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)

Sofie Lindström[a*], Randall B. Irmis[b], Jessica H. Whiteside[c], Nathan D. Smith[d], Sterling J. Nesbitt[e], and Alan H. Turner[f]

[a] Geological Survey of Denmark and Greenland, Øster Voldgade 10, DK-1350 Copenhagen K, DENMARK, sli@geus.dk

[b] Natural History Museum of Utah and Department of Geology & Geophysics, University of Utah, Salt Lake City, UT 84108-1214, USA

[c] Ocean and Earth Science, National Oceanography Centre Southampton, University of Southampton, European Way, Southampton SO14 3ZH, UNITED KINGDOM

[d] Dinosaur Institute, Natural History Museum of Los Angeles County, Los Angeles, CA 90007, USA

[e] Department of Geosciences, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24601 USA

[f] Department of Anatomical Sciences, Stony Brook University, Stony Brook, New York 11794-8081, USA

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 (*Enzonalasporites, 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 poposauroids, 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*

bryansmalli, *Tawa hallae*, and *Daemonosaurus chauliodus*) (Irmis et al., 2007; Nesbitt et al., 2009a; Sues et al., 2011), and coelophysoid theropods (Colbert, 1989; Heckert et al., 2003; Irmis et al., 2007). Similar to other North American Triassic assemblages (Irmis, 2011), the Chama Basin lacks any evidence of sauropodomorph and ornithischian dinosaurs. Because sauropodomorph dinosaurs are abundant at coeval higher-paleolatitude localities in Europe and Gondwana, they reinforce ideas about faunal provincialism across Pangaea, perhaps controlled by climatic zones (Irmis et al., 2007; Nesbitt et al., 2009a; Ezcurra, 2010; Irmis, 2011; Whiteside et al., 2011; Kent et al., 2014). This hypothesis is supported by a recent high-resolution paleoclimate proxy dataset, which indicates that the Chama Basin during this time experienced an unpredictable arid climate that fluctuated between extremes within the context of pervasive wildfires and elevated and rising atmospheric pCO_2 (Whiteside et al., 2012, 2015).

One of the main sites in the Chama Basin that documents this paleoclimate and fossil record is the Hayden Quarry, which consists of three separate paleochannels in the lower part of the Petrified Forest Member (for more information on the Hayden Quarry see Downs, 2005; Irmis et al., 2007, 2011; Whiteside et al., 2015). Together, these deposits preserve abundant organic material suitable for isotopic analysis, fossil charcoal, and the single most diverse vertebrate fossil assemblage in the basin (Irmis et al., 2007; Whiteside et al., 2012, 2015). The abundant organic record preserved in the reduced (i.e. deposited under low-oxygen conditions) fine-grained sediments of these paleochannels makes them ideal for palynological sampling, and they comprise a significant proportion of the palynomorph samples presented here. Previous published palynological data from the Chama Basin are limited to a few isolated samples from the ‘siltstone’ member (Scott, 1982; Litwin et al., 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), Doher (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 *Brodispora 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 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 *Brodispora striata*, *Camerosporites secatus*, *Infernopollenites claustratus Lagenella martini*, and *Samaropollenites speciosus*, , the zone also contains the first occurrences of *Cycadopites stonei*, *Enzonalasporites 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 Foveolatitriletes potoniei*, *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 strew 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 reposited 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 osmundaceaous 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 *Pretricolpipollenites* 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 americus.* 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 circumpolloid 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

399 strategy. For example, the low sampling density of the Poleo Sandstone is a result of the rarity
400 of fine-grained channel fill facies in this coarse-grained unit, and the absence of productive
401 samples from the lower portion of the 'siltstone' member is a consequence of a lack of
402 organic-rich horizons in this interval. In all, over ninety spore/pollen form taxa were
403 identified (Fig. 2) and these have been grouped by their known or probable parent plant
404 affinities (Table 1; Fig. 3).
405
406 *5.1. Poleo Sandstone*
407 Five samples were studied from the Poleo Sandstone, but the uppermost sample (UMNH
408 PB 70) contains only twenty-three specimens and is therefore not statistically significant (Fig.
409 2). The two lowest samples from this unit are from approximately 10 m above the base of the
410 Poleo Sandstone, but because of limitations in outcrop exposure and correlation, it is unclear
411 exactly how far stratigraphically below they are in relation to the next highest sample. The
412 lowest sample (UMNH PB 71A) contains few palynomorphs and the majority of these (56%)
413 are marine acritarchs, including sphaeromorphs, *Leiosphaeridia* sp., *Cymatiosphaera* sp.,
414 *Micrhystridium* sp., which we interpret as being reworked. The *in situ* palynoflora is sparse
415 and only fifteen spore/pollen taxa have been identified, but the presence of *Praecirculina*
416 *granifer* is noteworthy (Fig. 2). The overlying sample (UMNH PB 71B), from slightly higher
417 in the section, contains abundant and well-preserved palynomorphs. The palynoflora is fairly
418 diverse, containing 43 spore-pollen taxa (Fig. 2). Bisaccate pollen dominate, with high
419 abundances of *Alisporites opii* and *Klausipollenites gouldii*, together with *Patinasporites*
420 *densus.* Single specimens of *Infernopollenites claustratus* and *Equisetosporites chinleanus* are
421 also present in the sample. The next two samples (UCMP PA1178 and UCMP PA1177) from
422 the Poleo Sandstone contain abundant palynomorphs, and they are characterized by
423 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

498 occurrences within the most diverse assemblages. Even though several of the FOs within the
499 upper portion of the Poleo Sandstone and the Petrified Forest Member consist of taxa
500 occurring only in one sample, the first occurrence rates are higher in the Poleo Sandstone
501 Member than in overlying strata. LOs show a three-fold stepwise pattern, with increased
502 numbers of disappearances in the upper portion of the Poleo Sandstone Member (UCMP
503 PA1177), in the lower portion of the Petrified Forest Member (UCMP PA1092 to UCMP
504 PA1095a), and within the 'siltstone' member (UCMP PA1088b). In all, there is a 50% loss in
505 diversity from the maximum range-through diversity in the Poleo Sandstone Member (70
506 taxa) to the topmost assemblage (35 taxa) in the 'siltstone' member. However, a rarefaction
507 analysis of the Chama Basin palynomorph assemblages (Fig. 5) indicates that when
508 accounting for the number of palynomorphs counted in each sample, the 'siltstone' member is
509 just as diverse as the Poleo Sandstone, but the Petrified Forest Member is clearly lower in
510 diversity. This does not necessarily mean that the drop in diversity between the Petrified
511 Forest and siltstone members is purely a sampling artifact, but is certainly influenced on some
512 level by the lower number of palynomorph grains in the 'siltstone' member samples.
513
514 **6. Discussion**
515
516 *6.1. Ecosystem and palaeoclimatic interpretations*
517 Except for the lowermost sample, assemblages from the Poleo Sandstone are remarkably
518 diverse, indicating vegetation dominated by corystospermous seed ferns, with abundant
519 majonicacean and voltziacean conifers (Fig. 3). The corystosperms most likely inhabited
520 lowland areas, as suggested by macrofloral taphonomic evidence from the lower portion of
521 the Chinle Formation (Demko et al., 1998) and later during the Jurassic Period (Abbink,
522 1998). Ash (1999) described an upland macroflora from Petrified Forest Member-equivalent
523 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

549 further expression of an increasingly more arid climate less suitable for palynomorph
550 preservation, as fine-grained channel fills are still present in this part of the section (Figs. 2–
551 3). A return to at least seasonally slightly wetter conditions in the upper portion of the
552 ‘siltstone’ member is suggested by the presence of a fairly diverse palynoflora with a decrease
553 in abundance of majonicacean conifers, and more common hygrophytic ferns, though these
554 assemblages are still less diverse than those of the underlying Petrified Forest Member (Figs.
555 2–3). The high amount of single sample occurrences in the Poleo Sandstone and lower portion
556 of the Petrified Forest members may be a reflection of a high stress environment. The marked
557 50% drop in range-through diversity from the Poleo Sandstone member to the ‘siltstone’
558 member suggests increasingly harsh conditions within this part of the Chinle Formation (Fig.
559 2).

560 New palaeoclimate evidence from organic carbon isotopes, pCO_2 estimates from
561 pedogenic carbonates, and fossil charcoal indicate that the Petrified Forest and 'siltstone'
562 members experienced arid and warm conditions, fluctuating between extremes (Whiteside et
563 al., 2012, 2015). In particular, the isotopic values of bulk organic carbon correlate with the
564 relative abundance of several common palynomorphs (*Alisporites*, *Camerosporites*, and
565 *Enzonalasporites*-group). These data are consistent with estimated mean annual precipitation
566 (MAP) based on paleosols and estimated mean annual palaeotemperature (MAT) from
567 pedogenic carbonates (Cleveland et al., 2008a,b), which indicate that MAT increased
568 substantially and MAP decreased through time in the Petrified Forest and 'siltstone' members
569 (Cleveland et al., 2008b). There is also evidence for rising pCO_2 during this interval
570 (Cleveland et al., 2008b). Together, these data fit well with our palynological evidence for
571 progressive aridification during deposition of the upper Chinle Formation in the Chama Basin
572 of northern New Mexico. This climate change makes sense in the context of a northward-
573 moving Pangaea, as the Chama Basin would have moved from approximately 10°N to 15°N

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

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

598 resource limitations may explain the complete lack of large herbivorous sauropodomorph
599 dinosaurs in the Triassic Pangaean low paleolatitudes (c.f., Whiteside et al., 2015).
600
601 *6.2. Biostratigraphic correlation*
602 The overall composition of the spore/pollen assemblages from the Poleo Sandstone and
603 the Petrified Forest Member, with abundant members of the *Enzonalasporites*-group,
604 *Froelichsporites traversei*, and *Klausipollenites gouldii*, suggests correlation with zone III of
605 Litwin et al. (1991). However, there are a few elements that are typical of zone II, namely
606 *Cycadopites stonei*, *Equisetosporites chinleanus* and *Lagenella martini* (Litwin et al., 1991).
607 In the Chama Basin, *C. stonei* and *L. martini* are last observed within the upper portion of the
608 Poleo Sandstone, whereas *E. chinleanus* is present in both the Poleo Sandstone and the lower
609 part of the Petrified Forest Member (Fig. 6). The upper occurrence of *E. chinleanus* consists
610 of a single poorly preserved specimen. Similarly, *Infernopollenites claustratus* is present in a
611 single sample in the lower part of the Poleo Sandstone. Reworking of specimens of all four
612 taxa from older strata within the lower part of the investigated succession is a real possibility
613 given their rarity in the samples (1–2 grains) and the presence in these samples of various
614 reworked marine acritarchs (Plate 6), especially in the Poleo Sandstone. Rare occurrences of
615 pollen specimens assigned to *Lueckisporites* sp. and *Potonieisporites* sp. may be reworked
616 from marine strata of the Pennsylvanian Madera Group, which are exposed below the Chinle
617 Formation in this area (NMBGMR, 2003). Alternatively, detrital zircon data from the Poleo
618 Sandstone suggest some input of late Paleozoic age source sediments from the Ouachita
619 orogen to the southeast (Dickinson and Gehrels, 2008, 2010).
620 The LO of *L. martinii* in the Chinle Formation is otherwise in the lowermost Bluewater
621 Creek Member of the Chinle Formation near Fort Wingate, New Mexico (Litwin, 1985;
622 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-Lockatong 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. *Brodispora 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

747 sampling across paleolatitudes (and therefore climate zones). Even within the Chinle
748 Formation, variations in composition of age-equivalent assemblages show no clear patterns
749 (cf. Fig. 6). Although several authors (Litwin et al., 1991; Litwin and Ash, 1993; Reichgelt et
750 al., 2013) have noted major decreases in diversity through time within particular sections of
751 the Chinle Formation, there are few consistent patterns of extinction between local areas (Fig.
752 6). In the Chama Basin, there is a 50% range-through diversity drop between the palynoflora
753 of the Poleo Sandstone Member and the upper 'siltstone' member, marked by the LOs of
754 *Camerosporites secatus, C. verrucosus, Cordaitina minor, Equisetosporites chinleanus,*
755 *Froelichsporites traversei, Heliosaccus dimorphus,* and *Playfordiaspora cancellosa* . A
756 similar drop in diversity is observed between the Petrified Forest Member and the overlying
757 Church Rock Member in Utah, with the disappearance of *Alisporites gottesfeldii,*
758 *Enzonalasporites vigens, Foveolatitriletes potoniei, Minutosaccus crenulatus, Ovalipollis*
759 *ovalis*, and possibly *Camerosporites secatus* (Litwin et al., 1991), but the LO of *C. secatus* is
760 the only event potentially shared between the two regions (Fig. 6). As mentioned above,
761 independent age constraints show that the LO of *C. secatus* in these two areas are not
762 synchronous (Fig. 6). Although floras of the Chinle Formation can be expected to have been
763 adapted to seasonally harsh conditions, the increased aridity as Pangaea drifted northward
764 during the Late Triassic (Kent and Tauxe, 2005; Kent and Irving, 2010; Cleveland et al.,
765 2008a,b; Whiteside et al., 2011, 2012, 2015) must have caused long-term on-going
766 environmental stress to the ecosystem. The variations in extirpation patterns among
767 penecontemporaneous strata of the Chinle Formation are most likely the result of the
768 local/regional floras reacting differently depending on variations in local conditions, such as
769 groundwater availability, precipitation, nutrients, and temperature. A similar on-going
770 aridification also took place in northwestern Europe during the Late Triassic which, albeit
771 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 Herngreen, 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 (Onoue et al., 2012) and Britain (214.7 ± 2.5 Ma $^{40}Ar/^{39}Ar$ 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. Onuoe 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., Onuoe 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 Onuoe 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

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

7. Conclusions

822 The new palynological data reported here from the upper portion of the Chinle Formation in
823 the Chama Basin, northern New Mexico, provide evidence of continuing ecosystem change
824 during the deposition of the Poleo Sandstone, Petrified Forest, and 'siltstone' members. The
825 spore-pollen assemblages are dominated by corystospermous seed fern and voltziacean
826 conifer pollen, and are correlated with Chinle palynomorph zone III of Litwin et al. (1991).
827 Major changes in palynological plant group abundances from the Poleo Sandstone to the
828 Petrified Forest Member, with marked increases in the latter in the abundances of the
829 *Enzonalasporites*-group (*Enzonalasporites, Patinasporites, Pseudoenzonalasporites,*
830 *Vallasporites*) and the enigmatic fused tetrad *Froelichsporites traversei*, indicate restructuring
831 of the terrestrial ecosystem during deposition of the lower part of the Petrified Forest
832 Member. A detrital zircon U-Pb radioisotopic date from this part of the succession has
833 provided a maximal depositional age of 211.9 ± 0.7 Ma, i.e. a late Norian age (Irmis et al.,
834 2011), demonstrating that the entire investigated Chama Basin succession is Norian–Rhaetian
835 in age. A total 50% range-through drop in diversity is registered through the sampled
836 sequence of the Chama Basin. Marked step-wise losses of species richness, along with only
837 minor appearances of new taxa, are interpreted as a possible consequence of increased aridity
838 as Pangaea drifted northward (Kent and Tauxe, 2005; Kent and Irving, 2010; Cleveland et al.,
839 2008a,b; Whiteside et al., 2011, 2012, 2015). However, it is interesting to note that some
840 major biotic changes might be synchronous to the middle Norian Manicouagan impact
841 (Hodych and Dunning, 1992; Ramezani et al., 2005; Onoue et al., 2012). Comparison with
842 other penecontemporaneous palynofloras from the Chinle Formation in Utah and Arizona
843 show discrepancies in the last occurrences of specific taxa between these areas, and this
844 probably reflects local environmental variations within the western United States. Similarly,
845 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.

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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 [1] Ramezani et al. (2011), [2] Irmis et al. (2011), and [3]Atchley et al. (2013). Palynological data after this study, [4]Litwin et al. (1991), and [5]Reichgelt 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.

Plate I. Photographs of selected spores from the Chinle Formation at Ghost Ranch. The specimens are photographed under interference contrast in transmitted light with a Leica DFC 295 digital camera on a Leica DM 2000 microscope. The scale bar is 20 µm. Each specimen is marked by locality, sample and slide number, as well as England Finder coordinates. Individual specimen numbers are listed in Appendix 1.

1. *Deltoidospora toralis* UCMP PA1178:1, J33/2
2. *Dictyophyllidites mortonii* UCMP PA1178:2, N41/3
3. *Dictyophyllidites mortonii* UCMP PA1092:2, U34/3
4. *Gleicheniidites* sp. cf. *G. senonicus* UCMP PA1178:2, Q39/2
5. *Gordonispora fossulata* UCMP PA1177:2, C37/2
6. *Deltoidospora australis* UCMP PA1178:1, K28/1

7. *Iraqispora speciosa* UCMP PA1178:1, S46/3
8. *Nevesisporites* sp. UCMP PA1177:2, F20/1
9. *Foveolatisporites* sp. UCMP PA1178:1, N26/2
10. *Punctatisporites globosus* UCMP PA1092:2, G10/4
11. *Osmundacidites* sp. UCMP PA1177:2 M24/4
12. *Punctatisporites globosus* UCMP PA1178:1, U40/1
13. *Reticulatisporites* sp. UCMP PA1178:1, U36/2
14. *Reticulatisporites* sp. UCMP PA1178:2, F46/3
15. *Reticulatisporites* sp. UCMP PA1178:1, J45/1

Plate II. Photographs of selected spores and pollen from the Chinle Formation at Ghost Ranch. The specimens are photographed under interference contrast in transmitted light with a Leica DFC 295 digital camera on a Leica DM 2000 microscope. The scale bar is 20 µm. Each specimen is marked by locality, sample and slide number, as well as England Finder coordinates. Individual specimen numbers are listed in Appendix 1.

1. *Camerosporites secatus* UCMP PA1178:1, G16/2
2. *Camerosporites secatus* UCMP PA1177:2, C37/4
3. *Camerosporites secatus* UCMP PA1177:2, F40/4
4. *?Camerosporites* sp. UCMP PA1177:2, D44/2
5. Circumpolloid tetrad, possibly underdeveloped *Camerosporites,* UCMP PA1092:2, R47/3
6. *Camerosporites verrucosus* UCMP PA1178:1, G21/1
7. *Classopollis* sp. cf. *C. torosus* UCMP PA1178:2, H43/3
8. *Enzonalasporites vigens* UCMP PA1092:2, O24/2
9. *Pseudoenzonalasporites summus,* UMNH PB 71B:1, M27/1

10. Circumpolloid tetrad, UCMP PA1092:2, S47/3
11. *Vallasporites ignacii* UCMP PA1178:2 O39/3
12. *Vallasporites ignacii* UCMP PA1092:2, N16/4
13. *Vallasporites ignacii* UCMP PA1092:2, N22/3
14. *?Vallasporites ignacii* UCMP PA1095B-1:1, Y28/2
15. *?Enzonalasporites* sp. UCMP PA1178:1, O41/2
16. *Monosulcites* sp., finely granulate, UCMP PA1178:1, O13/2
17. *Podosporites* sp., finely granulate, UCMP PA1178:1, O27/2
18. *Monosulcites* sp. A, UCMP PA1178:1, F44/2
19. *Patinasporites densus,* UCMP PA1178:1, H47/2
20. *Monosulcites* sp. A, UCMP PA1177:2, F20/1
21. *Monosulcites* sp. A, UCMP PA1178:1, O15/1
22. *Pretricolpipollenites bharadwajii,* UCMP PA1092:2, O27/2
23. *Pretricolpipollenites bharadwajii,* UCMP PA1177:2, L39/4
24. *Patinasporites densus,* UCMP PA1092:2, N45/4
25. *Cycadopites stonei,* UCMP PA1177:2, F24/3
26. *Cycadopites* sp., weakly granulate, UCMP PA1178:1, U43/2
27. *Playfordiaspora cancellosa,* UCMP PA1178:2, N41/3
28. *Patinasporites densus,* UCMP PA1178:1, H43/3

Plate III. Photographs of selected bisaccate pollen from the Chinle Formation at Ghost Ranch. The specimens are photographed under interference contrast in transmitted light with a Leica DFC 295 digital camera on a Leica DM 2000 microscope. The scale bar is 20 µm. Each specimen is marked by locality, sample and slide number, as well as England Finder coordinates. Individual specimen numbers are listed in Appendix 1.

1. *Falcisporites australis,* UCMP PA1092:2, N21/3
2. *Alisporites* sp., UCMP PA1178:1, F44/4
3. *Samaropollenites speciosus,* UCMP PA1178:1, N10/2
4. Aberrant bisaccate pollen with two normal and two small sacci, UCMP PA1095B-1:1, O24/2
5. *Alisporites thomasii,* UCMP PA1178:1, H41/4
6. *Alisporites* sp., UCMP PA1178:1, H26/2
7. *Alisporites* sp., UCMP PA1177:2, D25/3
8. *Alisporites opii,* UCMP PA1178:1, Q34/2
9. *Alisporites opii,* UCMP PA1178:1, H19/3
10. *Alisporites* sp., UCMP PA1092:2, W45/3

Plate IV. Photographs of selected pollen from the Chinle Formation at Ghost Ranch. The specimens are photographed under interference contrast in transmitted light with a Leica DFC 295 digital camera on a Leica DM 2000 microscope. The scale bar is 20 µm. Each specimen is marked by locality, sample and slide number, as well as England Finder coordinates. Individual specimen numbers are listed in Appendix 1.

1. *Klausipollenites gouldii,* UCMP PA1178:1, N14/1
2. *Klausipollenites gouldii,* UCMP PA1178:1, H43/3
3. *Klausipollenites gouldii,* UCMP PA1092:2, N24/3
4. *Klausipollenites gouldii,* UCMP PA1092:2, U33/1
5. *Protodiploxypinus americus,* UCMP PA1178:1, J31/2
6. Small bisaccate, UCMP PA1092:2, U34/3
7. Small bisaccate, UCMP PA1092:2, G39/2
8. *Platysaccus triassicus,* UCMP PA1178:2, H28/2

9. *Platysaccus* sp., UCMP PA1178:1, G22/1
10. *Triadispora* sp. cf. *T. verrucata,* UCMP PA1095B-1:1, X45/1
11. *Triadispora* sp. cf. *T. verrucata,* UCMP PA1178:1, M32/1
12. *Triadispora* sp. cf. *T. verrucata,* UCMP PA1178:1, J26/4
13. *Triadispora* sp. cf. *T. verrucata,* UCMP PA1178:1, O27/2
14. *Triadispora* sp., UCMP PA1178:1, M26/4
15. *Ovalipollis* sp., UCMP PA1178:1, M15/3
16. *Triadispora* sp., UCMP PA1178:1, H16/3
17. *Ovalipollis ovalis,* UCMP PA1178:1, L40/1
18. *Colpectopollis ellipsoideus,* UCMP PA1178:1, M45/2
19. *Ovalipollis ovalis,* UCMP PA1092:2, V14/1
20. *Colpectopollis ellipsoideus,* UCMP PA1092:2, S46/2
21. *Colpectopollis ellipsoideus,* UCMP PA1092:2, S27/4

Plate V. Photographs of selected pollen from the Chinle Formation at Ghost Ranch. The specimens are photographed under interference contrast in transmitted light with a Leica DFC 295 digital camera on a Leica DM 2000 microscope. The scale bar is 20 µm. Each specimen is marked by locality, sample and slide number, as well as England Finder coordinates. Individual specimen numbers are listed in Appendix 1.

1. *Equisetosporites chinleanus* UMNH PB 71B:2, H20/2
2. *Lunatisporites rhaeticus* UCMP PA1178:2, N10/2
3. *Infernopollenites* sp. cf. *I. claustratus* UMNH PB 71B:1, G29/3
4. *Protodiploxypinus* sp. UCMP PA1092:2, U17/1
5. *Protodiploxypinus* sp. UCMP PA1178:1, S38/1
6. *Protodiploxypinus* sp. UCMP PA1178:1, S37/3

7. *Protodiploxypinus* sp. UCMP PA1092:2, W35/4
8. *Protodiploxypinus* sp. UCMP PA1178:1, S38/1
9. *Protodiploxypinus* sp. UCMP PA1178:1, Q34/1
10. *Protodiploxypinus* sp. UCMP PA1092:2, O32/2
11. *Protodiploxypinus* sp. UCMP PA1092:2, Y14/3

Plate VI. Photographs of enigmatic pollen and reworked acritarchs from the Chinle Formation at Ghost Ranch. The specimens are photographed under interference contrast in transmitted light with a Leica DFC 295 digital camera on a Leica DM 2000 microscope. The scale bar is 20 µm. Each specimen is marked by locality, sample and slide number, as well as England Finder coordinates. Individual specimen numbers are listed in Appendix 1.

1. *Froelichsporites traversei* UCMP PA1178:1, M40/1
2. *Froelichsporites traversei* UCMP PA1095B-1:1, P19/4
3. *Froelichsporites traversei* UCMP PA1095B-1:1, O18/4
4. *Froelichsporites traversei* UCMP PA1095B-1:1, O13/4
5. *Cymatiosphaera* sp. UMNH PB 71A:1, J18/4
6. *Concentricystes* sp. UCMP PA1178:1, M14/3
7. Unknown sporomorph, UCMP PA1178:1, K37/4
8. *Inaperturopollenites* sp. UCMP PA1178:2, Q43/4
9. *Cymatiosphaera* sp. UCMP PA1178:1, F41/2
10. *Cymatiosphaera* sp. UCMP PA1177:2, E23/1
11. *Micrhystridium* sp. UCMP PA1177:2, L39/3
12. *Micrhystridium* sp. UCMP PA1178:1, R39/3
13. *Micrhystridium* sp. UCMP PA1178:1, J47/3

14. *Micrhystridium* sp. UMNH PB 71B:1, Y18/1

15. *Veryhachium* sp. UCMP PA1177:2, H21/3

16. *Multiplicisphaeridium* sp. UMNH PB71B:1, P32/2

17. *Multiplicisphaeridium* sp. UCMP PA1178:1, T46/2

1526 Appendix 1. List of specimen numbers for studied samples.

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