$ dating of dinosaur origins. *Science* 260, 794–797.
- Scott, R.A., 1982. Aspects of the palynology of the Chinle Formation (Upper Triassic), Colorado Plateau, Arizona, Utah, and New Mexico. U.S. Geological Survey Open-File Report 82–937, 1–19.
- Seff, P., 1966. Stratigraphy and paleo-environments of the Blue Mesa area, Petrified Forest National Park, Arizona. Unpublished National Park Service Report, pp. 1–43.
- Stewart, J.H., Poole, F.G., Wilson, R.F., 1972. Stratigraphy and origin of the Chinle Formation and related Upper Triassic strata in the Colorado Plateau region. U.S. Geological Survey Professional Paper 690, 1–336.
- Stewart, J.H., Anderson, T.H., Haxel, G.B., Silver, L.T., Wright, J.D., 1986. Late Triassic paleogeography of the southern Cordillera: the problem of a source for voluminous volcanic detritus in the Chinle Formation of the Colorado Plateau region. *Geology* 14, 567–570.

- 1272 Stone, J.F., 1978. Pollen and spores. Brigham Young University Geology Studies 25, 45–59.
- 1273 Sues, H.-D., Nesbitt, S.J., Berman, D.S., Henrici, A.C., 2011. A late-surviving basal theropod
1274 dinosaur from the latest Triassic of North America. Proceedings of the Royal Society of
1275 London, Biological Sciences 278, 3459–3464.
- 1276 Therrien, F., Fastovsky, D.E., 2000. Paleoenvironments of early theropods, Chinle Formation
1277 (Late Triassic), Petrified Forest National Park, Arizona. Palaios 15, 194–211.
- 1278 Tipper, J.C., 1979. Rarefaction and rarefaction-the use and abuse of a method in paleoecology.
1279 Paleobiology 5, 423–434.
- 1280 Traverse, A., 2007. Paleopalynology, Second Edition. Springer, Dordrecht, The Netherlands.
1281 ISBN 978-1-4020-5610-9 (e-book).
- 1282 Trendell, A.M., Atchley, S.C., Nordt, L.C., 2013. Facies analysis of a probable large-fluvial-
1283 fan depositional system: the Upper Triassic Chinle Formation at Petrified Forest National
1284 Park, Arizona, U.S.A. Journal of Sedimentary Research 83, 873–895.
- 1285 Vakhrameev, V.A., 1981. Pollen *Classopollis*: indicator of Jurassic and Cretaceous climate.
1286 Palaeobotanist 28–29, 301–307.
- 1287 Vakhrameev, V.A., 1991. Jurassic and Cretaceous floras and climate of the Earth. Cambridge
1288 University Press, Cambridge.
- 1289 Van Konijnenburg-van Cittert, J.H.A., 2002. Ecology of some Late Triassic to Early
1290 Cretaceous ferns in Eurasia. Review of Palaeobotany and Palynology 119, 113–124.
- 1291 Vidal, G. 1988. A palynological preparation method. Palynology 12, 215–220.
- 1292 Visscher, H., van der Zwan, C.J., 1981. Palynology of the circum-Mediterranean Triassic:
1293 phytogeographical and palaeoclimatological implications. Geologische Rundschau 70,
1294 625–634.

- 1295 Visscher, H., Van Houte, M., Brugman, W.A., Poort, R.J., 1994. Rejection of a Carnian (Late
1296 Triassic) “pluvial event” in Europe. *Review of Palaeobotany and Palynology* 83, 217–
1297 226.
- 1298 Visscher, H., Looy, C.V., Collinson, M.E., Brinkhuis, H., van Konijnenburg-van Cittert,
1299 J.H.A., Kürschner, W.M., Sephton, M.A., 2004. Environmental mutagenesis during the
1300 end-Permian ecological crisis. *Proceedings of the National Academy of Sciences* 101,
1301 12952–12956.
- 1302 Walkden, G., Parker, J., Kelley, S., 2002. A Late Triassic impact ejecta layer in southwestern
1303 Britain. *Science* 298, 2185–2188.
- 1304 Walker, M.V., Felton, J.B., 1935. Where did the trees grow? Unpublished National Park
1305 Service Report, 1–12.
- 1306 Whiteside, J.H., Grogan, D.S., Olsen, P.E., Kent, D.V., 2011. Climatically driven
1307 biogeographic provinces of Late Triassic tropical Pangea. *Proceedings of the National*
1308 *Academy of Sciences* 108, 8972–8977.
- 1309 Whiteside, J.H., Dunlavey, M., Lindström, S., Irmis, R.B., Kasprak, A.H., Glasspool, I.,
1310 Nesbitt, S., Smith, N., Turner, A., 2012. Continental ecosystem instability during the Late
1311 Triassic rise of dinosaurs. *American Geophysical Union Fall Meeting Abstract*, PP11C-
1312 2034.
- 1313 Whiteside, J.H., Lindström, S., Irmis, R.B., Glasspool, I.J., Schaller, M.F., Dunlavey, M.,
1314 Nesbitt, S.J., Smith, N.D., Turner, A.H. 2015. Extreme ecosystem instability suppressed
1315 tropical dinosaur dominance for 30 million years. *Proceedings of the National Academy*
1316 *of Sciences* 112, 7909–7913.
- 1317 Woody, D.T., 2006. Revised stratigraphy of the lower Chinle Formation (Upper Triassic) of
1318 Petrified Forest National Park, Arizona. *Museum of Northern Arizona Bulletin* 62, 17–
1319 45.

- Wotzlaw, J.-F., Guex, J., Bartolini, A., Gallet, Y., Krystyn, L., McRoberts, C.A., Taylor, D., Schoene, B., Schaltegger, U., 2014. Towards accurate numerical calibration of the Late Triassic: high-precision U-Pb geochronology constraints on the duration of the Rhaetian. *Geology* 42, 571–574.
- Zavada, M.S., 1990. The ultrastructure of three monosulcate pollen grains from the Triassic Chinle Formation, western United States. *Palynology* 14, 41–51.
- Zavialova, N., van Konijnenbrug-van Cittert, J., Zavada, M., 2009. The pollen structure of *Williamsoniella coronata* Thomas (Bennettitales) from the Bajocian of Yorkshire. *International Journal of Plant Sciences* 170, 1195–1200.
- Zeigler, K.E., 2003. Taphonomic analysis of the Snyder Quarry: a fire-related Upper Triassic vertebrate fossil assemblage from north-central New Mexico. *New Mexico Museum of Natural History and Science Bulletin* 24, 49–62.
- Zeigler, K.E., Geissman, J.W., 2011. Magnetostratigraphy of the Upper Triassic Chinle Group of New Mexico: implications for regional and global correlations among Upper Triassic sequences. *Geosphere* 7, 802–829.
- Zeigler, K.E., Lucas, S.G., Heckert, A.B., 2002. Taphonomy of the Late Triassic Lamy Amphibian Quarry (Garita Creek Formation: Chinle Group), central New Mexico. *New Mexico Museum of Natural History and Science Bulletin* 21, 279–283.
- Zeigler, K.E., Heckert, A.B., Lucas, S.G., 2003. The vertebrate fauna of the Upper Triassic (Revueltian) Snyder Quarry. *New Mexico Museum of Natural History and Science Bulletin* 24, 71–79.
- Zeigler, K.E., Kelley, S., Geissman, J.W., 2008. Revisions to stratigraphic nomenclature of the Upper Triassic Chinle Group in New Mexico: new insights from geologic mapping, sedimentology, and magnetostratigraphic/paleomagnetic data. *Rocky Mountain Geology* 43, 121–141.

Zhang, W., Grant-Mackie, J.A., 2001. Late Triassic–Early Jurassic palynofloral assemblages from Murihiku strata of New Zealand, and comparisons with China. *Journal of the Royal Society of New Zealand* 31, 575–683.

Captions

Fig. 1. a) Palaeogeographical map of Pangaea during the Norian Stage of the Upper Triassic (modified from Blakey, 2011). Star shows location of present-day New Mexico, United States. b) Map of Triassic outcrops in New Mexico (modified from Irmis et al., 2011). GR= Ghost Ranch.

Fig. 2. Semi-quantitative range chart of spore-pollen taxa for the Chinle Formation in the Chama Basin. Composite stratigraphic column modified from Irmis et al. (2007). The locations of the Hayden Quarry sections (H2-4; from Whiteside et al. 2015), as well as that of the sample radioisotopically dated to 211.9 ± 0.7 Ma (Irmis et al., 2011), are marked on the composite stratigraphic column in Fig. 3.

Fig. 3. Quantitative stratigraphic palynology for the Chinle Formation in the Chama Basin, arranged in groups after known or hypothesized plant affinity according to Table 1. Note the differences in abundance scale. tri* = trilete. The position of the Hayden Quarry sections is marked on the composite stratigraphic column with H2, H3 and H4, respectively (from Whiteside et al. 2015). SQ = Snyder Quarry. CaQ = Canjilon Quarry. CoQ = *Coelophysis* Quarry. In addition, the location of the sample radioisotopically dated to 211.9 ± 0.7 Ma (Irmis et al., 2011) is marked by a star.

Fig. 4. Diversity, first and last occurrences of pollen and spores within the succession for the Chinle Formation in the Chama Basin. A) Taxonomic diversity; black line shows the range-through diversity, red line shows the taxonomic richness for each sample. B) Extinction and origination based on last and first occurrences, respectively.

Fig. 5. Rarefaction plots of taxonomic richness for palynomorph assemblages from each member of the Chinle Formation in the Chama Basin.

Fig. 6. Correlation of Chinle members and palynoevents across the western United States.

Geochronological ages after ¹Ramezani et al. (2011), ²Irmis et al. (2011), and ³Atchley et al. (2013). Palynological data after this study, ⁴Litwin et al. (1991), and ⁵Reichgelt et al. (2013). B.W.C. = Bluewater Creek Member. Please note that no palynological information exists for the lowermost part of the Chinle Formation in the Arizona succession.

Fig. 7. Correlation of the Chinle Formation in the Chama Basin with the Newark Supergroup in eastern North America and northwestern Europe. Newark Supergroup palynodata compiled from Cornet (1977, 1993), Litwin et al. (1991), and Litwin and Ash (1993). European palynodata compiled from Kürscher and Herngreen (2010).

Table 1. Hypothesized plant affinities and ecological preferences.

Figure 1

Figure 2a

Figure 2 (part 1)

Figure 2b

Figure 2 (part 2)

Figure 3

Figure 4

Figure 5

Figure 6

Figure 7

Table 1. Probable plant affinities and ecological preference

Taxa	Plant affinity	Comments on <i>In situ</i> occurrence (* in Chinle floras)	Habit
<i>Alisporites</i> spp.	Seed fern, Corystosperm	<i>Alisporites</i> pollen have been recovered from a variety of corystospermous reproductive structures (see Balme, 1995 for references).	Canopy
<i>Alisporites opii</i>	Seed fern, Corystosperm	Balme (1995) remarked that the structure and, hence, probably affinity of <i>Alisporites opii</i> remains unresolved. It is here tentatively included in Corystosperms.	Canopy
<i>Alisporites robustus</i>	Seed fern, Corystosperm	See under <i>Alisporites</i> spp.	Canopy
<i>Alisporites thomasi</i>	Seed fern, Corystosperm	See under <i>Alisporites</i> spp.	Canopy
<i>Alisporites toralis</i>	Seed fern, Corystosperm or Voltziales	<i>Willsiostrobus cordiformis</i> (Grauvogel-Stamm) Grauvogel-Stamm et Schaarschmidt 1978	Canopy
<i>Chordasporites</i> spp.	Seed fern, Corystosperm	Tentatively included in Corystosperms. No <i>In situ</i> occurrences.	Canopy
<i>Falcisporites australis</i>	Seed fern, Corystosperm	<i>Falcisporites</i> pollen have been recovered from a variety of corystospermous reproductive structures (see Balme, 1995 for references).	Canopy
<i>Sulcosaccisporites alaticonformis</i>	Seed fern	This form taxon may include aberrant forms of bisaccate pollen.	? Canopy
<i>Vitreisporites bjuvensis</i>	Seed fern, Caytoniales	See under <i>Vitreisporites pallidus</i> .	Canopy
<i>Vitreisporites pallidus</i>	Seed fern, Caytoniales	<i>Caytonanthus arberi</i> (Thomas) Harris 1941, see references in Balme (1995).	Canopy
<i>Vitreisporites</i> sp.	Seed fern, Caytoniales	See under <i>Vitreisporites pallidus</i> .	Canopy
<i>Platysaccus triassicus</i>	Seed fern or Conifer		Canopy
<i>Platysaccus</i> spp.	Seed fern or Conifer		Canopy
<i>Protodiploxypinus americus</i>	Seed fern or Conifer	* <i>Pramelreuthia dubielii</i> Ash and Litwin 1996, placed under Probable Coniferales by Balme (1995).	Canopy
<i>Protodiploxypinus doubingerii</i>	Seed fern or Conifer	No known <i>In situ</i> occurrences.	Canopy
<i>Protodiploxypinus fastidioides</i>	Seed fern or Conifer	No known <i>In situ</i> occurrences.	Canopy
<i>Protodiploxypinus</i> sp.	Seed fern or Conifer	No known <i>In situ</i> occurrences.	Canopy
<i>Araucaricites</i> sp.	Conifer, Pinales, Araucariaceae		Canopy
<i>Callialasporites</i> sp. cf. <i>C. dampieri</i>	Conifer, Pinales, Araucariaceae		Canopy
<i>Camerosporites secatus</i>	Conifer, Pinales, Cheirolepidiaceae	No known <i>In situ</i> occurrences, but included in the Cheirolepidiaceae due to morphological similarity to <i>Classopollis</i> .	Canopy
<i>Camerosporites verrucosus</i>	Conifer, Pinales, Cheirolepidiaceae	No known <i>In situ</i> occurrences, but included in the Cheirolepidiaceae due to morphological similarity to <i>Classopollis</i> .	Canopy
<i>Classopollis torosus</i>	Conifer, Pinales, Cheirolepidiaceae	<i>Hirmeriella muensterii</i> (Schenk) Jung 1968	Canopy
<i>Cordaitina minor</i>	Conifer		Canopy
<i>Potonieisporites</i> spp.	Conifer		Canopy
<i>Duplicisporites granulatus</i>	Conifer, Pinales, Cheirolepidiaceae	No known <i>In situ</i> occurrences, but included in the Cheirolepidiaceae due to morphological similarity to <i>Classopollis</i> .	Canopy
<i>Patinasporites densus</i>	Conifer, Voltziales, Majonicaceae	<i>Glyptolepis</i> Schimper 1872, see discussion in Axsmith and Taylor 1997.	Canopy
<i>Enzonalasporites vigena</i>	Conifer, Voltziales, ? Majonicaceae	Tentatively included in Majonicaceae due to morphological resemblance to <i>Patinasporites</i> .	Canopy

<i>Enzonalasporites</i> spp.	Conifer, Voltziales, ? Majonicaceae	Tentatively included in Majonicaceae due to morphological resemblance to <i>Patinasporites</i> .	Canopy
<i>Inaperturopollenites</i> spp.	Conifer, Araucariaceae		Canopy
<i>Klausipollenites gouldii</i>	Conifer, ?Voltziales, ?Voltziaceae		Canopy
<i>Lueckisporites</i> sp.	Conifer, Voltziales, Majonicaceae		Canopy
<i>Lunatisporites</i> sp.	Conifer, Voltziales, Voltziaceae		Canopy
<i>Minutosaccus crenulatus</i>	Conifer		Canopy
<i>Ovalipollis ovalis</i>	?Conifer		Canopy
<i>Podosporites</i> “granulatus”	Conifer		Canopy
<i>Podocarpidites</i> spp.	Conifer, Pinales, Podocarpaceae		Canopy
<i>Pseudoenzonalasporites summus</i>	Conifer		Canopy
<i>Samaropollenites speciosus</i>	Conifer	Balme (1995) commented that <i>in situ</i> pollen from <i>Dinophyton spinosum</i> Ash 1970, originally referred to <i>Alisporites</i> by Krassilov and Ash (1988) more closely resemble <i>Samaropollenites</i> .	Canopy
<i>Spheripollenites</i> spp.	Conifer		Canopy
<i>Triadispora</i> spp.	Conifer, Voltziaceae		Canopy
<i>Triadospora verrucata</i>	Conifer, Voltziaceae		Canopy
<i>Vallasporites ignacii</i>	Conifer, Voltziales, ? Majonicaceae	Tentatively included in Majonicaceae due to morphological resemblance to <i>Patinasporites</i> .	Canopy
<i>Cycadopites</i> spp.	Cycad/Ginkgo/Bennettitales		Canopy
<i>Cycadopites stonei</i>	Cycad/Ginkgo/Bennettitales	Granulate monosulcate pollen grains similar to <i>Granamonocolpites luisae</i> Herbst have been found <i>in situ</i> in a Middle Jurassic <i>Williamsoniella coronata</i> , which is of Bennettitalean affinity (Zavialova et al. 2009)	Canopy
<i>Ephedripites</i> spp.	Gnetopsids, Ephedrales		Understory
<i>Equisetosporites chinleanus</i>	Gnetopsids, Ephedrales	* <i>Masculostrobus clathratus</i> Ash 1972	Understory
<i>Eucommiidites/Pretricolpites</i>	Erdtmanithecales	The morphologically similar genus <i>Eucommiidites</i> has been recovered from	Canopy
<i>Lagenella martini</i>	Gnetopsids, Ephedrales		Understory
<i>Monosulcites</i> sp. cf. <i>M. minimus</i>	Cycad/Ginkgo/Bennettitales/Peltasperms	<i>Monosulcites minimus</i> has been found <i>in situ</i> in the bennettitalean <i>Vardekloeftia sulcata</i> Harris 1932, by Pedersen et al. 1989.	Canopy
<i>Monosulcites</i> sp. A	Cycad/Ginkgo/Bennettitales/Peltasperms		Canopy
<i>Monosulcites</i> spp.	Cycad/Ginkgo/Bennettitales/Peltasperms		Canopy
<i>Colpectopollis ellipsoideus</i>	Unknown gymnosperm		
<i>Heliosaccus dimorphus</i>	Unknown gymnosperm		
<i>Quadraesporites anellaeformis</i>	Unknown gymnosperm		
<i>Retisulcites perforatus</i>	Unknown gymnosperm		
<i>Gordonispora fossulata</i>	Bryophyte		Ground cover
<i>Nevesisporites</i> sp.	Bryophyte		Ground cover
<i>Retusotriletes</i> sp.	Bryophyte		Ground cover

<i>Calamospora</i> spp.	Sphenopsids, Equisetales	Triassic <i>in situ</i> occurrence include <i>Echinostachys cylindrical</i> Schimper et Mougeot 1844, <i>E. oblongus</i> Brongniart 1828, <i>E. verticillata</i> Grauvogel-Stamm 1978, <i>Equisetostachys nathorstii</i> Halle 1908, <i>E. suecicus</i> (Nathorst) Halle 1908, and <i>Schizoneura harrisii</i> Ash 1985. (See Balme, 1995 for references)	Ground cover
<i>Aratrisporites</i> sp.	Lycopod, Isoetales, Pleuromeiaceae	(See Balme, 1995)	Ground cover
<i>Limbosporites</i> sp.	Lycopod	No known <i>In situ</i> occurrences.	Ground cover
<i>Uvaesporites</i> sp.	Lycopod, Selaginellales	<i>Uvaesporites</i> has been found <i>in situ</i> in <i>Selaginellites hallei</i> Lundblad 1950. See Balme (1995) for references.	Ground cover
<i>Anapiculatisporites</i> sp.	Fern or Lycopod	(See Balme, 1995)	Ground cover
<i>Cyclogranisporites</i> spp.	Fern, Osmundaceae		Ground cover
<i>Deltoidopora</i> spp.	Fern, Dipteridaceae, Dicksoniaceae, Matoniaceae, Cyathaceae	This taxon has e.g. been found <i>in situ</i> in the Triassic-Jurassic dipterids <i>Dictyophyllum exile</i> (Braun) Nathorst 1978, <i>Thaumatopteris brauniana</i> Popp 1863, and <i>Thaumatopteris schenkii</i> Nathorst 1878. See Balme (1995) and van Konijnenburg-van Cittert (2002) for additional <i>in situ</i> occurrences.	Ground cover/ Understory
<i>Dictyophyllidites mortonii/harrisii</i>	Fern, Matoniaceae	* <i>Phlebopteris smithii</i> (Daugherty) Arnold 1947 emend. Ash et al. 1982	Ground cover
<i>Gleicheniidites</i> sp. cf. <i>G. senonicus</i>	Fern, Gleicheniaceae	No Triassic <i>in situ</i> occurrence, but from the Jurassic in <i>Gleichenites nitida</i> Harris 1931.	Ground cover
<i>Granulatisporites infirmus</i>	Fern, Dipteridaceae	* <i>Clathropteris walkeri</i> Daugherty 1941	Ground cover
<i>Iraqispora</i> “granulatus”	Fern	No known <i>In situ</i> occurrences.	Ground cover
<i>Iraqispora laevigata</i>	Fern	No known <i>In situ</i> occurrences.	Ground cover
<i>Iraqispora speciosa</i>	Fern	No known <i>In situ</i> occurrences.	Ground cover
<i>Laevigatosporites</i> spp.	Fern, Marattiales	(See Balme, 1995)	Ground cover
<i>Osmundacidites</i> sp.	Fern, Osmundaceae	* <i>Todites fragilis</i> Daugherty emend. Litwin 1985	Ground cover
<i>Polypodiisporites</i> spp.	Fern, Schizaceae, Polypodiaceae	(See Balme, 1995)	Ground cover
<i>Punctatisporites globosus</i>	Fern, Osmundaceae	(See Balme, 1995)	Ground cover
<i>Punctatisporites</i> spp.	Fern, Osmundaceae	* <i>Wingatea plumosa</i> (Daugherty) Litwin 1985	Ground cover
<i>Reticulatisporites</i> spp.	Fern	Carboniferous <i>in situ</i> occurrences are ferns of uncertain order (Balme, 1995).	Ground cover
<i>Retitriteles</i> sp. cf. <i>R. austroclavatidites</i>	Fern	No known <i>In situ</i> occurrences.	Ground cover
<i>Thymospora</i> spp.	Fern, Marattiales	(See Balme, 1995)	Ground cover
<i>Verrucosisporites</i> spp.	Fern, ? Osmundaceae	No known <i>In situ</i> occurrences.	Ground cover
<i>Froelichsporites traversei</i>	Unknown	No known <i>In situ</i> occurrences.	
<i>Playfordiaspora cancellosa</i>	Unknown	No known <i>In situ</i> occurrences.	