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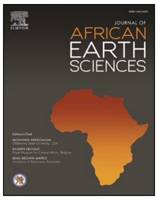

The influence of taphonomy and time on the paleobotanical record of the Permian–Triassic transition of the Karoo basin (and elsewhere)

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ABSTRACT

Terrestrial fossil assemblages preserved in the upper Permian–Lower Triassic strata of the Karoo Basin, South Africa, have played a central role in the interpretation of ecosystem patterns and end-Permian extinction models. However, these models need to be carefully reconsidered because of the limitations of the rock record. Four lessons learned from a multidisciplinary approach to the rocks, lithology, stratigraphy, and dating are relevant to other paleofloras in large continental basins. In reality, the Karoo paleofloral record is very sparse. Hence, reports of a near continuous fossil record in this basin should be considered as the near continuous record of erosion and time lost with sporadic plant-fossil assemblages.

A review of the debate over the rate and timing of the Permian–Triassic in the Karoo Basin reinforces the need for extensive stratigraphic mapping, the analysis of depositional environments of the plants, as well as the application of a variety of dating methods. First, Late Permian to Early Triassic paleobotanical assemblages are extremely rare in the basin with only a handful of sites in the Free State and Eastern Cape Provinces. These fossil data originate from >3750 m of total measured section wherein megafloral remains are preserved in <1% of the available rock record (0.9% all megafloral elements; permineralized wood = 0.1%, adpressions = 0.8%), with spore-and-pollen assemblages only slightly more frequently encountered at 1.3%. This low occurrence is comparable with other basins. Thus, any continental fossil assemblage represents a very short temporal window into the paleobiosphere because of taphonomic effects of the soils, pedogenesis, and controls on depositional environments. Second, geochronometric and rock magnetic data, developed in a sequence stratigraphic context, are critical to constrain time and biological trends in continental successions. The missing time, diastems and hiatuses, are critically important. Third, the spatial relationships of plant-fossil assemblages are not easily correlated across the basin without an extensive dataset of the paleolandscape. In general, the Late Permian Beaufort rocks represent channels, floodplains, and braided streams rather than lakes and oxbows that are conducive to the preservation of plant parts. Finally, the temporal distribution of paleobotanical assemblages is complicated by the missing time (sediments) that has resulted in the apparent scarcity of vegetation before and after the end Permian extinction. The reported uncharacteristic diversity and abundance of plants in the Carnian–Norian Molteno Formation is most likely due to an environment conducive to preserving fossil-plant assemblages combined with a record of intensive collecting. Overall, the large inland Karoo Basin, without any marine influence or extensive volcanic deposits, has favored the preservation of vertebrate assemblages.

1. Introduction

Terrestrial assemblages preserved in the upper Permian–Lower Triassic strata of the Karoo Basin, South Africa, have played a central role in the interpretation of ecosystem patterns (e.g., Smith and Botha-Brink, 2014) and modeled terrestrial dynamics (e.g., Angielczyk et al., 2005; Roopnarine et al., 2019) related to the end-Permian crisis. The reported extinction-and-replacement of vertebrates, used to interpret a short-term, mass-extinction event over a very thin stratigraphic interval (e.g., Viglietti et al., 2021), is predicated on a hypothesis about the catastrophic demise of a landscape forested and dominated by seed-bearing, gymnosperm taxa of the Glossopteridales (e.g., Retallack

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et al., 2003; Ward et al., 2005). This vegetation is thought to have been "replaced" rapidly, first, by horsetails (Equisetaleas) and, then, club mosses (Lycopsida) and other gymnosperms which were adapted to climatically stressed conditions. Arid and semi-arid environments are interpreted to have prevailed into the Late Triassic (~Carnian; Bordy et al., 2020) before seasonally warm and humid conditions (Bordy et al., 2005) returned. This change in climate state is evidenced by the preservation of a highly diverse megaflora in the Molteno Formation (Anderson and Anderson, 1985; Bamford, 2004). The interpretation of such patterns is dependent not only on the taphonomy (the processes responsible for transfer of an organism or its parts from the biosphere to the lithosphere and its preservation) and nature of the mega- and microfloral assemblages (e.g., Gastaldo et al., 2005, 2021), but also on their frequency of occurrence and sampling intensity over the stratigraphic interval of interest (DiMichele and Gastaldo, 2008). Ultimately, though, the interpretations of such patterns are controlled by the rock record, itself.

Rocks of the main Karoo Basin are exposed across nearly two-thirds of South Africa and are assigned to the Karoo Supergroup (Fig. 1). They represent deglacial sediments of the latest Carboniferous and early-to-middle Permian that transition to fully continental pedogenically modified floodplain (paleosols of various type), fluvial, and lacustrine deposits that persisted into the Triassic. Fully terrestrial deposition began in the middle Permian (Guadalupian; Rubidge et al., 2012) and continued into the Early Jurassic (Bordy et al., 2020) before the emplacement of the extensive Karoo-Ferrar Dolerites across southern Africa and Antarctica (Pliensbachian; Svensen et al., 2012). The strata reported to straddle the Permian–Triassic boundary (PTB) have been interpreted to represent a "continuous" record of sedimentation in localities of the Eastern Cape and Free State provinces (e.g., Smith, 1995; Ward et al., 2005; Smith and Botha-Brink, 2014; Botha et al., 2020; Viglietti et al., 2021). It is these geological and paleontological records that form the basis of the basin's legacy.

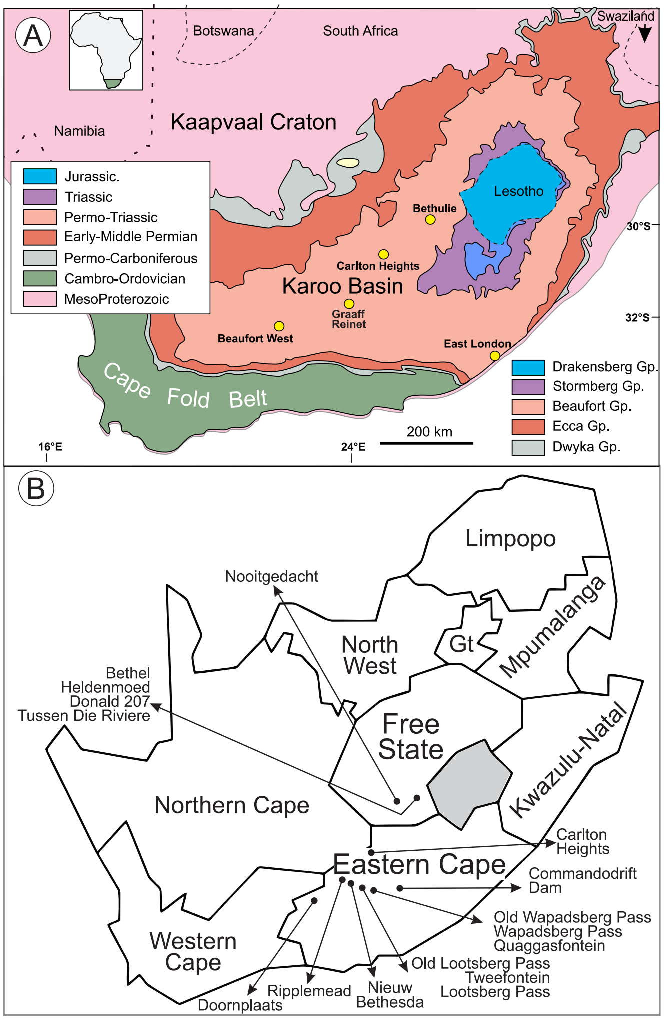


Fig. 1. Maps of the main Karoo Basin, South Africa. (A) Geologic map showing the geographical distribution and ages of the lithostratigraphic groups recognized in the basin. (B) Generalized political map of South Africa's provinces (Gt = Gautang) and the locations in which upper Permian and Lower Triassic rocks have been described in the literature, many of which are reported to contain the end-Permian extinction event and Permian–Triassic Boundary.

1.1. *The legacies of the Karoo basin, South Africa*

South Africa's Karoo Basin has been a golden spike for the Permian and Triassic since Alex Du Toit, a Cape Town-born mining engineer and geologist employed to map the Cape Province, published his book *Our Wandering Continents* (Du Toit, 1937). Du Toit noticed similarities between South African rocks and those of other southern hemisphere continents (Gondwana) and, thus, provided supporting evidence for Continental Drift (Wegener, 1915). Evidence for Wegener's "hypothesis, " the basis for modern plate tectonic theory, comes from various disciplines. Of relevance, here, are the similarities in rock formations and their fossil assemblages recovered from southern hemisphere continents, now well-separated across the globe. Du Toit correlated the South African Dwyka Group (Late Carboniferous to Early Permian; Fig. 1A) glacial deposits with similar glacial deposits in Brazil (Paraná Basin), Australia (Canning Basin), and India (Talchir Basin). Dr Edna Plumstead added palaeobotanical evidence of an exclusively southern hemisphere flora, the extinct gymnosperm *Glossopteris* (tongue-shaped leaf) flora that occurs in the Early Permian Ecca Group, the Antarctic Transantarctic Mountains (Plumstead, 1962), the Rio Bonito Formation coals (Iannuzzi, 2010) in Brazil, the Australian Bowan and Sydney Basins (McLoughlin, 2011), and India (Anderson et al., 1999; Srivastava and Srivastava, 2016). In addition, Permian and Triassic faunal elements, such as pariasaurs (plant-eating cheek lizards) and captorhinids (primitive lizard-like reptiles; see overviews in Rubidge, 2005; and Rubidge et al., 2016) also were shown to be closely related, although preserved on seemingly distant continents today. One iconic example is the taxon *Lystrosaurus*, a Late Permian to Triassic mammal-like reptile, that has been documented from all southern hemisphere paleocontinents and recently reported from Pangaea (China; Angielczyk et al., 2022). Not only have reptiles, "mammal-like reptiles", mammals, and dinosaurs been used for intercontinental biostratigraphic correlation, but nearly the all of the Karoo Basin record has permitted developmental and evolutionary studies of these taxa (for an opinion piece on Karoo vertebrate evolution, see Abdala, 2021). Biostratigraphic frameworks, though, are refined over time as new data are acquired. Our knowledge gaps are filled in due course when additional exploration reveals more information, dating techniques are refined, and genuine stratigraphic gaps, such as basin-wide erosional events or localized hiatuses, are recognized. The Karoo Basin's sedimentary, floral, and faunal records have served as the legacy model for the Late Carboniferous to the Jurassic because it is one of the most robust continental successions encompassing nearly 100 million years. More importantly, these records were deposited on a relatively stable tectonic plate that was capped and preserved by massive outpourings of basalt, the Drakensberg volcanics (Torsvik and Cocks, 2013), during Gondwanan disassembly.

1.1.1. *The Karoo's biostratigraphic legacy*

Paleontological research of the basin began in earnest in the small southern Karoo town of Nieuw Bethesda (Fig. 1B) when Robert Broom, a medical doctor with interests beyond medicine, noticed the strange fossil animals in the rocky outcrops of surrounding farms (Broom, 1909). He employed a local road builder, Coenie Kitching in 1912, to collect fossils. In 1934, James Kitching joined his father in collecting fossils for

Broom and a local doctor, Sydney Rubidge. Old man Kitching was fatally wounded in the Second World War but young James continued collecting and was to become the world's leading fossil collector of his time. These collections, housed at the University of the Witwatersrand where James Kitching was employed from 1946, and in the Rubidge collection near Graaff Reinet (southern Karoo Basin; Fig. 1A), form the basis of the Permian and Triassic Karoo vertebrate biostratigraphy. These faunas are dominated by pre-mammal terrestrial tetrapods and have been used as the basis for its subdivision (Smith et al., 2020). Kitching (1970) proposed the first formal Karoo vertebrate biozones, later refined by Bruce Rubidge (grandson of Sydney Rubidge; Rubidge, 1995; Rubidge, 2005) and students (e.g., Smith et al., 2020).

Locally, the basin's stratigraphy and vertebrate biozones (use of key or index taxa to characterize a time interval) have formed the framework for fossil-plant biozones, including those for wood (Bamford, 1999) and pollen (MacRae, 1988; Aitken, 1994; Barbolini et al., 2016a, 2016b, 2018). This biostratigraphic framework has been extended into southern and eastern Africa. For example, in Zambia, James Kitching described and correlated the rocks of the Luangwa Basin with those of the Karoo (Kitching, 1963), and Lacey and Smith (1972) correlated the floras. More recently, Barbolini et al. (2016a) reviewed and revised the fossil plants from Zambia. Fauna from Mozambique has been correlated with that of the Karoo Basin (Araújo et al., 2020), and in southern Tanzania with the Ruhuhu Basin (Angielczyk et al., 2014), to list but a few. The legacy of the Karoo Basin goes far beyond the African continent. The biostratigraphic framework and interpreted extinction events therein (e.g., Smith and Botha-Brink, 2014; Viglietti et al., 2021) have been applied to rocks in Brazil, Argentina, Australia, Antarctica, and India. A biostratigraphic framework, however, is just that; a hypothesis to be tested, corrected, adjusted, and refined as new data and advanced analytical techniques become available.

There have been advances in developing sequence-stratigraphic models (identification of spatial lithological relationships in a temporal framework where genetically related units are underlain and overlain by erosional surfaces or correlative conformities; details in Sec. 4.4.1) in continental basins (e.g., Gastaldo and Demko, 2011). These concepts have been applied in parts of the Karoo Basin. The application of a sequence-stratigraphic framework, coupled with geochronometric and paleomagnetic data in classic PTB localities, now constrain much of the paleontological record and provide a more comprehensive understanding of the basin (Gastaldo et al., 2015, 2018, 2020a, 2021; Rochín-Bañaga et al., 2023). In the following text we provide several more recent examples of how this framework has been tested and refined in South Africa. We will explore these advances that allow us to assess: the distribution, through space and time, of paleobotanical assemblages, therein; and the vegetational response in the Karoo Basin, testing the rapidity of turnover in this part of Gondwana. We will present lessons learned and ways in which this legacy can be used in the future on other continents and across the Phanerozoic.

1.1.2. *Organization of this contribution*

We will attempt not only to provide the historical and legacy basis for our understanding of the Late Permian and Early Triassic paleobotany of the Karoo Basin, but also integrate multidisciplinary data collected over the past 20+ years about its plant-fossil record and their implications in the Karoo and other continental basins. We will attempt to provide insights to better constrain what we know, how we know, where in space and time do we know, what paleontological patterns might we decipher from the record, and how these insights are applicable to other Phanerozoic rocks. The stage is set with an overview of Karoo Basin geology (Sec. 2) that, then, anchors the discussion on the nature and character of the upper Permian and Lower Triassic rocks in which plants are preserved. A general consideration follows of the typical plants found in megafloral (compressions/impressions [adpressions] and permineralized wood) and microfloral (palynology) assemblages of the Eastern Cape and Free State provinces (Sec. 3). These assemblages, then, are reviewed in stratigraphic, spatial, and temporal (geochronologic and magnetostratigraphic) context relative to their proximal (Eastern Cape) or distal (Free State) locations in the basin (Sec. 4). The final section (Sec. 5) analyzes and discusses these data to demonstrate that a wide array of biological, taphonomic, and physical factors influence what we are able to deduce from the plant-fossil record, and how that record can be used to interpret paleontological patterns, especially over critical intervals in Earth history. We show that paleontological assemblage patterns only can be understood using such a multidisciplinary approach that incorporates, at least, sequence stratigraphic, geochronologic, and rock magnetic data and, where possible, the application of other pertinent disciplinary information (e.g., elemental and stable-isotope geochemistry).

2. Considerations of Upper Permian and Lower Triassic geology

In this section we first present a stratigraphic overview of the Karoo succession that spans the Upper Carboniferous to Jurassic, and then focus our attention on rocks assigned to the upper Permian and Triassic in which plant-fossil assemblages are preserved. Biostratigraphic age constraints follow palynostratigraphy for Gondwana, the southern hemisphere supercontinent before a discussion on the vertebrate biostratigraphic model used to subdivide these rocks. Certainly a lithostratigraphic PTB can be identified whereupon the oldest Permian rocks are overlain by younger Triassic deposits. But the PTB in the Karoo has been equated with the end-Permian extinction event, which complicates any discussion because of this paradigm. We recognize and discuss factors that influence whether or not a biostratigraphic PTB can be identifiable in the classic sections where a vertebrate-defined boundary is reporteed.

2.1. *Karoo Supergroup lithostratigraphy*

The sedimentary succession known as the Karoo Supergroup is subdivided into the Dwyka (Fig. 1A; Carboniferous–Lower Permian), Ecca (Lower–Middle Permian), Beaufort (Middle Permian–Middle Triassic), Stormberg (Upper Triassic–Lower Jurassic), and Drakensberg (Lower Jurassic) Groups. The Beaufort Group (Fig. 2) is exposed in the main Karoo Basin (Fig. 1A; Johnson et al., 2006) and the Lebombo Basin in the eastern part of South Africa (Bordy and Prevec, 2008, 2015). It consists mainly of a sandstone-and-mudstone succession, which is monotonous in physical characteristics, and attains a thickness of >2500 m in the southern part of the basin (Viglietti et al., 2017). The absence of a distinct set of physical criteria to separate lithostratigraphic units led early workers to rely on an abundant and diverse fossil-vertebrate fauna (see Sec. 1.1.1). Geochronometric (Fig. 2; Rubidge et al., 2013; Day et al., 2015; Gastaldo et al., 2015, 2021; Rochín-Bañaga et al., 2023) and paleomagnetic (Gastaldo et al. 2018; 2020a, 2021) constraints in lithostratigraphic context now allow for traditional litho- and biostratigraphic paradigms to be evaluated and better correlated with global standards. What once was promoted as a simple solution to distinguish Permian–Triassic rocks, using vertebrate biostratigraphy, is now demonstrated to be complicated and problematic (see discussion in Gastaldo et al., 2021).

The latest Permian and earliest Triassic deposits occur in the Balfour and Katberg formations where several formal and informal lithostratigraphic members are recognized (Fig. 2). Latest Permian (Changhsingian) deposits likely begin in the Daggaboersnek or Barberskrans (informal Ripplemead Member; Viglietti et al., 2017) member and extend through the Elandsberg and Palingkloof members into the basal Katberg Formation (Gastaldo et al., 2020a, 2021). Currently, the remainder of the Katberg Formation is assigned to the Triassic. The end-Permian terrestrial event in Australia (e.g., Fielding et al., 2019), as identified by palynostratigraphy and constrained by geochronology, is first identified in the Katberg Formation (Gastaldo et al., 2019). In Australia, vegetational change (*Dulhuntyispora parvithola* to

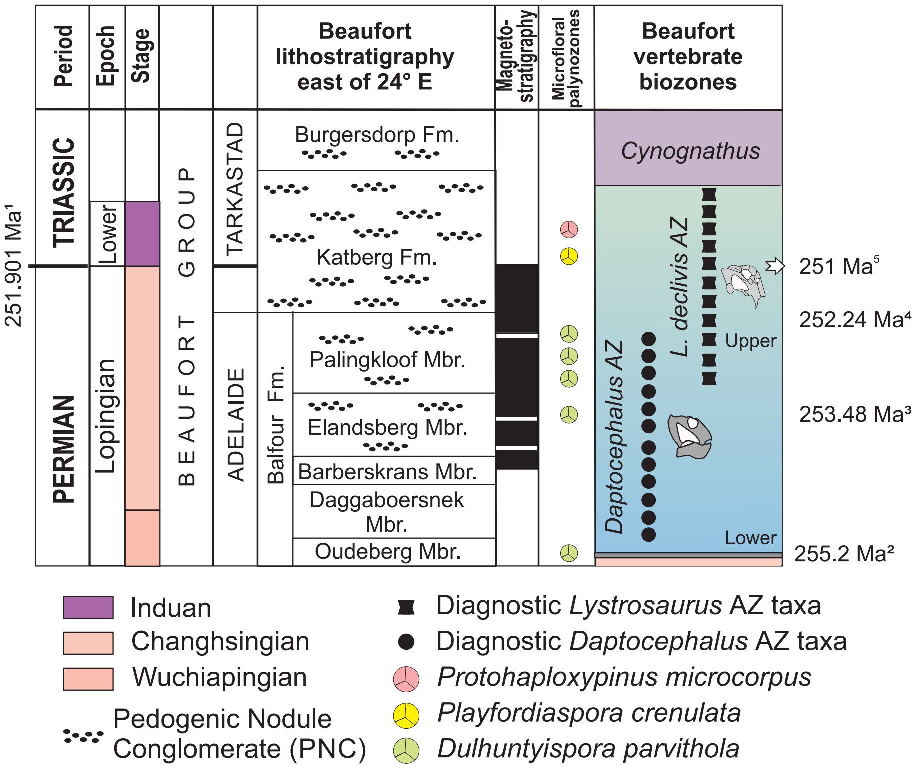


Fig. 2. Generalized stratigraphy of the continental Beaufort Group and lithostratigraphic subdivision east of 24° longitude as recognized by the South African Committee on Stratigraphy (Johnson et al., 2006; Cole et al., 2016). Magnetostratigraphy of the Beaufort Group from Gastaldo et al. (2017, 2018a, 2019, 2020a, 2021). U–Pb ages are from [1]Shen et al. (2019), [2]Rubidge et al. (2013), [3]Gastaldo et al. (2015), [4]Gastaldo et al. (2020a), and [5]Rochín-Bañaga et al., 2023. The biostratigraphic overlap of the Last Appearance Datum of the diagnostic vertebrate taxa used to define the latest Permian *Daptocephalus* Assemblage Zone (Viglietti, 2020) and First Appearance Datum of the diagnostic vertebrate taxa used to define the base of earliest Triassic the *Lystrosaurus declivis* AZ (Botha and Smith, 2020) are depicted (see Gastaldo et al., 2020a). The stratigraphic range of the *Dulhuntyispora parvithola* (Changhsingian), *Playfordiaspora crenulata* (Changhsingian–Induan) and *Protohaploxypinus microcorpus* (Induan) palynozones are shown. The placement of the Permian–Triassic boundary in the Katberg Formation follows Gastaldo et al. (2021).

Playfordiaspora crenulata palynozones; Mays et al., 2020) dates before 252.3 ± 0.07 Ma (Fielding et al., 2019). Evidence of this turnover in the Karoo is found in a fluvial-siltstone trough fill positioned above the vertebrate-defined PTB as reported on farm Nooitgedacht (Botha et al., 2020) and is younger than 251 ± 3 Ma (Rochín-Bañaga et al., 2023).

The initial vertebrate-defined extinction-and-assemblage turnover model (Ward et al., 2000, 2005; Smith and Ward, 2001) was reported over a stratigraphic thickness of ~60 m in the Palingkloof Member, temporally constrained to represent between 10 ka and 100 ka (Smith and Botha-Brink, 2014). With the addition of the high-resolution age date in the Palingkloof Member (Gastaldo et al., 2020a), Viglietti et al. (2021) revised the model and now interpret a change in the vertebrate assemblage having occurred over a stratigraphic interval of 100 m, with a protracted mass-extinction event lasting 1 Ma. In this model, the pre-extinction vertebrate assemblage (Upper *Daptocephalus* Assemblage Zone; *L. maccaigi*–*Moschorhinus* subzone) is replaced by new taxa reported to have their first appearance datums (FAD) in the post-extinction *Lystrosaurus declivis* Assemblage Zone (AZ). Recently, Gastaldo et al. (2021) demonstrated that the diagnostic taxa used to circumscribe each of these assemblage zones are preserved in coeval strata in the Eastern Cape Province (Fig. 2). These purportedly pre-extinction and post-extinction diagnostic taxa are in Changhsingian deposits yielding microfloral assemblages that are of the Late Permian, *Glossopeteris*-dominated, *D. parvithola* palynozone (Fig. 2).

The lithostratigraphic position of the PTB in the Karoo, if present, likely is somewhere in the lower Katberg Formation (Gastaldo et al., 2021). Viglietti et al. (2017) reaffirm the disparity in available stratigraphic sections between southern localities in the Eastern Cape Province (e.g., Lootsberg Pass), close to the provenance of sediment supply, and those in distal parts of the basin in the Free State Province (e.g., Bethulie; Fig. 1). Criteria to identify the Katberg Formation throughout the basin relied heavily on the presence of intraformational conglomerate lag in thick fluvial sandstone (e.g., Smith, 1995; Retallack et al., 2003). The presence of pedogenic nodule conglomerate (PNC) was considered as a unique and diagnostic feature of Triassic rivers assigned to the Katberg Formation. These were reported to have formed in the wake of the aridity interpreted to have been associated with the end-Permian event and loss of vegetation (Ward et al., 2000, 2005; Smith and Ward, 2001; Smith and Botha-Brink, 2014). Other workers have demonstrated that these intraformational lag deposits are a common feature of the Beaufort Group. They occur in the Middle Permian Abrahamskraal Formation (Katsiaficas et al., 2010) and extend throughout the upper Permian Balfour Formation (Fig. 2; e.g., Viglietti et al., 2017; Gastaldo et al., 2017, 2019, 2021). Such intraformational lag deposits are the result of landscape degradation (Gastaldo and Demko, 2011), concentrating resistant calcite-cemented soil nodules at the base of newly established rivers and their adjacent floodplains. In contrast to their concentration as river sediment, soil remnants–very fine sand, silt, and clay–were eroded and transported basinward, removing any evidence of their existence except for when reworked tuffaceous deposits are encountered and can be dated geochronometrically (Gastaldo et al., 2018a; 2021). The presence of PNC lags in rivers, then, represent "ghost" landscapes (Gastaldo et al., 2020b); they are the only evidence of conditions that prevailed where no stratigraphic record now exists. Landscape erosion (riverine and floodplain paleosols) resets sediment accumulation in a new depocenter, and changes the potential for preservation of floral elements (Gastaldo and Demko, 2011). This episodic, but ongoing, set of processes on land results in a stratigraphic record replete with highly condensed sections of variable thickness and temporal resolution in different parts of the basin. Hence, it is highly unlikely that a lithostratigraphic interval in either the Balfour or Katberg formations will record the PTB interval. This is the case at Nooitgedacht (Fig. 1B) where approximately 1.25 My of stratigraphic record is missing across the critical extinction interval (Fig. 2; Rochín-Bañaga et al., 2023).

3. Paleobotany over the Permian–Triassic transition

Our knowledge of the reported megafossil and microfossil assemblages in the Balfour and Katberg formations, to date, are restricted to a few localities. In Kwazulu-Natal Province these include: farms Christina and Moorfield (Claassen, 2008) and Clouston farm (Prevec et al., 2009), previously assigned to the Normandien Formation that is now combined with the Balfour Formation (Groenewald et al., 2022); several isolated megafloral localities that are unconstrained in that formation (Mooi River [Lacey et al., 1975]; Wagendrift, [Zavada and Mentis, 1992; Selover and Gastaldo, 2003]; Bulwer [Lacey, 1976; Gastaldo et al., 2005]; and Loskop [Gastaldo et al., 2005; McLoughlin et al., 2021]); and a number of localities from which permineralized wood is reported (Bamford, 1999, 2004). In the Eastern Cape Province (Fig. 3A), paleobotanical assemblages are known from: Wapadsberg Pass (Prevec et al., 2010; Gastaldo et al., 2014), farms Blaauwater and Tweefontein (Gastaldo et al., 2017, 2021), Old Lootsberg Pass (Gastaldo et al., 2018a), and Carlton Heights (Retallack et al., 2003; Gastaldo et al., 2005). And, localities in the Free State Province (Fig. 3B) include: farms Donald 207 (=Fairydale; Smith and Botha-Brink, 2014; Barbolini et al., 2018), Bethel (Gastaldo et al., 2005, 2019) and Tussen die Riviere, and Nooitgedacht (Botha et al., 2020; Gastaldo et al., 2020a). A general overview of the character and diversity of megafloral and microfloral assemblages are presented in this section.

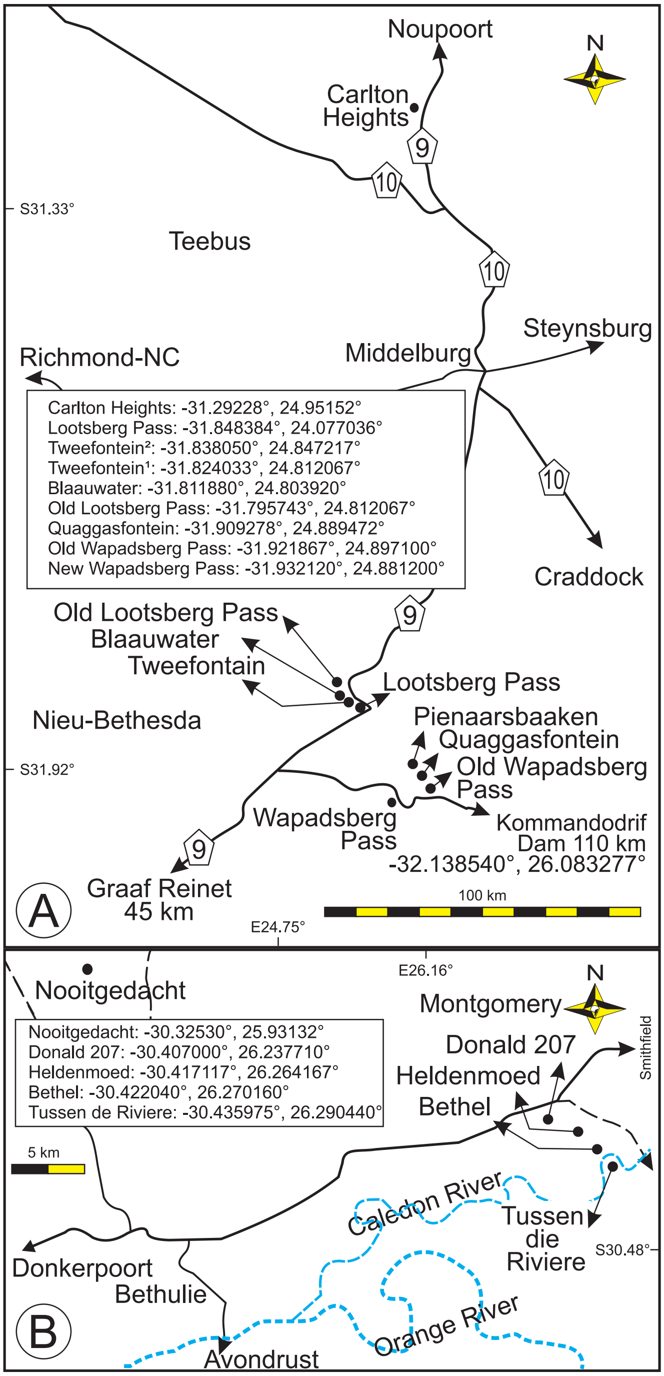


Fig. 3. Maps of classic localities where the Permian–Triassic transition and event boundary (=PTB) are reported in the literature. (A) Eastern Cape Province localities reviewed in this manuscript with generalized GPS (WGS84 standard) coordinates. (B) Free State localities reviewed in this manuscript with generalized GPS (WGS84 standard) coordinates. See text for details.

3.1. *Megaflora*

3.1.1. *Adpression floras*

The predominant preservational mode of megafloral assemblages is adpression (coalified compression/impression; Shute and Cleal, 1987) where, in some instances, cuticular remains (resistant biopolymer covering leaves) can be retrieved from bedding surfaces. In many cases, though, organic remains have decayed or been lost, leaving faint-to-well defined morphological features impressed into the sediment in which these were buried. Robust axes, such as the horsetail *Paracalamites*, as well as club mosses and unidentifiable axes, are preserved in fine-to very fine-grained sandstone and finer clastic strata. In contrast, leaves and other aerial parts are almost exclusively restricted to coarse-to-fine siltstone; claystone is uncommon in this part of the succession and, where encountered, may preserve cyclical beds of leaf litter (e.g., Bulwer; Gastaldo et al., 2005). Leaves in fine-grained sandstone and siltstone can be identified by their persistent venation without intervening lamina (the flat and extended section of the leaf), most often as impressions. Rarely have *in situ* roots and/or rooting systems been encountered (e.g., *Vertebraria*–gymnosperm rooting systems of glossopterids; Gastaldo et al., 2014) despite the fact that paleosols dominate the sedimentological record in the basin.

Wetland taxa are most common and include horsetails, rare club mosses and ferns, and gymnosperms; the most common elements are assigned to Glossopteridales (an extinct seed-bearing group spread across the southern paleohemisphere; Fig. 4A and B). Aerial parts of horsetails include axes and lateral branches with whorled leaves, and reproductive cones. These are assigned to two orders and three families: Schizoneuraceae (e.g., *Schizoneura*) and Phyllothecaceae (e.g., *Paracalamites*, *Phyllotheca*) in the Equisetales, and Sphenophyllaceae (e.g., *Trizygia*) in the Sphenophyllales (Fig. 4C). Very few examples of club mosses have been recovered, and assignment of defoliated specimens to this group are complicated by their preservational state (e.g., Prevec et al., 2009). This is not the case for ferns or some other gymnosperm groups. This is despite their mainly small specimen size and generalized shapes, resulting in their placement in the form taxon *Sphenopteris*. In contrast, *Glossopteris* leaf shapes are relatively diverse and vary in both size and venation patterns. Early reports assigned specimens to established species (Lacey, 1976); but, with recognition that leaf characteristics vary in sample populations, a morphotype approach is applied to their systematization (e.g., Claassen, 2008; Prevec et al., 2009, 2010; Botha et al., 2020). At least 30 different *Glossopteris* morphotypes are recognized, to date, in these latest Permian assemblages. These morphotypes are in addition to leaves formally assigned to *Glossopteris conspicua* and *G. elongata* (Lacey, 1976), *G. symmetrifolia* (Gastaldo et al., 2017), and *G. angustifolia* and *G. linearis* (Botha et al., 2020). Often it is possible to find evidence of plant-insect interaction in glossopterids (Fig. 5; Prevec et al., 2009, 2010; McLoughlin et al., 2021).

There is a dearth of paleobotanical material, to date, in rocks assigned to the Lower Triassic. Isolated and dispersed fossils in the Katberg Formation are preserved on bedding in fluvial fine-grained sandstone and sandy siltstone and, generally, unidentifiable (e.g., Gastaldo et al., 2005). Retallack et al. (2003, p. 1147), though, report the presence of what were, then, considered to be exclusively Triassic taxa from Bethulie and Carlton Heights (Fig. 1B). These were described as "plant hash" but not illustrated. The samples were transferred to the authors subsequent to the paper's publication, and now are curated in

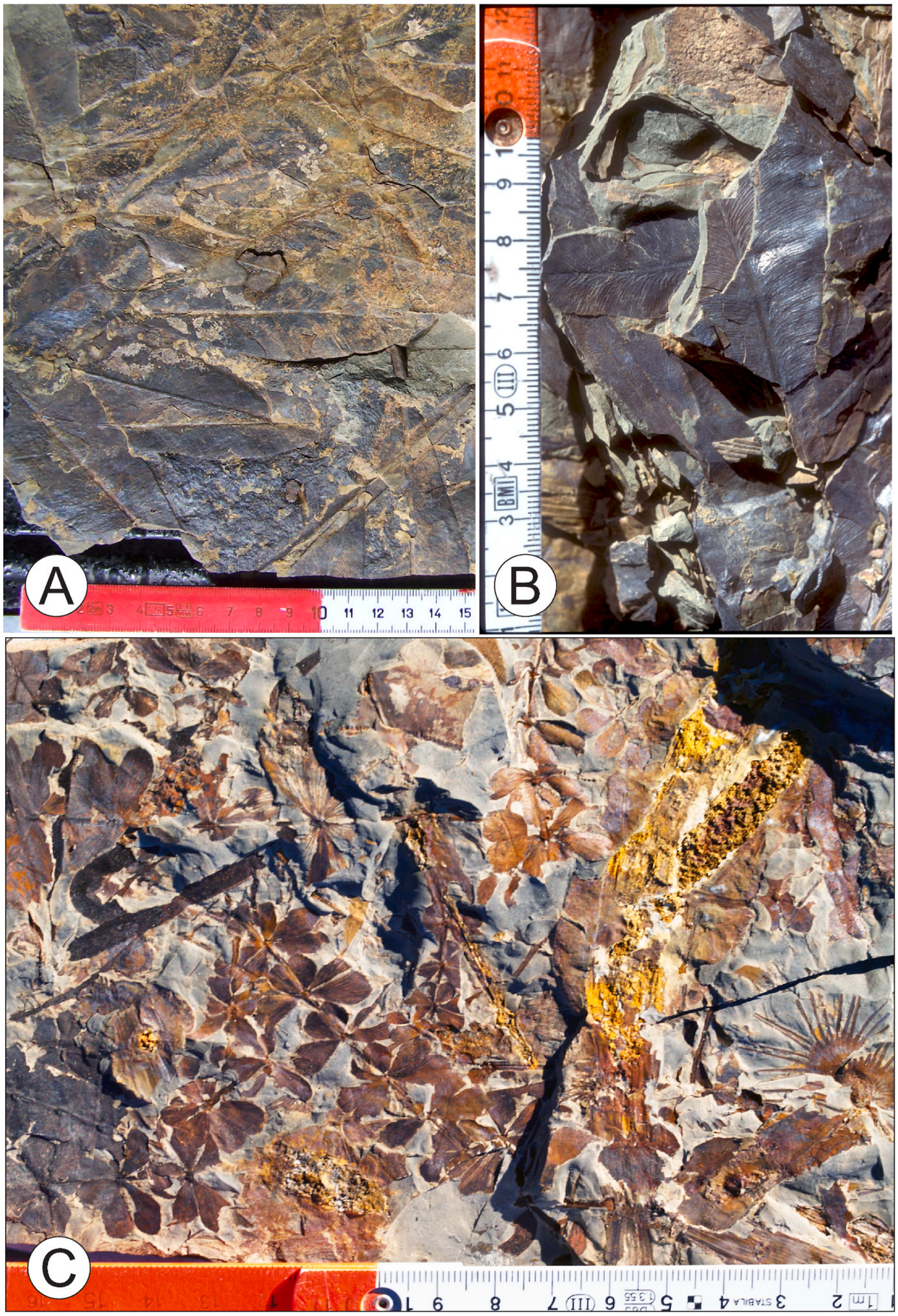


Fig. 4. Characteristic megafloral elements of the Beaufort Group. (A) Leaf mat of randomly oriented, mineralized impressions of *Glossopteris* leaves, Onder Karoo, Northern Cape Province. (B) Leaf mat of randomly oriented, mineralized impressions of *Glossopteris* leaves preserved in an abandoned channel deposit, Clouston farm, KwaZulu Natal Province (Prevec et al., 2009). (C) Equisetalean dominated assemblage of isolated whorls of *Phyllotheca* (Ph), axes with whorled leaves assigned to *Tryzigia* (Tr), and associated three-dimensionally preserved reproductive strobili (Str), Old Wapadsberg Pass, Eastern Cape Province (Prevec et al., 2010). Scales in mm and cm.

the paleobotanical collections of the Evolutionary Studies Institute (University of the Witwatersrand, Johannesburg). The small collection includes the original specimen number as assigned by Retallack and a letter of transmittal (samples curated in the paleobotanical collection, University of Witwatersrand, Johannesburg). Taxa identified to genus include: *Lepidopteris* (Fig. 6A and B), *Pagiophyllum* (Fig. 6C and D), *Cladophlebis* (Fig. 6E), and *Samaropsis* (Fig. 6F).

3.1.2. *Permineralized wood*

Permineralized wood (Fig. 7) is less common in latest Permian and Lower Triassic rocks, which may explain their low taxonomic diversity. Bamford (1999, 2000, 2004) identified a single genus in this interval in which two species are recognized: *Agathoxylon africanum* and *A. karooensis*. *Agathoxylon africanum* (Fig. 7E) is a long ranging taxon that appears in the Late Permian (Lopingian) and continues into the Middle Triassic of southern Africa (Bamford and Phillippe, 2001). In contrast, *A. karooensis* (Fig. 7F) is only known from uppermost Permian strata. Recently, Bamford et al. (2020) recognized wood assignable to *Australoxylon natalense* and *A. teixeirae* (Fig. 7D) in the latest Permian Middleton Formation of the Eastern Cape Province. This wood type is very similar to that of the woody roots (*Vertebraria*) of glossopterid trees.

3.2. *Microfloras (spores and pollen)*

There are rare occurrences of spore-and-pollen (palynomorph) assemblages documented from surficial outcrops in the upper Permian–Lower Triassic succession (e.g., Prevec et al., 2009, 2010; Barbolini et al., 2016a, 2018; Gastaldo et al., 2015, 2017, 2019, 2020a, 2021). There are a few studies conducted on drill core in the main Karoo and southern Africa, focused mainly in the coal-bearing Ecca Group (e.

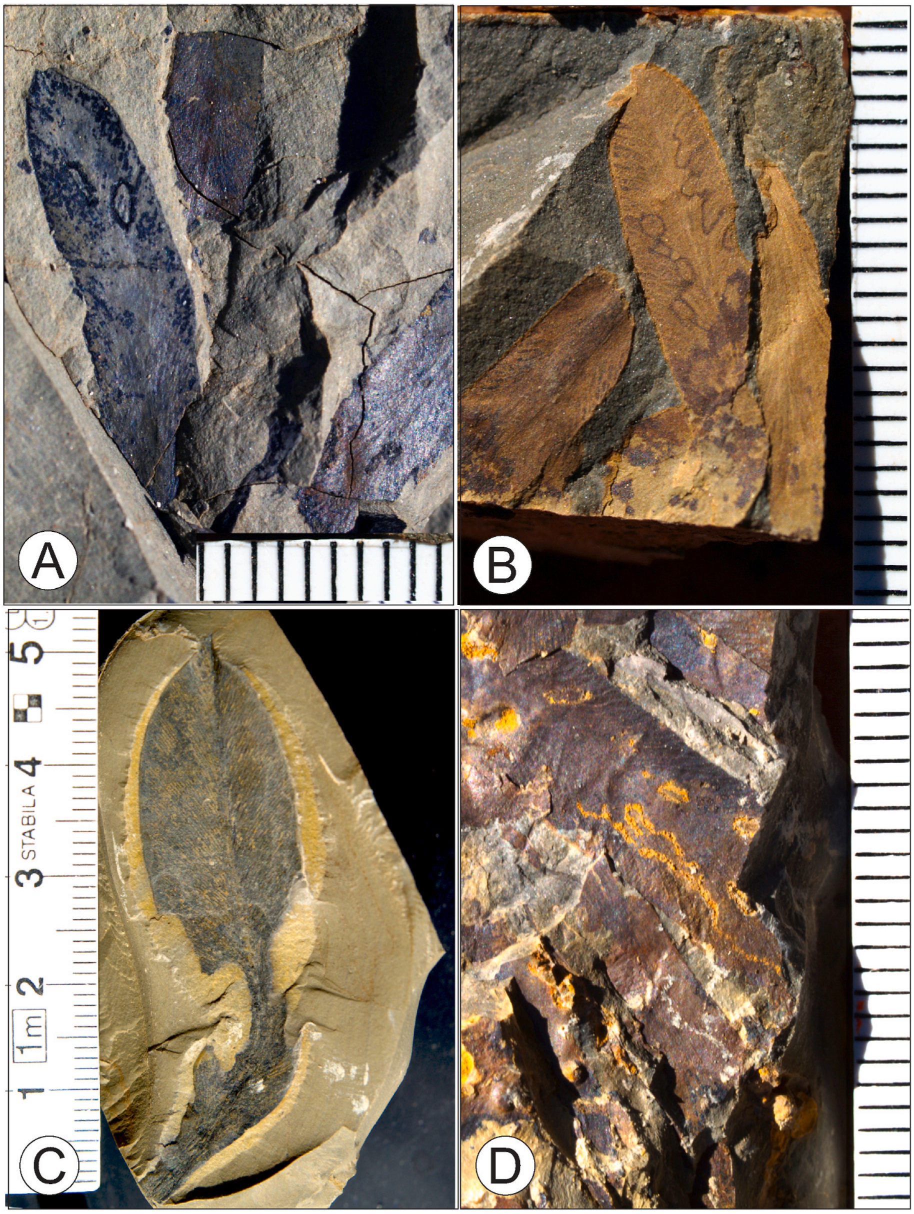


Fig. 5. *Glossopteris* herbivory. (A) Feeding holes penetrating *Glossopteris* morphotype W1 of Prevec et al. (2010). (B) Surface feeding. (C) Deeply incised margin feeding. (D) Leaf mining. Wapadsberg Pass, Eastern Cape Province. Scale in mm and cm.

g., MacRae, 1988; Falcon, 1989; Aitken, 1994; Wagner et al., 2019) where results are available in unpublished theses and dissertations (e.g., Mahabeer, 2017). Other studies (Ruckwied et al., 2014; Götz et al., 2017) have misinterpreted the stratigraphy and palaeoenvironments (see comments by Cole, 2017; Cole and Barbolini, 2019) and have not taken this field further. Basin-wide sampling from the vertebrate biozones, together with radiometric dating, has produced a broad overview and pollen biostratigraphy (Barbolini et al., 2016a; 2018). But, a high resolution, core-sourced profile is still lacking for the South African Karoo Basin. The quality of dispersed assemblages is dependent on the depth of weathering of surficial exposure and, more importantly, the thermal history of the rocks in which they are preserved. Palynomorph color ranges from orange-yellow (e.g., Fig. 8C), indicative of a thermal maturation index (TMI) ~2, to brownish black and black (Fig. 8D, F), indicative of a TMI approaching or >4 (Marshall, 1990). Hence, post-depositional preservation potential is dependent, primarily, on the emplacement of Jurassic-aged dolerite dykes associated with the Karoo-Ferrar Large Igneous Province. Thermal maturation of the host rock where temperatures exceeded 200° C has resulted in the “cooking” of organics and, in many instances, the loss of diagnostic features that would allow for systematic identification of any palynomorphs.

Dolerite intrusions are ubiquitous throughout the Main Karoo basin but are rare in the Waterberg Coalfield located in the Ellisrus Basin, a small basin in northern South Africa. Here, Wagner et al. (2019) have correlated the maceral types (an organic clast found in coal or oil shale that analogous to the term ‘mineral’ as applied to igneous or metamorphic rocks) with palynology and environmental interpretations. They processed bulk samples from coal seams in the Vryheid and overlying Grootegeluk formations and found that these assemblages correlated with the previous work of Falcon (1986, 1989). Inertinite (in reflected light these clasts appear white and bright) was found to be dominant together with tree-fern spores and a diversity of other palynomorphs, indicating a wetland setting and cooler climate. In contrast, the overlying Grootegeluk Formation has high vitrinite/vitrite (clasts that are medium to light gray in reflected light) and is dominated by pollen grains with two bladders (bisaccates; Fig. 8G), indicating a wet

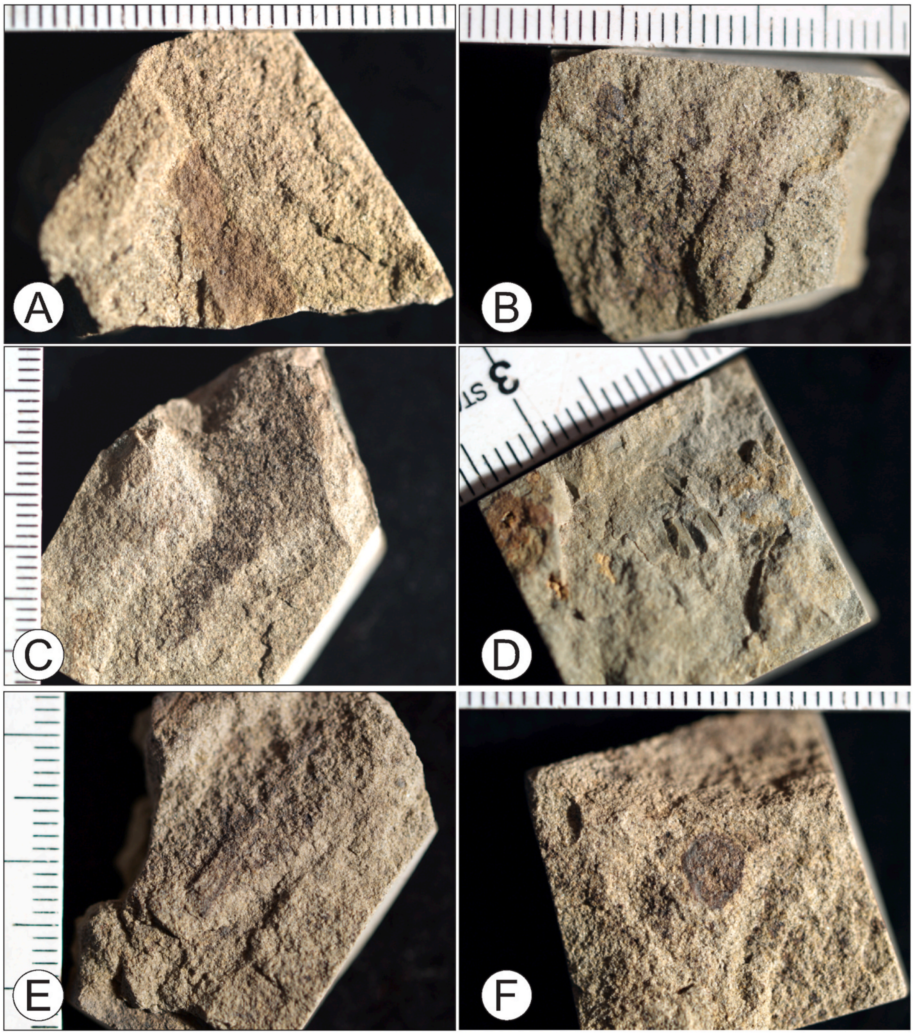


Fig. 6. Megafloral elements reported by Retallack et al. (2003, p. 1147) from Carlton Heights. Collection sent to the first author along with letter with identifications, currently curated in the Paleobotanical collection of the Evolutionary Studies Institute, Johannesburg. (A) *Lepidopteris*, Retallack collection number 4643; (B) *Lepidopteris*, Retallack collection number 4635; (C) *Pagiophyllum*, Retallack collection number 4645; (D) *Pagiophyllum*, Retallack collection number 4637; (E) *Cladophlebis*, Retallack collection number 4664; (F) *Samaropsis*, Retallack collection number 4646. Scales in mm.

gymnosperm forest under a warmer and more seasonal climate that promoted rapid growth (Wagner et al., 2019).

Most productive assemblages are dominated by taeniate pollen assigned to the Glossopertidales (Fig. 8E–G) and spores of groundcover sphenophyllaleans (Fig. 8B and C) and ferns (Fig. 8D). These spores and pollen come from plants that grew in wetlands and landscapes that experienced seasonally wet conditions. In several rare instances, though, Late Permian assemblages contain a low-to-moderate proportion of other gymnosperm groups, macroscopic remains of which are not found in these rocks (Prevec et al., 2010; Gastaldo et al., 2015, 2017). These taxa include conifer pollen (early, primitive Voltzians) and various "seedferns" (peltasperm and corystosperm affinities; Fig. 8I–K), and are preserved in sediments associated with seasonally dry paleosol intervals where calculated Mean Annual Temperatures averaged ~8.7 ± 4.4 °C and Mean Annual Precipitation was 890 ± 181 mm/yr (Gastaldo et al., 2020c). Many of these taxa were once considered as recovery plant of the Triassic by other workers (e.g., Eshet et al., 1995) but, now, are known to have their first appearance datums in the Permian (e.g., Blomenkemper et al., 2019).

3.3. Summary of the upper Beaufort Group vegetation

Paleobotanical assemblages recovered from paleolandscapes of the Balfour Formation (Fig. 2) are dominated by taxa of the gymnosperm *Glossopteris*. Representatives are preserved more commonly as adpressions whereas permineralized wood is less common (Sec. 4). Glossopterids grew in seasonally wet soils and peat, and the group is considered to have preferred wetlands. Palynological assemblages recovered from where megafloras are preserved also show a dominance of this gymnosperm group in the spore-and-pollen spectrum. Horsetails assigned to three different groups, and represent groundcover plants or vines. Rarely are other lower vascular plant groups (e.g., club mosses and ferns) or gymnosperms encountered in megafloras. Yet, these groups, and particularly other gymnosperms (corystosperms, peltasperms, conifers) are preserved as part of the palynological spectrum in sediments deposited under more seasonally dry conditions. Although members of the corystosperms and peltasperms have been considered to represent post-extinction communities, their existence in the latest Permian precludes such an interpretation.

4. Spatial and temporal distribution of Karoo plant assemblages

The majority of the Karoo bedrock today is covered either in dwarf succulent shrubby vegetation, talus comprised of resistant sandstone and/or dolerite boulders, or both, which may be up to several meters in depth. Upper Paleozoic and Lower Mesozoic Karoo strata typically are exposed either as thin surface outcrops in quarries of a few meters in relief, or in narrow erosional drainage gullies (dongas). Dongas vertically traverse escarpments, which are capped by resistant lithologies. In some instances it is possible to measure a stratigraphic section that approaches 300 m, although gradients at higher elevations often are difficult to access limiting observations to resistant sandstones. In

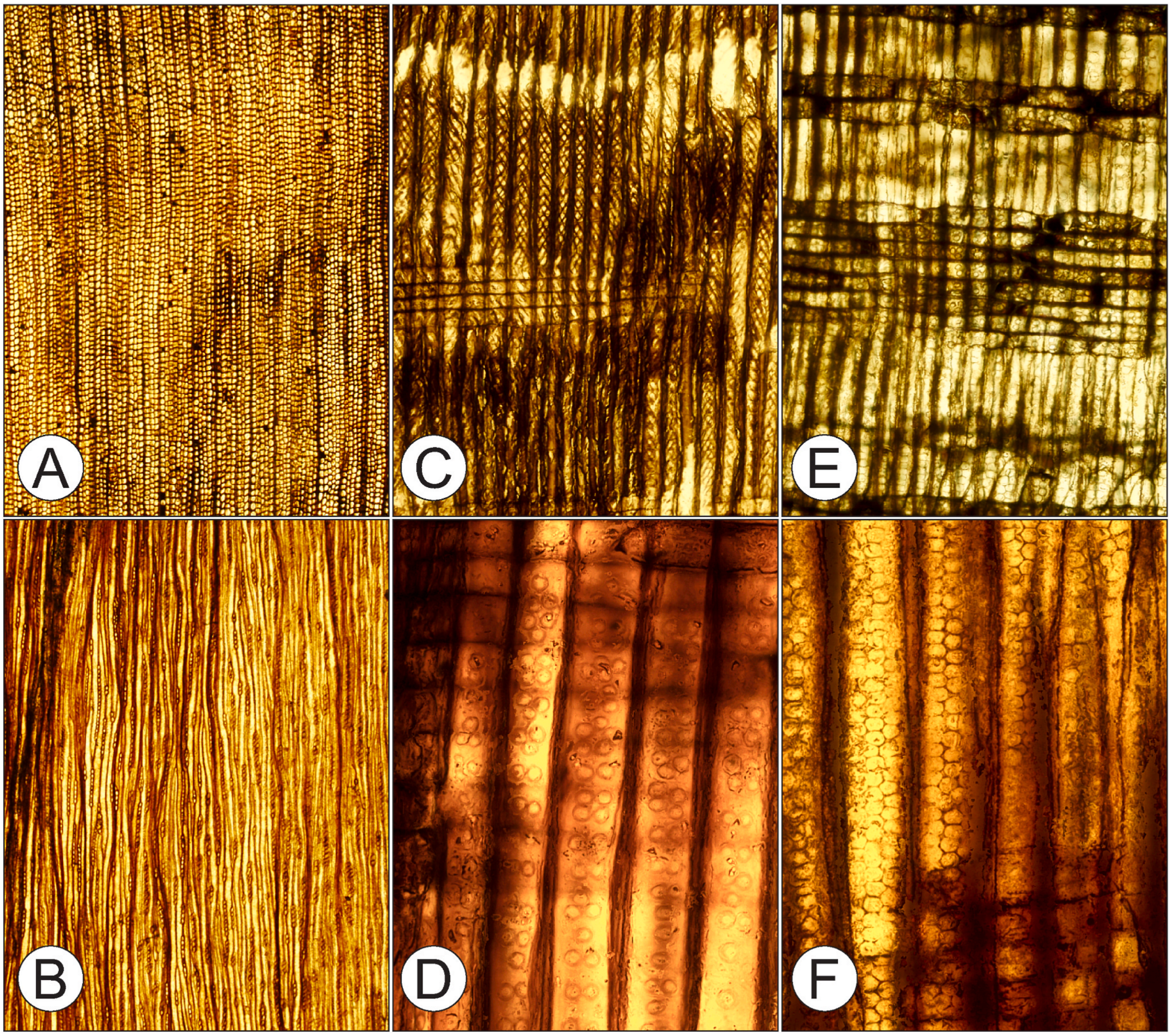


Fig. 7. Karoo Fossil Wood, where generic identification is best discriminated in Radial Longitudinal thin Sections (RLS = section through the center of the axis). (A) Cross (transverse) section of a typical Permian conifer-type wood with uniform rows of round to square conducting cells (tracheids). Magnification 40x. (B) Longitudinal section cut tangential to the center of the plant of a typical Permian conifer-type wood with longitudinal conducting cells (tracheids) and rays comprised of a single-row (uniseriate) of similar-sized (homocellular) cells. (C) RLS of Early Permian *Prototaxoxylon uniseriale* with spiral thickenings on the conducting cells (tracheids) and bordered pits. Bordered pits (intracellular pores) conform to those found in found in several gymnosperm families. (D) RLS of *Australoxylon teixeirae* (Permian) with clusters of bordered pits on the tracheid walls. (E) RLS of *Agathoxylon africanum*, the most common wood spanning Late Permian–Triassic, with two rows (biseriate) of bordered pitting arranged in an alternating pattern. (F) RLS of Late Permian *Agathoxylon karooensis* with bi-to-triseriate (two-to-three rows) alternate bordered pitting. Scale: all tracheids are 35–40 μm in diameter.

general, though, donga exposures are limited in width to less than a few meters, depending on their elevation on the mountainside. Hence, the availability of exposures where fossiliferous plant beds can be encountered or traced laterally, described in context, and sampled is limited to lower elevations. In contrast, vertebrate remains have been collected from surface exposures where surrounding rock has weathered around calcified skeletons and skeletal elements.

Before the incorporation of geochronology and magnetostratigraphy, vertebrate biostratigraphy served as the way in which the monotonous sandstone-and-siltstone succession of Karoo rocks were assigned relative ages. Hence, vertebrate biostratigraphy served as the only temporal paradigm into which fossil plants could be placed. We provide the reader with data derived from more than 20 years of investigations on the occurrence and frequency of plant fossils in the Eastern Cape and Free State provinces. We will demonstrate that the occurrence of paleobotanical assemblages in this part of the basin is rare; very rare. These occurrences will be set in a temporal context showing that geochronometric age constraints can be obtained in greater numbers in Eastern Cape rocks, proximal in the basin, than in Free State successions, which are in a distal basinal position. We provide examples of how combining geochronometric and magnetostratigraphic data, in conjunction with other techniques, constrain time and sedimentation patterns in this part of the Karoo Basin.

4.1. Historical and geographic context of plant sites

Vertebrate paleontology has been the driving force in South Africa for more than a century, and many of the upper Permian–Lower Triassic fossil-plant localities are tied directly to collection sites where megafaunal elements are reported. In essence, though, there are two, basic geographic areas from which the Permian–Triassic vertebrate database originates. The first is in the Eastern Cape Province where they are described as “classic” PTB sections. Here, localities (variously named in the literature for same site; Fig. 3) include: Old Wapadsberg Pass (−31.921867°, 24.897100°), Lootsberg Pass (−31.848384°, 24.077036°), Tweefontein of Ward et al. (2005; −31.838050°, 24.847217°); Tweefontein[1] (−31.824033°, 24.812067°) and Tweefontein[2] (−31.843067°, 24.847783°) of Gastaldo et al. (2018, 2021; to

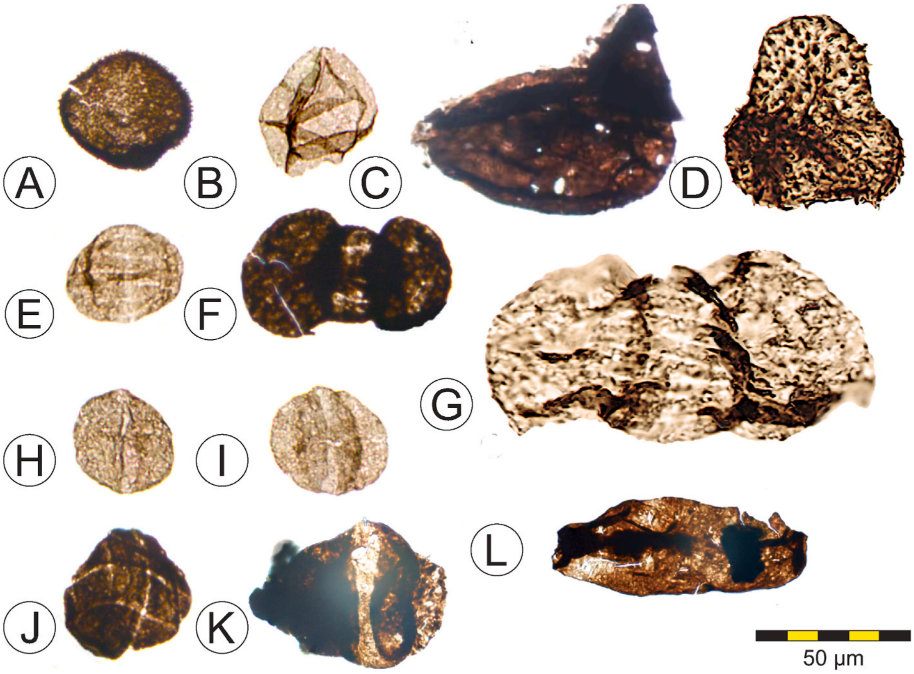


Fig. 8. Representative Beaufort Group palynomorphs. Algae: (A) *Mehlisphaeridium* sp., Quaggasfontein farm, Eastern Cape (UCMP PA1476, UCMP 390326, WAP803–2, H18-2). Equisetales: (B) *Calamospora* sp., Quaggasfontein farm, Eastern Cape (UCMP PA1476, UCMP 390327, WAP803-3, O32-2); (C) *Columinsiporites* cf. *peppersii*, Wapadsberg Pass, Eastern Cape (Prevec et al., 2010; UCMP PA1179, UCMP 398617, SA-NWP2.A, E37-1). Pteridophytales: (D) *Horriditriletes teretangulatus*, Clouston Farm, Kwazulu Natal (Prevec et al., 2009; UCMP PA1179, UCMP 398623, SA-CA0.5–9, H37-4.). Glossopteridales: (E) *Protohaploxypinus* sp., Quaggasfontein farm, Eastern Cape (UCMP PA1476, UCMP 390328, WAP803-3, O31–O), (F) *Striatiopodocarpites* sp., Quaggasfontein farm, Eastern Cape (UCMP PA1476, UCMP 390329, WAP803-1, P26–O), (G) *Striatiopodocarpites cancellatus,* Clouston Farm, Kwazulu Natal (Prevec et al., 2009; UCMP PA1179, UCMP 398628, SA-CA0.5–5, C44-3); Peltaspermales and Voltzialeas: (H) *Scheuringipollenites* sp., Quaggasfontein farm, Eastern Cape (UCMP PA1179, UCMP 390330, WAP803–3, H29-1), (I) *Alisporites* sp., Quaggasfontein farm, Eastern Cape; ?Voltzialeas (UCMP PA1476, UCMP 290221, WAP803–2, K28-3); (J) *Guttulapollenites* sp., Quaggasfontein farm, Eastern Cape. Gymnospermales (?Peltaspermales; UCMP PA1476, UCMP 390332 WAP803–2, M25-4); (K) *Falcisporites australis*, Quaggasfontein farm, Eastern Cape. Fungal/algal (Gastaldo et al., 2019; UCMP PA351.2m UCMP 398655,G37-3/4: (L) *Reduviasporonites* sp., Donald 207 farm (Gastaldo et al., 2019; UCMP PA1351.1, UCMP 398664, M49-1). Note range of palynomorph color, ranging from yellow-brown (~100°C; thermal alteration index 2; Utting and Hamblin, 1991) to black (>200°C, thermal alteration index 4+), as a function of post-depositional thermal alteration in response to the emplacement of the Karoo-Ferrar dolorites. Taxonomic names are followed by a UCMP collection locality number code, the UCMP specimen number, and England Finder graticule coordinates. Scale = 50 µm. Images courtesy of C.V. Looy.

clarify confusion about vertebrate-collection sites, see Gastaldo et al. (2017), 2021; Old Lootsberg Pass (−31.795743°, 24.812067°); Carlton Heights (−31.29228°, 24.95152°), and KommandoDrif Dam (−32.138540°, 26.083277°). The geographic straight-line distance between Lootsberg Pass and (1) Old Lootsberg Pass is 9.5 km to the NW, (2) Wapadsberg Pass is 9.5 km to the SE, (3) Carlton Heights is 45 km to the N, and (4) Kommandodrif Dam is 115 km to the E (Fig. 1B). The second generalized area is in the Free State Province, where the distance from Lootsberg Pass is > 200 km to the NE. Here, reported PTB localities include: Bethel (−30.422040°, 26.270160°) and Heldenmoed (−30.417117°, 26.264167°) farms, Donald 207 (=Fairydale of Smith and Botha-Brink, 2014; −30.407000°, 26.237710°), and Nooitgedacht (−30.32530°, 25.93132°). Retallack et al. (2003, their Fig. 3B) report a laminated succession at Bethel farm, located in Tussen die Riviere game park (Fig. 3B), that is fault bounded and cannot be correlated with rocks on other localities (Gastaldo et al., 2009). Greater than 80% of the vertebrate specimens used in the development of the interpreted vertebrate-defined extinction event, equated to the PTB marine extinction (Ward et al., 2005; Smith and Botha-Brink, 2014; Viglietti et al., 2021), were recovered from an ~10 km^2 area on farms Bethel, Heldenmoed, and Donald 207, and Tussen die Riviere nature reserve (Gastaldo et al., 2019). Hence, these “classic” Eastern Cape and Free State localities have been the primary focus of our efforts over the past 20 years.

4.2. *Stratigraphic context of plant sites*

The lithostratigraphy of the upper Balfour Formation (Fig. 2), in general, consists of repetitive fining-up successions of fine-to very fine-grained lithic wacke overlain by, and laterally equivalent to, coarse-to-fine siltstone (e.g., Neveling et al., 2016). This is true in both the Eastern Cape and Free State province localities. Lithic sandstone bodies range in color from yellowish gray to light to-medium gray and vary in architectural elements and hierarchies. Individual sandstone bodies attain thicknesses of ~12 m and thin laterally along strike (e.g., Gastaldo et al., 2021). Erosional channel bases may be overlain by intraformational conglomerate-lag deposits comprised of calcite-cemented pedogenic nodules (remants of ghost landscapes; Gastaldo et al., 2020b), mudchip clasts ranging from millimeter-to-decimeter scale, vertebrate skeletal elements and bone fragments, and rare mm-scale euhedral pyrite supported in a sandstone matrix. Gastaldo et al. (2021) note that intraformational conglomerate, including mudchip conglomerate, is rare, comprising a very low proportion of the rock record. To date, we have not encountered coarse woody detritus (CWD) in any lag or in any channel sandstone deposit. Sandstone bodies are organized into trough cross-bedded bedsets that fine upwards to very thin, low angle cross beds where ripples and small-scale trough cross beds are found across bed contacts. Fining up sandy siltstone and siltstone commonly are interbedded with thin, decameter-scale lenticular wacke (Gastaldo et al., 2020a, 2020c, 2021). Abandoned channel deposits are infrequently encountered and, when present, are heterolithic and exhibit planar lamination wherein beds fine upward (very fine sandstone to coarse siltstone; coarse to fine siltstone). Individual beds may be greenish-gray or reddish-gray, the latter color being a function of the presence of hematite (Li et al., 2017).

Fine clastic deposits include coarse and fine siltstone, silicified siltstone (porcellanite; Gastaldo et al., 2015), and rarely claystone (devitrified volcanic airfall ash; Gastaldo et al., 2020a). Siltstone occurs both in, and adjacent to, channel bodies and, in general, is massive in character. Massive in-channel siltstone conforms to trough fills whereas siltstone in floodplain deposits has undergone various pedogenic processes ranging from immature soils (Inceptisols; Gastaldo et al., 2014) to mature soils (Calcic Vertisols; Gastaldo et al., 2020c). Individual siltstone beds may show a lateral change in color from greenish-gray to reddish gray, interpreted as a function of fluxes in groundwater geochemistry (Li et al., 2017).

The total stratigraphic thickness of measured sections that form the basis of the current contribution is > 3750 m, encompassing the above localities in which each is reported to contain the vertebrate-defined PTB. Where outcrop is limited or inaccessible, such as the Carlton Heights, Kommandodrif Dam, or Nooitgedacht localities, a single measured section was acquired beginning at the base of the knoll (kopjie). In other localities where several dongas traverse the mountainside, as many as ten or more measured sections of various stratigraphic length were correlated across the escarpment using laterally extensive sandstone bodies (e.g., Gastaldo et al., 2021). Table 1 presents the number of measured sections, their total stratigraphic thickness, the number and type of plant-bearing intervals for each locality, and pertinent citations.

4.2.1. Eastern Cape Province

Ten stratigraphic sections are published for Old and New Wapadsberg Pass (Prevec et al., 2010; Gastaldo et al., 2014), and for donga exposures on farm Quaggasfontein (Gastaldo et al., 2020c); two measured sections have been described on farm Pienaarsbaaken (Fig. 3B). A total of 1130 m of section are detailed from these 12 successions. Leaves of the gymnosperm, *Glossopteris* (Figs. 4 and 5), dominate these assemblages and are preserved as bedded litters in the basal intervals of the Old and New Wapadsberg sections (Prevec et al., 2010). Isolated aerial debris is rare higher in the section, and we have not encountered large, coarse-woody detritus (CWD) in either any fluvial sandstone or associated paleosol in any section. Here, only nine beds and paleosol horizons account for our understanding of the adpression assemblages, and permineralized wood fragments have been encountered scattered over only two surfaces. In contrast, we have recovered ten spore-and-pollen assemblages and palynomorphs display a range of preservational qualities and thermal indices of alteration (Fig. 8). Palynological assemblages are associated with bedded litters in the basal intervals, whereas other beds preserve them in fine-grained laminated siltstone higher in these sections. In contrast to megafloral assemblages, glossopterid pollen grains are often mixed with those of other gymnosperm groups for which there is no evidence in the megafloral record (Gastaldo et al., 2018b). To date, though, we have not encountered or recovered either adpression or palynological assemblages higher than the Balfour or Katberg formations in-and-around Wapadsberg Pass.

The area in-and-around Lootsberg Pass is the second classic region in which the vertebrate-defined extinction is reported and paleobotanical assemblages described. Exposures along farm roads and in dongas spread across the escarpment can be traced over a distance of ~10 km. These are found on the Kingwill farms, which include three geographically separate localities reported as Tweefontein and Blaauwater (Table 1; Fig. 3A). Over this expansive area we have reported >1650 m in 23 measured sections (Gastaldo et al., 2005, 2017, 2018, 2020a, 2020b, 2021). Similar to Wapadsberg Pass sites, glossopterids dominate

Table 1

The stratigraphic position of Eastern Cape and Free State province localities used in the current compilation noting: the number of measured sections and their total stratigraphic thickness; the number of intervals from which permineralized wood, macrofloras, and microfloras have been either reported or observed; and references for published fossil-plant assemblages. Note that measured sections published by earlier workers have not been included because their is uncertainty about where mega- or microfloras were recovered. [1] Thickness of measured sections is based only on work of the authors and colleagues unless specified. [2] The number of sections and total thickness of rock measured on Bethel and Heldenmoed farms includes both Palingkloof and Katberg intervals (see discussion in Gastaldo et al., 2019 for problems in the placement for the base of the Katberg Formation). [3]Tweefontain consists of three dongas geographically separated over a lateral distance of 4.5 km (See Gastaldo et al., 2021). [4]Number of productive samples reported in the literature; our palynology values indicate productive localities or stratigraphic intervals rather than number of productive samples.

Period	Stratigraphic Unit	Locality	# Measured Sections[1]	Total Thickness[1]	Permin. Wood	Adpression Macroflora	Palynoflora	Citation
Triassic	Burgersdorp Fm.	Boesmanshoek	1	75 m		1		Gastaldo et al. (2005)
Upper Permian	Katberg Fm.	Carlton Heights					22[4]	Steiner et al. (2003)
		Carlton Heights				1		Retallack et al. (2003)
		Carlton Heights	8	380 m		1		Gastaldo et al. (2005); Pace et al. (2009)
	Balfour Fm. Palingkloof Mbr	Carlton Heights	1	60 m		1		Gastaldo et al. (2005); unpublished
	.	Nooitgedacht	2	86 m		5		Botha et al. (2020)
		Nooitgedacht	1	70 m			2	Gastaldo et al. (2020)
		Donald 207/Fairydale	8	340 m			1	Barbolini et al. (2018) Gastaldo et al. (2019)
		Bethel/Heldenmoed farm[2]	13	685 m		2		Gastaldo et al. (2005, 2009, 2019, 2020)
		CommandoDrift	2	210 m		2	12[4]	Gastaldo et al. (2005); unpublished Coney et al. (2007)
		Old Lootsberg Pass (Blaauwater)	13	880 m	2	6	1	Gastaldo et al. (2017)
		Tweefontein[3]	7	780 m				Gastaldo et al. (2017, 2021)
		Lootsberg Pass	3					Gastaldo et al. (2021); unpublished
		Pienaarsbaaken	2	180 m		1	1	unpublished
		Quaggasfontein	1	155 m	1	4	3	Gastaldo et al. (2020)
		Quaggasfontein					2	Gastaldo et al. (2018); unpublished
		Old Wapadsburg Pass/ Pienaarsbaaken	8	730 m	1	2	3	Gastaldo et al. (2005); Prevec et al. (2010)
		New Wapadsburg Pass	1	65 m		2	1	Gastaldo et al. (2014, 2018b); Prevec et al. (2010); unpublished
	Elandsberg Mbr. ?	Tweefontein				1	1	Gastaldo et al. (2017)

the megaflora and microflora in seven and two localities, respectively (Table 1). All fossils are preserved in olive-gray siltstone, and we have not encountered CWD in any outcrop.

Megafloral preservation in olive-gray siltstone is also the case at Kommandodrif Dam (N = 2 beds) and Carlton Heights (N = 2 beds) where isolated aerial debris is reported (Gastaldo et al., 2005). A single bed of isolated debris occurs in the Palingkloof Member at Carlton Heights in a heterolithic "laminite" interval that was reported to represent the PTB (Retallack et al., 2003). The assignment of that succession to the end-Permian marine equivalent was based on the assumption, at the time, that a unique "laminite" facies occurred at a single, basin-wide horizon and marked the event. This assumption of a single, heterolithic, contemporaneous interval with a basin-wide correlation has been shown to be in error at the Bethel farm locality (Gastaldo et al., 2009) where it was first introduced into the literature (Smith, 1995). The most recent data demonstrate that the "laminite" interval believed to mark the PTB as reported by previous authors at Lootsberg Pass (Ward et al., 2000, 2005; Retallack et al., 2003), for example, lies stratigraphically below an early Changhsingian U–Pb CA-ID-TIMS age of 252.43 ± 0.19 Ma (Gastaldo et al., 2021). And, similar to Wapadsberg Pass, we have not encountered assemblages higher in the Katberg Formation except at Carlton Heights.

Isolated aerial fossil-plant debris is rarely encountered in the Katberg Formation, where we have measured 380 m of stratigraphy in eight sections (Pace et al., 2009). Here, plant hash is scattered atop bedding in very fine sandstone, identifiable plant debris is found on a single bed (Gastaldo et al., 2005), and no CWD has been encountered. Additional, scattered megafloral elements (Retallack et al., 2003; Fig. 6) and 22 intervals have been reported to yield microfloral assemblages, spread over an thickness of 59 m (Steiner et al., 2003). The succession from which these palynological assemblages recovered by Steiner et al. (2003) appears not to have been sampled at the classic exposure along the M9. Rather, sampling was done on exposures somewhere along the M10 motorway (N. Tabor, pers. comm. 2019; Fig. 3A) for which no GPS coordinates are published. We have been unable to replicate the observations of Steiner et al. (2003) in the Carlton Heights succession (Pace et al., 2009).

4.2.2. *Free State province*

The vertebrate database on which the end-Permian vertebrate extinction is interpreted (Ward et al., 2005; Smith and Botha-Brink, 2014; Viglietti et al., 2021) originates from three adjacent farms in the Free State Province: Bethel, Heldenmoed, and Donald 207/Fairydale (Fig. 3B; Gastaldo et al., 2019). We have reported a total of 1130 m of stratigraphy encompassing 22 measured sections of various lengths across the area in addition to several, unpublished short stratigraphic sections (Table 1; Neveling et al., 2016; Li et al., 2017; Gastaldo et al., 2009; 2019). Although isolated resistant horsetail or unidentifiable narrow axes may be encountered infrequently, identifiable megafloral remains are very rare. To date, only two fossiliferous intervals have been found on the Bethel and Heldenmoed farms; no bedded litter has been encountered on farm Donald 207. There is a similar dearth of recoverable palynological assemblages, with a single productive interval reported from Donald 207 farm, high in the section, that is assigned to the *Protohaploxypinus microcorpus* palynozone (Table 1; Fig. 2; Gastaldo et al., 2019). Rocks on farm Nooitgedacht have been more productive.

Nooitgedacht outcrops occur around kopjies on the farm, called Loskop and Spitskop. Botha et al. (2020) illustrate one composite section, totaling 86 m of stratigraphy, from each hill. We have documented a single, 90-m section from Loskop (Gastaldo et al., 2020a). Botha et al. (2020) report five intervals in which megafloral remains are preserved, and figure specimens assigned to the horsetail *Paracalamites*, the gymosperm *Glossopteris* and its reproductive propagules, and an indeterminate fern genus. Gastaldo et al. (2020a) report two beds in which palynomorphs are well preserved. The lower interval occurs directly above a zircon-age date of 252.24 ± 0.11 Ma from a pristine ash-fall deposit, assigned to the *Dulhuntyispora parvithola* palynozone. The upper assemblage, assigned to the *Playfordiaspora crenulata* zone (Fig. 2), is preserved ~10 m higher in a fine-grained trough fill, where the base of the fluvial sandstone is erosional and overlain by an intraformational PNC lag deposit.

4.3. *Lesson 1: proportional representation of paleobotanical assemblages*

In total, 29 beds in which megafossil assemblages are encountered and described (bounding surfaces on which isolated axes or mesofossil organic drapes occur are excluded) and four beds from which permineralized wood (Gastaldo et al., 2015, 2017) span the uppermost Permian and Lower Triassic succession. In contrast, at least 48 beds (Table 1) are reported to yield productive palynological assemblages over the same interval. Considering that these data originate from >3750 m of total measured section, megafloral remains are preserved in <1% of the available rock record (0.9% all megafloral elements; permineralized wood = 0.1%, adpressions = 0.8%; Table 2). Although spore-and-pollen assemblages are encountered more frequently in the literature (1.3%; Table 1), they are preserved in only 0.4% of our measured sections. These very low values in the Karoo are consistent with data from other fully continental, upper Permian–Lower Triassic successions documented in the Bogda Mountains, Xinjiang Province, western China (Gastaldo et al., 2023). There, permineralized wood is encountered in <2% and adpression assemblages in <1% of depositional high-order cycles, which vary in stratigraphic thickness across nine localities extending over 100 km distance. In fact, if each western China assemblage was preserved throughout the entirety of 1 m of measured section, these intervals would represent a mere 0.55% of the entire Bogda Mountain measured stratigraphic record of 4709 m (Gastaldo et al., 2023). In reality, identifiable macrofloral remains generally are limited to intervals of centimeters to decimeters reducing their proportionality in the rock record. One should not anticipate encountering these assemblages on a routine basis.

4.4. *Time and stratigraphic relationships*

The continental stratigraphic record is notoriously incomplete and the temporal relationships between units are difficult to interpret, in large part, because of a scarcity of datable sediments. Considerable time is "locked" in paleosols as diastems, with most fluvial sediments in adjacent deposits representing various stages of river processes prior to either avulsion (channel switching), abandonment, or a resetting of the land surface in response to landscape degradation or a basinward shift in depocenters. Continued erosion and reworking of sediments on land are the norm, and not the exception, and these processes are influenced by a combination of climatic or tectonic factors, or both (Bull, 1991; Gastaldo

Table 2
Number of horizons and percentage of stratigraphic record from which permineralized wood has been recovered, adpression megafloras, paleosols with subaerial litters and subsurface rooting, and productive and figured palynological assemblages per locality in our database (see Table 1). In addition, numbers of individual samples from which palynological assemblages have been reported in the literature are separated. The value assumes that each fossil assemblage is preserved over a 1 m interval of rock; in reality, most are found over a few centimeters to decimeters of rock.

Total Meters of Measured Section	Permineralized Wood	Adpression assemblages	Paleosols w/ adpression leaf litters and rooting	Palynology
3960	4 0.10%	28 0.71%	1 0.03%	16 0.40%
Microfloras from literature				48 1.3%

and Demko, 2011). Erosional surfaces, often incised into underlying deposits and found at the base of fluvial sandstone bodies, are evidence of an interval when the land's surface underwent erosion and degradation. These surfaces mark a hiatus in time and, hence, a gap of some duration in the stratigraphic record longer than paleosol diastems. Nevertheless, continental successions in the Karoo, and elsewhere, often are reported to represent "continuous" sedimentation. Such broad assumptions have allowed workers, in turn, to interpret biological patterns from the paleontological assemblages preserved, therein, over the interval of interest no matter how infrequent these may be in the stratigraphic record (Gastaldo et al., 2023). Yet, without any geochronologic or rock magnetic data with which to place time constraints (temporal boundaries) onto the stratigraphic record, such ecological interpretations only can be considered as broad working hypotheses subject to revision. The stratigraphy and fossil record of the Karoo is no exception and can serve as a model for understanding other continental successions.

4.4.1. *Geochronology*

The gold standard for establishing a maximum age constraint on a deposit is a U–Pb CA-ID-TIMS age estimate obtained from individual zircon grains, of a euhedral, pristine nature, recovered from a volcanogenic sediment. Values of uranium-and-lead isotopes from individual crystals in a sample suite are plotted on a Concordia diagram, which is a graphical way to evaluate the internal consistency of U–Pb data. Concordant isotopic compositional space is marked by the concordia line, a curve, and isotopic ratio measurements are figured as confidence ellipses (see: Gastaldo et al., 2015, 2021). Concordant samples that plot near to, or overlap with, the concordia line represent geochronological reliability (Ludwig, 1998). Volcanogenic airfall deposits are exceedingly rare and easily eroded on land. A rule-of-thumb to identify these in the field is the "what doesn't belong here" approach, which is based on their unusual color (light gray [Munsell color N7] to white [N8], in general), texture (silicification, a lithology appearing fused and rings when struck, or devitrification to clay), and grain-size when compared with surrounding lithologies. But, these deposits often are overlooked because they are relatively thin (mm–cm) and discontinuous. Yet, when identified and sampled, often provide temporal insight.

4.4.1.1. Eastern Cape Province. Volcanogenic sediments are more common in the Eastern Cape localities where they occur in the form of silicified ash (e.g., porcellanite; Gastaldo et al., 2018a) or, more often, as a devitrified tuffite (claystone; Gastaldo et al., 2014, 2021, unpublished). Analytical results of all beds studied, to date, indicate that these deposits are Lopingian in age (Fig. 2). The youngest Changhsingian airfall deposits are found in close stratigraphic proximity to megafloral and microfloral assemblages on Tweefontein and Blaauwater farms. But, caution is advised on interpreting an age for a succession in which tuffites occur because older, reworked Wuchiapingian tuffs also occur as trough fills in fluvial crossbed sets situated stratigraphically above these airfall deposits (Gastaldo et al., 2021). In the absence of, or in conjunction with, U–Pb geochronometric constraints based on one or more suites of zircon crystals, rock magnetic data can provide broader temporal constraints (see 4.3.2).

4.4.1.2. Free State province. In contrast to volcanogenic beds in the Eastern Cape, only claystone (devitrified tuffite) has been encountered in the Free State at one locality, to date. A discontinuous, thin, cm-thick devitrified, light gray clay occurs on farm Nooitgedacht from which ~1000 pristine, euhedral zircon grains were recovered from ~800 g of the unit (Gastaldo et al., 2020a). Pristine zircon differs from detrital zircon recovered from siltstone directly below and above the ash. Zircon recovered from the ash exhibit long or short prismatic, equant, or multi-faceted grains that are translucent; in contrast, detrital zircons have a wide variation in grain size, morphology, and color, and exhibit variable surface abrasion and rounding. A suite of 13 pristine zircon grains analyzed by U–Pb CA-ID-TIMS gives a latest Changhsingian age of 252.24 ± 0.11 Ma (Gastaldo et al., 2020a) to the airfall ash, which is situated ~5 m above the vertebrate-defined PTB of Botha et al. (2020).

Botha et al. (2020, p. 6) report results of U–Pb LA-ICP-MS analyses on a suite of detrital zircon grains recovered from a sandstone in the Spitskop section ~8 m below their vertebrate-defined, mass-extinction event. The largest modal peak is latest Permian with all dates reported with uncertainties of several million years, which is a consequence of this analytical technique. An Early Triassic U–Pb ID-TIMS age of 251.7 ± 0.3 Ma, based on the five youngest detrital zircons, also is reported from a siltstone (Botha et al., 2020, their Table 2 and Fig. 3) ~8 m below their boundary extinction event. Neither analytical data of these five grains, nor any U–Pb ID-TIMS data of this sample suite, are provided by these authors. Gastaldo et al. (2020a) noted that this earliest Triassic, detrital zircon, maximum age for their upper *Daptocephalus* AZ postdates the end-Permian event in the oceans (251.941–250.880 Ma; Burgess et al., 2014). The terrestrial extinction event identified in coastal plain deposits of Eastern Australia began at 252.31 ± 0.07 Ma, predating the marine event by ~300 kyrs and, lasted ~100 ka (Mays et al., 2020; and others).

4.4.2. *Magnetostratigraphy*

Developments in the field of magnetostratigraphy have extended its application from an approach to date rocks with the identification of geomagnetic polarity reversals, to a suite of techniques includes measurements of all geomagnetic field parameters, environmental magnetism, and rock magnetic change sequestered in sedimentary rocks. Before a polarity stratigraphy can be demonstrated, the rocks in question must be shown to demonstrate a retention of a geomagnetic field, which might be either primary (at the time of sediment deposition) or secondary (reset as a consequence of subsequent processes including chemical changes or long-term exposure to the geomagnetic field that affect assemblages of magnetic phases after rock formation). That property is dependent on its coercivity (the ability of magnetic phases to resist an external magnetic field without demagnetization), and there are several ways by which a sedimentary rock can record a geologically stable natural remanent magnetization (NRM; Jovane et al., 2013). Three types of NRM are recognized based on how the rock aquired its paleomagnetic signal: thermoremanent magnetism (TRM), chemical remanent magnetization (CRM), and detrital remanent magnetization (DRM; Langereis et al., 2010).

Detrital magnetic phases of appropriate grain size lock in and retain the original magnetization of the Earth's geomagnetic field during deposition, early sediment compaction, and diagenesis. To unravel the signal, it is critical to accurately record the orientation of the rock sample when collected in the field. This is accomplished either through coring in the field using a portable drilling apparatus, collecting oriented block samples, or the extraction of small flakes of rock, oriented with respect to the vertical and geographic north, and placing them into non-magnetic ceramic boxes packed tightly with either cotton or glass wool, and firmly taping them shut (Gastaldo et al., 2021) before progressive alternating field and/or thermal demagnetization in the laboratory. This technique is used to remove the effects of secondary NRM from the primary component, retaining the primary NRM signal. Samples are subjected to stepwise increases in temperature or alternating field in a field-free (zero magnetic field) enclosure. After each demagnetization step, the residual magnetism is measured and the resulting directional and intensity changes are displayed and analyzed (Zijderveld, 1967; Langereis et al., 2010). Data from these experiments are displayed using two methods to reconstruct the component structure of the NRM; Zijderveld diagrams (after Zijderveld, 1967) and vector end-point demagnetization diagrams. Magnetic components are extracted from the Zijderveld diagrams using least-square analysis (Kirschvink, 1980), and the most stable and consistent component that can be isolated is considered the characteristic remanent magnetization (ChRM), the nature of which must be interpreted. Subsequently, ChRM is tested to determine if the geomagnetic field record is primary or secondary by several approaches, and reliability tests also are performed (consistency, reversal, and fold tests; Langereis et al., 2010). Once laboratory obtained data are analyzed and considered in the context of the field geologic setting, the NRM signal can be interpreted to represent a time of sediment deposition during which magnetization acquisition takes place during a time of either a normal or reverse polarity of the geomagnetic field.

Rock magnetic properties, if not reset by younger intrusive activity, can provide insight into the broad timing of when paleolandscapes developed. When attempting to discern time, magnetic polarity data obtained from closely spaced stratigraphic beds provide a magnetostratigraphy that can be evaluated in several ways. First, the thickness of the stratigraphic succession in which either a normal or reverse polarity magnetozone is documented produces a comparative record for an estimate of the duration of each. Although there is wide variance in the span of a chron over Earth history, the average magnetozone duration has been determined to be ~180 ka (Lowrie and Kent, 2004). Hence, normal and reverse magnetozones of a similar thickness in a fully continental succession roughly could be considered time equivalents, with caveats. When a magnetozone is truncated by an erosional unconformity, though, and overlain by rocks exhibiting the opposite magnetic signal, time is missing. The actual amount of missing time is difficult to discern. But, a thin magnetozone of a few meters thickness underlying the erosional unconformity certainly represents significantly more missing time than a thicker underlying magnetozone extending over decameters (Fig. 9). Secondly, correlative stratigraphic sections over distances of only several kilometers may not preserve the same magnetostratigraphic record, especially if thin, truncated magnetozones characterize the succession. Where one or more thin magnetozones, truncated at their upper boundary, may be present in one measured section, one or more of these intervals may be absent in a correlative section (see Gastaldo et al., 2021; Fig. 10). Both of these factors influence the interpretation of whether a “continuous” stratigraphic record is present in any specific part of a basin and the biological trends preserved therein.

4.4.2.1. Eastern Cape Province. Rocks in the Old Lootsberg Pass section record the presence of four normal polarity and three reverse polarity magnetozones (Fig. 10). All normal polarity intervals extend over tens of meters; in contrast, reverse polarity intervals are short and truncated by erosional unconformities. Only ~1.5 km to the east in the Tweefontein^1 section, two normal and one reverse polarity magnetozones are identified (Gastaldo et al., 2021), where the latter occurs in a stratigraphic position that is below that of the Old Lootsberg Pass reverse magnetozone (Fig. 10). The interval in which the upper reverse polarity magnetozone may occur at Tweefontein^1, if not eroded away, was not sampled due to logistics. Only a single normal polarity magnetozone is documented in the rocks ~4 km farther to the east in the Tweefontein^2 section, the thickness of which encompasses both the lower and upper reverse polarity magnetozones at Old Lootsberg Pass. Hence, depending on where sections are measured and sampled for rock magnetic properties, very different impressions and interpretations of time are manifested over a short lateral distance in-and-around these classic localities.

Rocks at both Old and New Wapadsberg Pass have been remagnetized by dolerite intrusions with the emplacement of the Jurassic Karoo-Ferrar Large Igneous Province (LIP; Neveling et al., 2016). It has not been possible to recover their primary magnetization. Approximately 3 km to the northwest of these classic sites, though, Akatakpo et al. (2022) report the rock magnetic properties for two measured sections on farm Pienaarsbaaken. Here, two normal and one reverse polarity magnetozones are encountered. The reverse magnetic polarity magnetozone occurs near the base of the 180 m section (Table 1) and is bracketed by normal polarity intervals. The upper normal polarity intervals are interpreted to be of Changhsingian age based on an associated palynoflora (Gastaldo et al., 2018a).

4.4.2.2. Free State province. Rock magnetic properties of strata in the classic Bethel farm site have allowed for the development of a magnetostratigraphy in three measured sections, correlated across the valley, encompassing >100 m in thickness (Gastaldo et al., 2019, 2020a). Two intervals sampled in close proximity to dolerite intrusives show polarity resets, with these effects documented only within several meters of the contact with the surrounding sedimentary units. Two normal and one reverse polarity magnetozone are identified, wherein the vertebrate-defined PTB (=End Permian Extinction; Ward et al., 2000; 2005; Retallack et al., 2003; Smith and Botha-Brink, 2014; Viglietti et al., 2022) occurs in a reverse polarity interval (Gastaldo et al., 2019, Fig. 5). We note that the marine-defined PTB occurs in a normal polarity magnetozone (Shen et al., 2019). To date, there are no constraining geochronometric data published from the Bethel/Heldenmoed/Donald 207 sites. In contrast, the vertebrate-defined PTB (Botha et al., 2020) on farm Nooitgedacht occurs in a normal polarity magnetozone. Here, the bed in which the PTB is reported occurs below a U–Pb dated to 252.24 ± 0.11 Ma (see 4.3.2.1). The upper bounding surface of the normal-polarity magnetozone is erosional and overlain by a fluvial sandstone body with a basal pedogenic conglomerate-lag deposit (Gastaldo et al., 2020a). Rochín-Bañaga et al., 2023 report a U–Pb LA-ICPMS

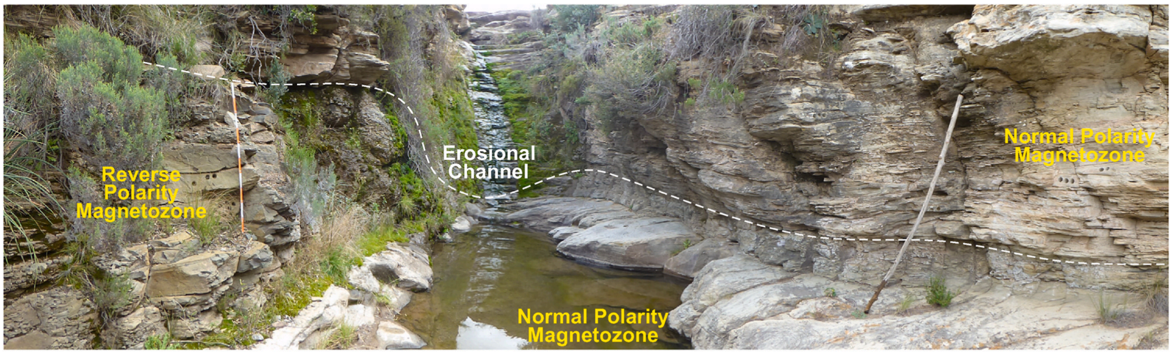
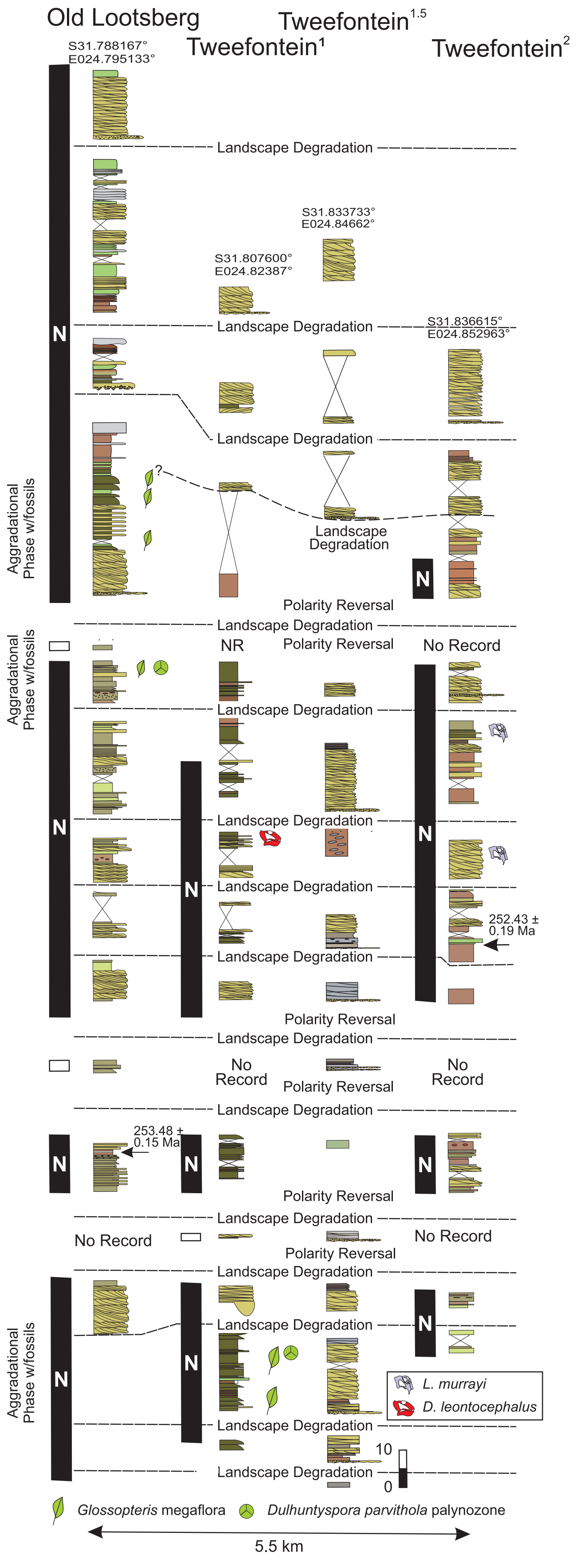


Fig. 9. Cryptic reverse polarity magnetozone exposed beneath an erosional unconformity (S 31.795125°, E 024.798815°) at Old Lootsberg Pass, Blaauwater farm (Gastaldo et al., 2018a). The landscape was reset by the erosion of sediments deposited during a reverse-polarity chron with the emplacement of an 11-m thick fluvial deposit at the onset of a degradational (erosional) phase in this part of the basin. Sampled anywhere else, the presence of a subjacent and suprajacent normal polarity magnetozone in contact with each other would evidence an impression of a continuous time interval over which these sediments accumulated. The presence of a reverse polarity magnetozone, though, demonstrates a significant temporal hiatus in the stratigraphic record. Borehole sample sites are evident in the walls of the donga; scale in decimeters.



(caption on next column)

Fig. 10. A modified Wheeler diagram in which four correlated stratigraphic sections over a 5.5 km distance along the escarpment from Old Lootsberg Pass to Lootsberg Pass (Gastaldo et al., 2018a; 2021) are shown in time-equivalent units. Time-equivalent units are bounded at the base by either: (1) an intraformational pedogenic lag deposit of a fluvial channel, the contact with the underlying lithology represents an erosional unconformity that signals a phase of landscape degradation; or (2) the identification of a non-conforming magnetozone between the subjacent and suprajacent lithologies indicating significant missing time at the contact. U–Pb CA-ID-TIMS ages constrain time, beds in which fossil plants are preserved are identified, and the position of diagnostic vertebrates used to separate the *Daptocephalus* AZ from the overlying *L. declivis* AZ as reported in the literature (Viglietti, 2020; Botha and Smith, 2020). Magnetostratigraphy shown for Old Lootsberg Pass, Tweefontein^1, and Tweefontein^2 sections (Gastaldo et al., 2021). Note the absence of any evidence of reverse polarity magnetozones in most sections, which is a function of either erosion or logistical sampling of weathered lithologies. GPS coordinates (WGS84 standard) are presented for the top of measured sections; see Gastaldo et al. (2018a, 2021) for detailed sections and their correlation across Blaauwater–Tweefontein–Lootsberg Pass.

age date of 251 ± 3 Ma from pedogenic carbonate nodules contained in this channel lag. The critical stratigraphic interval in which the PTB would have been found is missing at Nooitgedacht.

4.5. Paleobotanical assemblages in geochronologic and magnetostratigraphic context

The oldest *Glossopteris*-dominated megafloras and microfloras exposed in the Eastern Cape Province are preserved in early Changhsingian beds on Tweefontein^1. These lie below an age of 253.48 ± 0.15 Ma at an equivalent stratigraphic position in the correlative Old Lootsberg Pass section (Fig. 10; Gastaldo et al., 2021). Both age-constrained beds are in an unequivocal normal polarity magnetozone which, in the Karoo, falls in a long, reverse polarity magnetozone of the global composite of Hounslow and Balabanov (2016). Currently, there is neither a reliable age constraint on, nor a magnetostratigraphic context for, the only paleosol in which a leaf-litter (O) horizon is preserved and found at New Wapadsberg Pass (Prevec et al., 2010; Gastaldo et al., 2014). Although reworked tuffite occurs in the paleosol and a thin ashfall layer occurs within 1.5 m above the O-horizon (Gastaldo et al., 2014), these beds yielded only a few detrital zircon grains and rock magnetic properties are reset by dolerite intrusions. Without a sufficient number of high-resolution zircon analyses from pristine grains, with which a concordia plot can be developed, the age of the paleosol litter remains constrained to the Changhsingian by palynostratigraphy (*D. parvithola* zone; Gastaldo et al., 2021).

Younger, latest Permian assemblages are constrained by U–Pb ages in the Eastern Cape and Free State provinces. The *Glossopteris*-dominated mega- and microfloral assemblages at Old Lootsberg Pass (Gastaldo et al., 2017) lie ~65 m above a tuffite dated to 252.43 ± 0.19 Ma in the correlative Tweefontein^2 section (Fig. 10; Gastaldo et al., 2021). These assemblages are also in a normal polarity magnetozone that likely falls in the 1n.2n magnetozone (LT1n chron), which spans the PTB, of the global composite of Hounslow and Balabanov (2016). Beds in which *Glossopteris* leaves are preserved higher in the Old Lootsberg Pass section (Gastaldo et al., 2017) occur in a different normal polarity magnetozone. This interval overlies a very short, reverse polarity magnetozone that was truncated by erosion and landscape degradation (Fig. 9); this relationship is not recognized in the latest Permian, global composite by Hounslow and Balabanov (2016). These authors recognize the presence of a reverse polarity magnetozone 1n.1r in the Lower Triassic above the long normal magnetozone that encompasses the PTB. To date, we have not encountered any volcanogenic deposit in close proximity to the Old Lootsberg Pass floras that allow us to geochronometrically constrain their age. This is not the case for floras at Nooitgedacht.

A latest Permian age of 252.24 ± 0.11 Ma in the Free State Province at Nooitgedacht (Gastaldo et al., 2020a) overlies the *Glossopteris* floras reported by Botha et al. (2020). The U–Pb age also lies in the 1n.2n normal polarity magnetozone of the LT1n Chron of Hounslow and Balabanov (2016). Similarly, the presence of a palynological assemblage assigned to the *D. parvithola* zone, a few meters above the volcanogenic deposit, also lies in the same normal polarity magnetozone (Fig. 2). But, as previously described, this succession is truncated by an erosional contact with an intraformational conglomerate at the base of an overlying sandstone-channel. A younger microfloral assemblage, assigned to the *Playfordiaspora crenulata* palynozone, in which glossopterid pollen continues to comprise up to 40% of the assemblage (Mays et al., 2021), was recovered from siltstone in trough crossbed fills (Fig. 2; Gastaldo et al., 2020a). The upper boundary of this palynozone in Eastern Australia recently has been extended from the PTB (Mays et al., 2020) to the Griesbachian–Dienerian boundary (250.4 Ma; Mays et al., 2021). The recent U–Pb ICPMS age of 251 ± 3 Ma by Rochín-Bañaga et al., 2023 constrains the age of the *P. crenulata* microfloral assemblage to the Early Triassic. The same is not true for the spore-and-pollen assemblage recovered from Donald 207 farm.

Barbolini et al. (2018) first reported, and Gastaldo et al. (2019) reaffirmed, a microfloral assemblage on Donald 207 farm in close stratigraphic proximity to what other authors have termed the *Lystrosaurus* bone bed, interpreted to represent vertebrate recovery in the very earliest Triassic (e.g., Viglietti et al., 2013; Smith and Botha-Brink, 2014; Smith et al., 2022). The palynoassemblage is assigned to the *Protohaploxypinus microcorpus* palynozone which, at the time was interpreted to postdate the disappearance of *Glossopteris* in the latest Permian of Australia (Mays et al., 2020; Vajda et al., 2020). The presence of *Reduviasporonites* (Fig. 8L), an element of the Free State assemblage used to assign the assemblage to the *P. microcorpus* zone (Gastaldo et al., 2019), has been used as a proxy for the terrestrial environmental crisis in the latest Permian (e.g., Looy et al., 2001). More recently, though, Mays and McLoughlin (2022) place the lower boundary of the *P. microcorpus* palynozone at the Griesbachian–Dienerian boundary in the mid-Induan at ~251.5 Ma, and limit its temporal range to ~200 ka. To date, we have been unable to locate any volcanic generated deposit in any section on the farm from which a geochronometric constraint can be placed on this assemblage, nor have we rock magnetic properties due to an extensive dolerite intrusion in the shallow subsurface.

4.6. *Lesson 2: geochronometric and rock magnetic data, developed in a sequence stratigraphic context, constrain time and biological trends in continental successions*

The concepts of unconformity-bounded, lithostratigraphic successions at various scales (continent, region, basin) have been refined over the past 75 years following the incorporation of seismic stratigraphy in the 1970s (Hanneman and Wideman, 2010). Subsurface seismic lines revealed that the stratigraphic record is characterized by units that are partially bounded by unconformities. These features can be identified in both marine and continental basins and the successions therein. In effect, sequence stratigraphy is the analysis of sedimentary deposits in a time-stratigraphic context. Hanneman and Wideman (2010) note that not all terminology applied to marine rocks are applicable to contінetal basins because base-level changes in the former are influenced by oscillations in sea level. In contrast, fully continental settings are not affected by fluctuations in sea level. Nevertheless, continental sequences can be characterized as: (1) consisting of a relatively conformable succession of genetically related strata (fluvial, floodplain paleosols, lakes, etc.) bounded by lower and upper unconformities (or their correlative conformities); (2) being independent of spatial and temporal scales; and (3) the result of accommodation and base-level changes that are allogenic in origin (e.g., tectonism and climate; Gastaldo and Demko, 2011). Hence, accommodation in continental settings consists of the space that can be filled under the process-based regime (fluvial, limnic, aeolian, etc.) operating at the time. Each regime, in turn, is controlled by sediment load and stream power that are each a function of their response to changes in geomorphic base level (e.g., Bull, 1991). The ability to conserve these settings in the stratigraphic record occurs when subsidence brings sediments below the possible level of erosion (e.g., Blum, and Tornqvist, 2000). Hence, we can envision that each major sandstone body and its lateral correlative floodplain environments exposed in outcrop, bounded by basal and upper unconformities, represents what remains of a paleolandscape. Successive paleolandscapes either may be stacked one atop another. Or, paleolandscapes may be completely removed from the succession, with only the most resistant or lithified remnants of ghost landscapes (e.g., pedogenic carbonate nodules; Gastaldo et al., 2020b) incorporated into younger sediments. It is within each paleolandscape that fossil assemblages may be preserved.

We know from taphonomic studies that paleobotanical and, in fact, any continental fossil assemblage, represents a very short temporal window into the paleobiosphere. These temporal windows are dependent on a multitude of factors both operating at the time of accumulation and post deposition. Lesson 2 concerns the fact that stratigraphic successions touted as “continuous” continental records are never continuous, even when the presence of minor temporal diastems or hiatuses as recognized in paleosols are acknowledged. Time is constrained best when volcanogenic airfall ash deposits are encountered and a population of pristine zircon grains are subjected to high resolution CA-ID-TIMS analyses. Recognizing the fact that volcanogenic deposits are also a rarity, newly developed U–Pb LA-ICPMS techniques applied to calcite cements in pedogenic nodules hold promise to provide age constraints on continental successions where calcic paleosols occur (Davis and Rochín-Bañaga, 2021; Rochín-Bañaga et al., 2023). In the absence of geochronometry, the inclusion of a high-density sampling protocol to acquire rock magnetic properties is essential. Sampling for rock magnetic data in lithologies immediately below erosional surfaces of fluvial successions is critical in, potentially, identifying missing time. These data provide the basis for the development of a magnetostratigraphy with which the proportional representation of normal-and-reverse polarity magnetozones can be identified in the succession under consideration. Only a multi-disciplinary approach can constrain the time in the rock record and, hence, can be used to present and test hypotheses about the timing of events affecting the deep-time biosphere.

5. Discussion

The paleontological record of a stratigraphic succession is foundational in any, and all, interpretations of changes in the planet’s biosphere during critical intervals in Earth history. First, and foremost, the record is dependent on how much of the rock record is exposed, at which paleolatitudinal site they were deposited, where those rocks are now exposed, the proportion of exposed rock to the time interval under consideration, and whether or not they are accessible for study. Wall et al. (2009) calculated that Phanerozoic sedimentary rocks comprise ~27% marine carbonate, 45% marine terrigenous clastics, and ~28% continental terrigenous clastic settings, most of the latter represent the interface of coastal plain and nearshore marine regimes. Of the terrigenous clastic settings, Wall et al. (2011) estimate that the total outcrop area for the Upper Permian (Guadalupian–Lopingian) equals ~800,000 km^2 whereas the Lower Triassic (Induan–Olenekian) covers ~450,000 km^2, or 5.5% and 3%, respectively, of bedrock exposure. The time locked away in these rocks represent 7.61 Ma and 4.7 Ma, respectively (Cohen et al., 2013), and are distributed across both the southern and northern paleohemispheres in basins now surficially exposed in South America, southern Africa, Antarctica, Central Europe, the Russian platform, Siberia, India, China, and the United States. The plant-fossil record preserved in these areas was influenced and constrained by a number of inter-related factors which vary within, and across, depositional basins.

Taphonomic processes–including those related to preservation potential, biostratinomy, depositional setting, sedimentation, and various geochemistries–operating during any time of sediment-and-plant accumulation constrain the where-and-when of organic matter preservation

(DiMichele and Gastaldo, 2008; Locatelli, 2014). These inter-related factors portend a discontinuous record in space and time which is due to the inherent nature of preserving "soft" non-mineralized plant tissues. Subsequent tectonic and surficial processes operating over various time scales, ranging from 10s of thousands to 10s of millions or more years, will modify the potential record that can be recovered. These post-depositional, long-term processes also reduce the scope and number of fossiliferous intervals from which interpretations can be made (Gastaldo and Demko, 2011). Hence, it is not parsimonious to accept a stratigraphy at its face value when evaluating any biological or geochemical trend preserved therein. Only a high spatial and temporal resolution record can provide the insights needed when considering perturbations to Earth Systems and the response of ecosystems at various scales in, across, and between correlative basins.

To state the obvious, Earth's paleontological record from which ecological patterns are discerned is restricted to a very small proportion of sedimentary successions spread over, and clustered, in geologic time. It is demonstrated, unequivocally, that marine diversity, as well as ecological, turnover, and extinction patterns, are contingent upon the marine sequence stratigraphic framework from which invertebrate assemblages are collected and assessed (Patzkowsky and Holland, 2012). Turnover-and-extinction patterns in the marine-fossil record are not randomly distributed. The abrupt transitions in the invertebrate record are intricately tied to both unconformities of various nature as well as the spatial distribution of condensed stratigraphic intervals in a basin (Holland and Patzkowsky, 2015). Although the same principles apply in coastal and fully continental successions (DiMichele and Gastaldo, 2008; Gastaldo and Demko, 2011), these fundamental constraints often are discounted or overlooked for any number of reasons. Such reasons are not limited to, but may include: (1) the availability of outcrop, both as a consequence of the structural attitude of the rock and the extent of cover, limiting exposure; (2) the reliance on a single measured or composite stratigraphic section, or a small number of measured sections in close geographic proximity, in any locality from which to interpret regional or global biological patterns; (3) the assumption that the paleontological record, and the rocks in which they are preserved, in one area are temporally equivalent to patterns encountered in other regions that may be tens, hundreds, or thousands of kilometers distant without the presence of an unequivocal datum, independent of biostratigraphic presupposition, on which correlation can be made; and (4) the absence of a multi-disciplinary approach. Such a multi-disciplinary approach–employing rock magnetic properties, geochemistry, and geochronometry, where possible, has been used in the Karoo Basin to resolve time and allow for biological patterns to be better evaluated. All of these factors play a role in the paleontological, and particularly the paleobotanical, record of the upper Permian and Lower Triassic rocks of the Karoo Supergroup. And, contrary to an interpretation that these rocks represent a "continuous" succession with the presence of only minor hiatuses (e.g., Smith, 1995; Viglietti et al., 2021), our studies over the past two decades have shown this belief to be an oversimplification (Fig. 10; see 4.4.1 Lesson 2). The paleontological record in the Balfour and Katberg formations is more complex than what is proposed, and accepted, in the published literature.

5.1. Spatial relationships of plant-fossil assemblages in the Karoo basin

A taphonomic window exists under which subsurface and subaerial plant parts can potentially be added to, and preserved in, the fossil record. The criteria required for preservation vary in landscapes and across latitudinal zones at any, and all points in time. In fully continental basins where no marine influence on sedimentation is known, such as the Beaufort Group of the Karoo Basin (Fig. 2), there is a limited spectrum of depositional environments where there existed a potential for preservation resulting in a limited number of fossil-plant assemblages. The lowest plant-preservation potential exists in soils where both physical and biological processes continuously operate on the substrate across various climatically influenced soil types (pedotypes). Soil modifications of floodplain (interfluvial) sediments include, but are not limited to: hydrolysis (weathering of feldspathic minerals to clay), calcification ($CaCO_3$ enrichment and the precipitation of calcite-cemented nodules), salinization (precipitation of salts in the soil profile), and gleization (organic matter accumulation and iron reduction where water tables are high; Sheldon and Tabor, 2009). Bioturbation and utilization of soil biomass by invertebrates (e.g., *Katbergia*; Gastaldo and Rolerson, 2008) and vertebrates (e.g., Bordy et al., 2011), and phytoturbation of sediments via successive generations of roots, in conjunction with climate and rainfall patterns over the time span of pedogenesis, change both surficial and the pore-water geochemistries such that surficial litters decay and are recycled rapidly (e.g., Gastaldo and Staub, 1999). Under exceptional circumstances, vertical and subhorizontal rooting structures may be preserved either as adpressions or clay-lined impressions (Retallack, 1988), or act as nuclei for calcite-nodule precipitation in which roots are preserved (e.g., Gastaldo et al., 2014). When present, such rooting structures represent the final vegetation and phase of soil development before the landscape was rapidly removed from the soil-air interface and buried at a depth beyond the influence of renewed surficial pedogenic processes. Such a rapid, regional base-level change generally is tectonically influenced and accompanied by increased sedimentation as new accommodation is formed in response to changing depocenters and fluvial gradients (Gastaldo and Demko, 2011). In essence, marine obrution deposits (Brett, 1990) can be considered analogous to paleosols in which subterranean and, especially in exceptional circumstances, O-horizons are well preserved (e.g., Gastaldo et al., 2014).

Soils constitute the greatest volume and aerial distribution of sedimentary environments across any continental landscape. When mudrock paleosols account for the greatest proportion of the stratigraphic record, as they do in the Karoo succession, encountering any fossil-plant assemblage in rocks representing these settings is near impossible. To date, we have encountered only a single paleosol in the Balfour Formation at Wapadsberg Pass wherein both a macroflora (subterranean and leaf-litter assemblages) is preserved along with a microfloral assemblage (Prevec et al., 2010; Gastaldo et al., 2014). This single occurrence represents 0.03% of our upper Permian–Lower Triassic stratigraphic record (Table 2). Adpressions and palynolomorphs are preserved in other depositional environments, and preservation in these settings accounts for a higher percentage of paleobotanical assemblages in the Balfour and Katberg formations.

Rivers dissect the floodplain landscape on which soils develop. Sediment accumulation occurs primarily as bedload deposits in active river channels during times of floodplain pedogenesis. During each waning phase of any high-discharge event, plant debris transported in suspension load can settle on low-angle-cross bedded sand bodies, previously formed at higher velocities. Other in-channel locations where plant debris can accumulate include channel lags. If grain size is small (very fine sand [125–62.5 μm] and silt [62.5–3.9 μm]), as is the case in the Karoo Basin, sediment supply is periodically high, and sediment accumulation is coincident at the time of phytoclast (fragmentary detritus; Gastaldo, 1994) emplacement, plant debris may be buried increasing its preservation potential. Often, though, fluctuations in pore-water geochemistry (oxygen, redox, etc.), as well as fungal and bacterial activity, just below the sediment-water interface promote the decay of buried detritus (e.g., Gastaldo et al., 1987). In most instances, decay of these organic drapes results in an organic lamination in which only the most recalcitrant axes may be identifiable. Such beds comprised of comminuted or dispersed plant detritus (phytoclast fields) are a common feature of many, but not all, fluvial deposits. Their presence or absence is a function of fluvial discharge that operated at the time of sediment transport and deposition. The rates under which sediment accumulated can be broadly ascertained by the array of primary sedimentary structures found in channel deposits. The higher the discharge rates–reflected in the presence of trough cross, plane laminated, and massive bedding–the greater reworking of bedload and physical fragmentation of previously emplaced non-woody debris in the traction load (Gastaldo, 1994). Without consideration of the dominant primary structure in river deposits, one can be lead to the impression that adjacent floodplains were devoid of vegetation when, in all probability, the absence of phytodebris was a function of discharge energy and taphonomy. Beaufort Group (Fig. 2) river deposits are dominated by trough cross beds of various scale in which there are few examples of comminuted plant debris draping bedding (Gastaldo et al., 2021), and there is no evidence for the presence of CWD. This is in stark contrast to upper Permian and Lower Triassic fluvial deposits in the Bogda Mountains, Xinjiang Province, western China. Here, phytoclast fields (including palynomorphs) are the most commonly preserved plant assemblage found throughout river deposits dominated by low-angle crossbeds, and woody logs (CWD) are encountered in river deposits (Gastaldo et al., 2023). Although phytoclast fields may preserve identifiable plant detritus (Gastaldo et al., 2005), higher preservation potential exists for plant parts transported into standing bodies of water (abandoned and oxbow channels, open or closed lakes) that are enclosed in floodplain soils.

Not all standing bodies of water have the same preservation potential of plant debris introduced into a depression in any landscape. Preservation requires sufficient water depth and amenable bottom-water geochemistries, which may promote the development of surficial biofilms (Dunn et al., 1997) or entombment in microbial mats (Kerp et al., 1996; Iniesto et al., 2018). In most instances, preservation of transported (allochthonous) assemblages requires a higher suspension-load sedimentation rate wherein organic decay is impeded, rather than promoted. Surface-lake waters are thermally stratified and well oxygenated, with dysoxia (0.3–2 mg/l) or anoxia (0–0.2 mg/l) generally restricted to bottom waters at depths below the oxygen minimum zone (OMZ). In the case of modern sufficiently deep lakes, the OMZ is generally tens of meters below the water-air interface where invertebrate activity is restricted or curtailed at the sediment-water interface and shallow subsurface. And, the depth of the OMZ in a lake is influenced by its geographical and latitudinal position, as well as seasonality. Bedded litters and plant assemblages in laminated beds are indicative of their residency at the bottom of a standing water body below the OMZ, where the taphonomically active zone (TAZ) of invertebrate activity was suppressed at the time of emplacement of both the plant debris and entombing sediment. Seasonal changes and/or oscillations in bottom-water geochemistry (oxygenation, temperature, redox, etc.) will reinstate conditions for reactivation of invertebrate activity in bottom sediments, recycling organic matter both at the benthic-water interface and shallow subsurface. Even if the number of lakes in an area was high, and lakes were spread across one or more interfluvial landscapes, conditions in each lake would have differed at various points in time restricting the site(s) in which plants could have been preserved. Hence, coeval settings would not have had the same potential to preserve plant debris, which limits the probability of encountering a fossil assemblage in surficial exposures of these facies, particularly where outcrops are limited or found to be two dimensional.

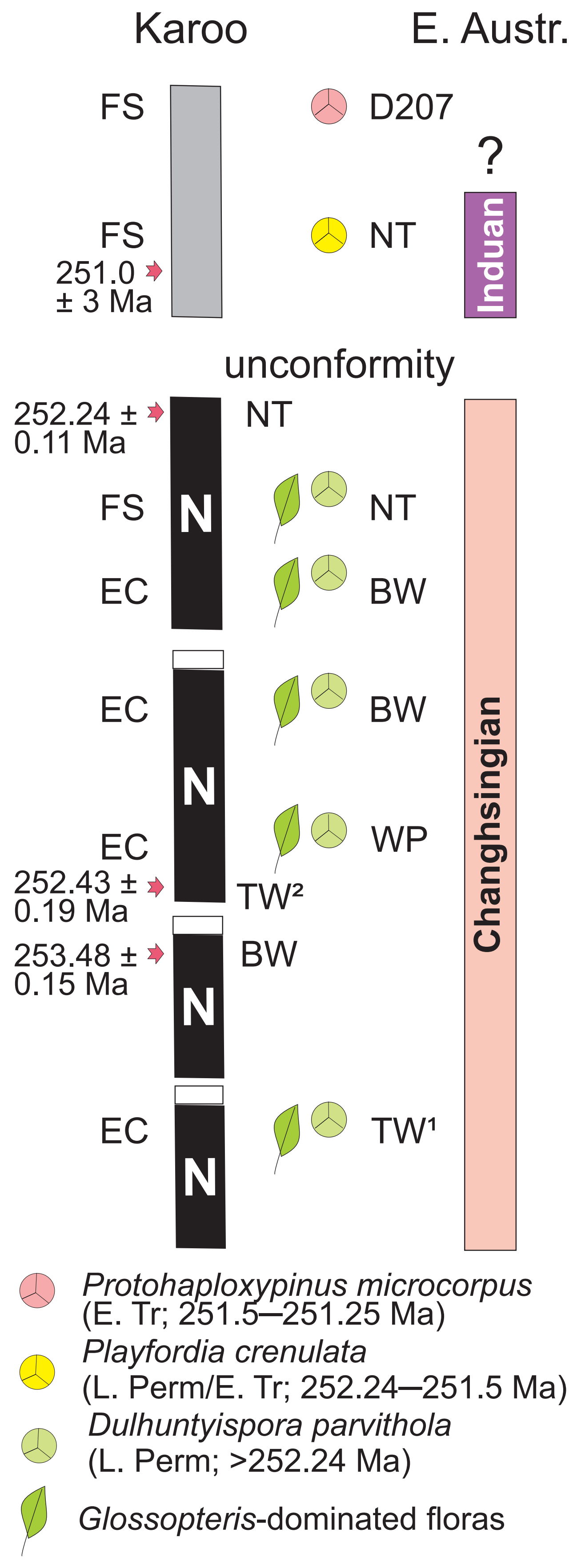
5.2. *Lesson 3: spatial distribution of paleobotanical assemblages in the Karoo basin*

Plant-fossil assemblages are neither distributed equally in nor across correlative sections in the Karoo Basin. Soft-tissue preservation, which is the most commonly encountered assemblage, requires a multitude of co-occurring factors which, at the most fundamental level, requires: (1) a depositional site in which plant-and-sediment accumulation occurs contemporaneously; (2) the isolation of plant debris under geochemical conditions conducive to constraining decay and increasing the potential for its conservation; and (3) the subsequent maintenance of that landscape allowing for its retention in the stratigraphic succession (Behrensmeyer et al., 2000; DiMichele and Gastaldo, 2008). Additionally, there is the low probability of encountering these facies in non-contiguous outcrops because of their geographic distribution in and across the original landscape. As demonstrated in the Karoo Basin, with similar data coming from the Hami-Turpan Basin, China (Gastaldo et al., 2023), megafloral assemblages constitute a very small proportion of lithostratigraphies in correlative sections. Hence, our understanding of vegetation in this part of the Karoo succession is contingent on a limited number of fossiliferous beds that, generally, are preserved over a rock thickness of a few decimeters, and are restricted in outcrops available for study at the present. Plant-rich deposits represent very limited spatial "windows" into the (paleo)biosphere and seem to be biased toward plant debris sourced from vegetation growing in soils adjacent to depositional settings (i.e., riparian plants adjacent to rivers and lakes). This appears to be true in all fully continental basins.

5.3. *Temporal relationships of plant-fossil assemblages in the Karoo basin*

Various perspectives about the timing of plant-rich assemblages in the Beaufort Group can be advanced. Here, we focus on the record of well-preserved plant assemblages (Figs. 10 and 11) and disregard the geographical distribution of potential depositional settings across that landscape (see 5.1.2). Gastaldo and Demko (2011) proposed that plant parts have a higher probability to be incorporated and preserved in the stratigraphic record during the initial phases of landscape aggradation (build up) in an active depocenter following a resetting of local and/or regional base level (see full discussion in Gastaldo et al., 2020b). This is because sediment-accumulation rates are highest during this initial phase of sediment transport and subsequent deposition. A coincidence of high sediment supply and depositional rates, along with biomass contribution from riparian (river and lake side) vegetation, results in the highest probability that plants will be buried and preserved in these deposits. Their conservation is the result of rapidly filling accommodation, embedding leaf litters in sediment that is unaffected by bioturbation (Fig. 4A and B). The residency times of phytodebris at the sediment-water interface are short, where there is a suppression of the TAZ, either via high suspension-load sedimentation or bottom-water geochemistries, that prevents invertebrate colonization. Many authors (e.g., Bull, 1991; Posamentier and Allen, 1999; Muto and Steel, 2000; Hanneman and Wideman, 2010) have noted that the stratigraphic "work" (deposition or erosion) effected in fluvial systems occur when these systems are in a state of disequilibrium. During the initial aggradational phase, overbank sedimentation is common, interfluvial paleosols increase in thickness, and there is an overall rise of the regional water table (Gastaldo and Demko, 2011; Gastaldo et al., 2020b). Climate is one factor that controls aggradation wherein poorly drained interfluvial soils are conserved, without further pedogenic maturation, under a seasonally wet climate. Changes in the regional fluvial gradient, sediment supply to the drainage system, or climate shift towards more seasonally dry or monsoonal conditions results in a slowing or cessation of floodplain sedimentation and landscape aggradation (Gastaldo and Demko, 2011). As floodplain sedimentation slows or ceases, pedogenesis results in more mature soil profiles (e.g., Calcic Vertisols, Calcisols, Gypsisols; Mack et al., 1993). Under these mature conditions (landscape stasis; Gastaldo et al., 2020b), a prevailing low sediment-accumulation rate precludes the burial and isolation of plant debris in depositional settings, resulting in their low preservation potential. As such, there is a dearth or absence of these assemblages in the final phase of an aggradational cycle, although similar depositional environments may have existed across the landscape in which plants previously were preserved.

We have encountered only a few *Glossopteris*-dominated megafloral assemblages in the Balfour Formation in aquatic settings of latest Permian age. All but one of these represents leaf-litter accumulations. The one exception is the immature paleosol and O-horizon found at Wapadsberg Pass (Prevec et al., 2010; Gastaldo et al., 2014) in the Eastern Cape Province. Glossopterid-dominated megafloras and microfloras are likely all Changhsingian in age. The Tweefontein[1] floras



(caption on next column)

Fig. 11. Summary diagram of *Glossopteris*-dominated and palynological assemblages in geochronometric and magnetostratigraphic context reported from classic Karoo localities in which the Permian–Triassic boundary is reported by various workers. Palynozones, their current age assignments, and age ranges as reported in Eastern Australia (Mays and McLoughlin, 2022) are illustrated against a composite section for the Karoo Basin. South African Provinces: EC = Eastern Cape; FS = Free State. Localities: BW = Blaauwater farm, Old Lootsberg Pass; TW^1 = Tweefontein^1, TW^2 = Tweefontein^2, WP = Wapadsberg Pass; NT = Nooitgedacht; D207 = Donald 207 farm. U–Pb ages for the EC from Gastaldo et al. (2018a, 2021) and FC from Gastaldo et al. (2020a) and Rochín-Bañaga et al. (2023). Gray bar indicates that no rock magnetic data are available for this part of the composite section.

(Gastaldo et al., 2017) are older than 253.48 ± 0.48 Ma, preserved in a normal polarity magnetozone (Fig. 10) but are unconstrained by a geochronometric age estimate, at present; the Wapadsberg Pass floras also are likely slighlty older (sec. 4.4). In the classic localities of the Eastern Cape, *Glossopteris*-dominated landscapes (Gastaldo et al., 2017, 2018, 2021) span at least four magnetozones in a succession of at least 18 aggradational and degradational sedimentation cycles (Fig. 10). It is likely that the Late Permian, Eastern Cape landscapes also underwent aggradational and degradational cycles during each reverse polarity magnetozone, given the estimates of an average-magnetozone duration of ~180 ka (Lowrie and Kent, 2004). The short and, at times, cryptic stratigraphic intervals in which reverse magnetozones are identified (Fig. 9), though, preclude any speculation about cycle number. In conjunction with evidence from the Free State locality of Nooitgedacht (Botha et al., 2020; Gastaldo et al., 2020a), these seasonally wet, *Glossopteris*-dominated megafloras continued into the latest Permian (Fig. 11). As previously noted at Nooitgedacht, an unconformity occurs a few meters above the bed from which we have obtained our U–Pb CA-ID-TIMS age, which is overlain by a fluvial channel deposit with a basal pedogenic nodule conglomerate lag. An overlying palynoflora conforms to the *P. crenulata* palynozone of Eastern Australia (Gastaldo et al., 2020a), which is now considered to range from 252.3 to 251.5 Ma (Mays and McLoughlin, 2022). Rochín-Bañaga et al. (2023; Fig. 11) report a U–Pb LA-ICPMS age from calcite, cementing a pedogenic nodule from the basal lag deposit, of 251 ± 3 Ma, indicating an Early Triassic age assignment to the palynoflora. Mays and McLoughlin (2022) report that glossopterid-type pollen constitute up to 40% of floras assigned to the *P. crenulata* palynozone. Pollen attributable to *Glossopteris* is present in the *P. crenulata* palynozone of the Karoo (Gastaldo et al., 2021) which also might indicate temporary persistence of the lineage into the Early Triassic in this basin.

Using the Australian palynozones, Barbolini et al. (2016, 2018) placed a palynoflora from the Donald 207 farm (Fig. 3) into the overlying *P. microcorpus* assemblage zone (Fig. 11). At the time, the base of this palynozone was considered to represent catastrophic vegetational turnover as a consequence of the terrestrial end-Permian extinction event (Fielding et al., 2019), and Mays et al. (2020, their Fig. 1) placed its upper boundary coincident with the marine event. Since then, Mays and McLoughlin (2022, their Fig. 5) have extended the *P. microcorpus* palynozone into the Dienerian (latest Induan). Hence, rather than it being indicative of the end-Permian terrestrial crisis, the Donald 207 palynoflora (Barbolini et al., 2016; Gastaldo et al., 2019) may be latest Induan (Fig. 11) or younger. We note that global analysis of megafloral and microflora data by Nowak et al. (2019) was unable to find evidence to support a mass extinction of vegetation across the PTB. Rather, a dramatic shift in palynofloras is reported in the Early Triassic, from the Griesbachian to the Dienerian (Hochuli et al., 2016; Schneebeli-Hermann et al., 2017). More recently, Schneebeli-Hermann (2020) proposed that Early Triassic, rather than latest Permian, terrestrial microfloral assemblage trends may reflect extreme compositional ecosystem shifts (extirpation) rather than outright turnover and extinction. Too few data are available in the Karoo Supergroup with which to test these hypotheses.

5.4. Lesson 4: temporal distribution of paleobotanical assemblages in the Karoo basin

The frequency of plant-bearing beds over a stratigraphic interval of interest will dictate one's perception of biological trends in time (DiMichele and Gastaldo, 2008). Each assemblage represents a short temporal "window" into the (paleo)biosphere, providing snapshots with which to connect-the-dots and discern biological patterns (see sec. 5.1). The presence of *Glossopteris*-dominated floras, beginning in the coals of the Vryheid Formation (279 Ma) and extending into at least the latest Changhsingian, demonstrates the presence of the glossopterid biome in South Africa for a duration of at least 28 My. Yet, the stratigraphy in which these assemblages are preserved, and interpreted to span the end-Permian crisis, must also be understood.

Stratigraphies must be investigated at a high temporal resolution in which diastems and hiatuses are identified and, where possible, semi-quantified before turnover, extirpation, or extinction patterns can be resolved. In the case of paleontological assemblages in the Karoo's Beaufort Group, the use of geochronological and magnetostratigraphic data in a sequence stratigraphic framework demonstrates that these rocks do not represent a "continuous" record of the Permian–Triassic transition, if that interval actually is absent as at Nooitgedacht (Rochín-Bañaga et al., 2023). Rather, the rocks of the Elandsberg through Katberg interval represent highly condensed successions (Figs. 10 and 11), of variable thickness in different parts of the basin, where a disproportionate amount of time is represented in sediments deposited during normal polarity magnetozones, and there is significant missing time as demontrated by the presence of short reverse polarity magnetozones. A major unconformity exists in the Nooitgedacht section, encompassing the terrestrial end-Permian crisis, making it impossible to detail biological patterns or trends that are proposed to have occurred at that time, let alone constrain such hypotheses to a temporal resolution of 10s to a 100 thousand years. Hence, it is not parsimonious to assume that fossils collected in close stratigraphic proximity to one another record a step-by-step biological pattern constrained to a short time scale. Neither is it parsimonious to use the stratigraphic position of a fossil assemblage to calculate confidence intervals with which to propose a taxon's range without, first, demonstrating how time is manifested in the rocks.

6. Conclusions

The demise of the *Glossopteris* gymnosperm flora that dominated the southern paleohemisphere for more than 26 million years–an equivalent time from the Miocene to the Anthropocene–has been interpreted as the first domino to fall at the onset of the terrestrial end-Permian crisis leading to systematic turnover and extinctions. The fossil record of the Karoo Basin, South Africa, has been considered as the "golden spike" in the end-Permian narrative to which biological trends and patterns on other continents have been compared. Here, the absence of megafloral remains in upper Changhsingian rocks became the basis for interpreting catastrophic deforestation that cascaded to vertebrate communities, and equated to the step-wise extinctions documented in latest Permian oceans. Yet, the interpretation of terrestrial patterns is dependent not only on the taphonomy of these plant assemblages and their overall presence in the stratigraphic record over the interval of concern, but also on their temporal context.

Glossopterid taxa dominate the Balfour Formation of the Beaufort Group where subordinate horsetail taxa with growth habits that include groundcover and lianas co-occur. These assemblages are preserved primarily as adpressions or impressions, with the occasional and isolated permineralized wood assemblage. All megafloral assemblages are biased to seasonally wet or wetland environments where they are preserved in river barforms, abandoned channels, and lakes in aggradational landscapes where they have the highest preservation potential. These depositional settings comprised a small proportion of the overall basinal geography at any point in time. In contrast, pedogenesis extended from river margins across the adjacent floodplains, and constitute the largest aerial extent of Karoo landscapes. Paleosols comprise the greatest proportion of the upper Permian and Lower Triassic stratigraphy. Balfour and Katberg formation soils range from immature (e.g., Inceptisol; Gastaldo et al., 2014) to mature (e.g., Calcic Vertisols; Gastaldo et al., 2020c), where soils have the lowest potential for plant-part preservation, as floodplain aggradation slowed in response to changes in prevailing regional climate and rainfall. Microfloras evidence shifts from predominantly wetland glossopterid-dominated pollen assemblages, with little evidence for the presence of other gymnosperm taxa, to pollen assemblages in which other gymnosperm groups (peltasperms, corystosperms, voltzialean conifers) indicative of seasonally dry conditions are found in higher proportions associated with calcic Vertisols (Gastaldo et al., 2018b).

The number of the depositional settings in which plants may be preserved and their geographic distribution across any Karoo landscape will control the potential for being encountered in any vertically exposed stratigraphic succession or in laterally equivalent rocks. It must also be recognized that coeval depositional settings will not have undergone the same physical and geochemical processes, resulting in a discontinuous paleobotanical record across any single landscape, reducing the probability of finding a bed in which plants are preserved. We have found that the paleontological record from which ecological patterns can be discerned in the Karoo Basin, and elsewhere, is restricted to a very small proportion of sedimentary successions spread over, and clustered, in geologic time.

We present paleobotanical data acquired from >3780 m of measured stratigraphic section in which permineralized wood, adpression, and microfloral assemblages are preserved in rocks spanning the upper Permian and Lower Triassic. Permineralized wood assemblages represent ~0.3% of the available rock record, with adpression assemblages found in <1% of the same stratigraphy. We have encountered no evidence of logs or other CWD in fluvial deposits, physically traced over several kilometers of lateral distance (e.g., Gastaldo et al., 2019, 2021), to date. Palynological assemblages have been recovered from <1.5% of the same stratigraphic interval. These data demonstrate that plant fossil assemblages represent vegetational snapshots of the Changhsingian landscapes that occupied Karoo soils over a duration of ~3 My (Fig. 11). Megafloral assemblages serve as windows into colonized landscapes in-and-around depositional settings, whereas microfloral assemblages represent ecologie components outside of that taphonomic window. These data, in conjunction with our sequence stratigraphic approach, continue to demonstrate that the continental stratigraphic record is notoriously incomplete due to the constant erosion and reworking of the land's surface. Hence, plant assemblages represent very short temporal "windows" into the paleobiosphere when preserved, and interpretations of abrupt vegetational change or turnover in any stratigraphic record should be considered in this light.

The accepted paradigm of rocks spanning the uppermost Permian and lowermost Triassic Karoo succession is one of a continuous depositional nature. Yet, temporal relationships between units are difficult to interpret, in large part, because of a scarcity of datable sediments. We demonstrate that geochronology coupled with magnetostratigraphy, and other rock-magnetic properties, provide a temporal context for continental successions. This approach not only assists in helping to resolve the overall duration of "time" that is represented in an area, but also provides an estimate of how much "time" is missing in that rock record. We caution that sampling regimes designed to acquire rock-magnetic properties of a succession may not result in the same magnetostratigraphy when undertaken in correlative sections, even when closely spaced, and especially true where one or more polarity magnetozones may thin as a consequence of their erosion during the emplacement of an overlying aggradational landscape cycle. Hence, it is not possible to rely solely on a single sampling regime in condensed, continental stratigraphic successions, to determine a relative timing of events. As we demonstrate here, once again, the Karoo succession spanning the uppermost Permian and lowermost Triassic is not a continuous record of events in the basin. Rather, these rocks record a disproportionate amount of time in successive landscapes. The duration of time in the Karoo succession is unequally divided. There is a disproportionate sedimentary record, with the greatest thickness of sediment, now lithified, deposited during chrons of normal polarity. These outweigh the proportion of time recorded in sediment that accumulated during chrons of reverse polarity, which are found in thin intervals that underlie erosional contacts at the base of aggradational cycles. This observation reinforces the conclusion that the Karoo lithostratigraphy represents a succession of mainly aggradational landscapes punctuated by degradational processes from which high-resolution biological patterns are difficult, at best, to resolve temporally. These lessons are applicable in all other Phanerozoic continental basins and need to be fully considered before vegetational trends including abrupt perturbations, extirpations, and extinction patterns, are interpreted and linked to other Earth Systems.

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Declaration of competing interest

None.

Data availability

Data will be made available on request.

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