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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 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. However, these models need to be carefully reconsidered because of the limitations of the rock record. Four lessons learned from a more robust approach to the rocks, lithology, continental sequence stratigraphy, and dating are relevant to other paleofloras in large terrestrial 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 phytoclast fields. A review of the debate over the rate and timing of the end Permian extinction as represented in the Karoo Basin reinforces the need for extensive stratigraphic mapping, the depositional environment of the plants, as well as the application of a variety of dating methods. First, the Karoo late Permian to early Triassic paleobotanical assemblages are extremely rare with only a handful of sites in the Free State and Eastern Cape Provinces. These 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, diatems 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 landscape. In general, the late Permian Beaufort rocks represent channels, floodplains, and braided streams rather than lakes and oxbows conducive to the preservation of phytoclasts. 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. Uncharacteristic diversity and abundance of plants in the Carnian–Norian Molteno Formation is most likely due to an environment conducive to preserving paleobotanical assemblages as well as 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 here and in other terrestrial basins.
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	Steve Holland stratum@uga.edu Steve Holland, better known for his studies in marine sequence stratigraphy, has recently applied his focus on terrestrial settings in which plant fossils may accumulate. His working knowledge of taphonomy, stratigraphy, and the paleontological record makes him ideal for reviewing this manuscript. Also, his recent co-author--Anik K. Regan (listed in the cover letter)--has focused on the continental plant-fossil record.
	Steffen Trümper steffen.truemper@hotmail.de In collaboration with Ronnie Roessler, Chemnitz, Steffen has been focused on Permian fossil-plant taphonomy, depositional environments, and paleoecology in central Europe.

Prof. Barbara J. Tewksbury
Hamilton College
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December 5, 2022

Dear Barbara and guest co-editors

Please find our invited contribution to the special volume of the Journal of African Earth Sciences focused on the paleobotanical record spanning the latest Permian and earliest Triassic interval in the Karoo Basin. The manuscript is a collaborative effort with Prof. Marion Bamford, and is entitled "The influence of taphonomy and time on the paleobotanical record of the Permian–Triassic transition of the Karoo Basin (and elsewhere)." As per your request and instructions, we have taken a "Lessons" approach to our manuscript, incorporating a multidisciplinary data set that our colleagues and ourselves have amassed over the past 20 years in the basin. We understand that the intent of the special issue is to review our current state-of-knowledge on the topic, which we have done. To provide the community with the necessary insights into how our work applies not only to the Karoo basin, but to any (and all) fully terrestrial settings, we have included several new analyses of the plant-fossil record in the succession, how that record parses in time (as determined via geochronology and magnetostratigraphy) and space (distribution of potential depositional environments), and provided reasons and rationale as to why megafloral assemblages are a rarity. Where appropriate, we compare our Karoo data with a similar data set from the Hami-Turpan Basin, western China (Gastaldo et al., in press, PALAIOS), demonstrating that our results are cosmopolitan and our conclusions applicable elsewhere. None of our analytical Karoo-Basin results have (or will) appear elsewhere; of course, much of our contextual data appear in a number of our previous publications.

Due to the mixed nature of a review article and the presentation of new analyses, we suggest the following colleagues who have demonstrable expertise in the array of topics and methodologies discussed in our manuscript.

- Prof. Jörg Schneider, TU Bergakademie Freiberg, Department of Palaeontology and Stratigraphy, D-09596 Freiberg, Germany; Joerg.Schneider@geo.tu-freiberg.de
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We look forward to learning of the reviewer's suggestions and comments, and a decision on our contribution after the New Year. We appreciate having been offered this opportunity to contribute to the Legacy volume.

Best Regards,

Bob

ABSTRACT

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. However, these models need to be carefully reconsidered because of the limitations of the rock record. Four lessons learned from a more robust approach to the rocks, lithology, continental sequence stratigraphy, and dating are relevant to other paleofloras in large terrestrial basins. In reality, the Karoo paleofloral record is verysparse. 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 phytoclast fields.

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Highlights

We present four lessons learned about the fossil-plant assemblages in the Karoo Basin, spanning the late Permian–early Triassic, that should be applied in other, fully continental settings regardless of age. The first lesson focuses on the proportional representation of the stratigraphic study interval, consisting of >3750 m of measured section. Here, fossiliferous horizons encountered account for <1% for megafloras and <1/5% for microfloras. The second lesson concerns the paradigm of "continuous" continental records across this interval. The Karoo succession is not continuous, even when the presence of minor temporal diastems or hiatuses in paleosols are acknowledged. Time is constrained best when using both geochronology and rock magnetic properties (i.e., magnetostratigraphy) in the absence of U-Pb datable minerals. Thirdly, Plant-fossil assemblages are neither distributed equally within or across correlative sections. 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 availabl outcrops. Lastly, the frequency of plant-bearing beds over a stratigraphic interval of interest will dictate one's perception of biological trends in time. This is because each assemblage represents a very short temporal "window" into the (paleo)biosphere, providing snapshots with which to connect-the-dots and discern biological patterns.

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 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. However, these models need to be carefully reconsidered because of the limitations of the rock record. Four lessons learned from a more robust approach to the rocks, lithology, continental sequence stratigraphy, and dating are relevant to other paleofloras in large terrestrial 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 phytoclast fields.

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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 *Glossopteris* taxa (e.g., Retallack et al., 2003; Ward et al., 2005). Glossopterid vegetation is thought to have been "replaced" rapidly, first, by equisetalean and, then, lycopsid and other gymnosperm taxa which were adapted to climatically stressed conditions. Arid and semi-arid conditions are interpreted to have prevailed into the Upper 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 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 begins in the Middle Permian (Guadalupian; Rubidge et al., 2012) and continues into the Lower Jurassic (Bordy et al., 2020) before the emplacement of the extensive Karoo-Ferrar Dolerites across southern Africa and Antarctica (Pleinsbachian; 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). Advances in discriminating a sequence-stratigraphic model (e.g., Gastaldo and Demko, 2011) in this part of the basin, coupled with geochronometric and paleomagnetic data in stratigraphic frameworks for classic PTB localities, now constrain this part of the paleontological record and provide a more comprehensive understanding of it (Gastaldo et al., 2015, 2018, 2020a, 2021). 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 that should be applied in other, fully continental settings regardless of age.

2. Considerations of Upper Permian and Lower Triassic Geology

The sedimentary succession known as the Karoo Supergroup is subdivided into the Dwyka (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. 1; Johnson et al., 2006) and the Lebombo Basin in the eastern part of South Africa (Bordy and

Prevec, 2008, 2015). It consists primarily of a sandstone-and-mudstone succession, that 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 distinguish lithostratigraphic units led early workers to rely on an abundant and diverse fossil-vertebrate fauna. These faunas are dominated by pre-mammalian terrestrial tetrapods and have been used as the basis for its subdivision (Smith et al., 2020) into what are accepted as Permian and Triassic-aged rocks. Geochronometric (Fig. 2; Rubidge et al., 2013; Day et al., 2015; Gastaldo et al., 2015, 2021) 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 stratigraphic units, the use of 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). Changhsingian-aged 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 Lower 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). Here, vegetational changeover (*Dulhuntyispora parvithola* to *Playfordiaspora crenulata* palynozones; Mays et al. 2020) dates younger than 252.24 ± 0.11 Ma (Gastaldo et al., 2020a) in a

fluvial-siltstone trough fill positioned above the vertebrate-defined PTB as reported on farm Nooitgedacht (Botha et al., 2020).

The initial vertebrate-defined extinction-and-assemblage turnover model (Ward et al., 2000, 2005) was reported to have occurred 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 vertebrate model and now interpret a protracted faunal assemblage change occurred over a stratigraphic interval of 100 m with a protracted mass-extinction event lasting 1 Ma. In this model, the pre-extinction Upper *Daptocephalus* Assemblage Zone (AZ; *L. maccaigi–Moschorhinus* subzone) is replaced by new taxa reported to have their first appearance datums (FAD) in the post-extinction *Lystrosaurus declivis* AZ. Recently, Gastaldo et al. (2021) demonstrated that the diagnostic taxa used to circumscribe each of the Upper *Daptocephalus* and *L. declivis* assemblage zones are preserved in coeval strata in the Eastern Cape Province. 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). Currently, though, it is unconstrained by either geochronologic or magnetostratigraphic data. 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, believed 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 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 and refractory 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–the fine siliciclastics (very fine sand, silt, and clay)–were eroded and transported basinward, removing any evidence of their existence except for when tuffaceous deposits can be dated geochronometrically (Gastaldo et al., 2018, 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 (fluvial and interfluvial 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 which the PTB will occur

exclusively in the Katberg Formation.

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 (Classen, 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., 2018), 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 follow.

3.1 Megaflora

3.1.1 Adpression floras

The predominant preservational mode of megafloral assemblages is adpression where, in some instances, cuticular remains can be retrieved from littered 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 equisetalean *Paracalamites*, as well as lycopsid and unidentifiable axes, are preserved in fine- to very fine-grained sand and finer clastic sediments. 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, most often as impressions. Rarely have *in situ* roots and/or rooting systems been encountered (e.g., *Vertebraria*; Gastaldo et al., 2014) despite the fact that paleosols dominate the sedimentological record in the basin.

Wetland taxa prevail in collections and include equisetaleans, rare lycopsids and ferns, and gymnosperms, whereas the most common elements are assigned to Glossopteridales (Fig. 4A, 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 Sphenophyllacae (e.g., *Trizygia*) in the Sphenophyllales (Fig. 4C). Very few examples of lycopsids have been recovered, and assignment of defoliated specimens to the club mosses can be complicated by their preservational state (e.g., Prevec et al., 2009). This is not the case for ferns. This is despite their generally small specimen size and generalized morphologies, resulting in their assignment to the form taxon *Sphenopteris*. In contrast, *Glossopteris* leaf morphologies 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 morphotypes of *Glossopteris* 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. 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 the paleobotanical collections of the Evolutionary Studies Institute. 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, B), *Pagiophyllum* (Fig. 6C, D), *Cladophlebis* (Fig. 6E), and *Samaropsis* (Fig. 6F).

3.1.2 Permineralized wood

Less common in latest Permian and Lower Triassic rocks are permineralized woods (Fig. 7), which may be reflected in the reported diversity of taxa. 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 Lopingian and continues into the Middle Triassic of southern Africa (Bamford and Philippe, 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 *Vertebraria*, the woody roots of glossopteridalean trees.

3.2 Microfloras

There are rare occurrences of palynological assemblages documented from surficial outcrops in the upper Permian–lower Triassic succession (e.g., Prevec et al., 2009, 2010; Barbolini et al., 2016, 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 primarily in the coal-bearing Ecca Group (e.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., 2016, 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 residual palynomorphs.

Dolerite intrusions are ubiquitous throughout the basin Main Karoo basin but are rare in the Ellisrus Basin, Waterberg Coalfield, a small basin in northern South Africa. Here, Wagner et al. (2019) have been able to correlate the maceral types with palynology and environmental interpretations. They processed bulk samples from coal seams in the Vryheid Formation and overlying Grootegeluk Formation and found that these assemblages correlated with the previous work of Falcon (1986, 1989). Inertinite 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 and is dominated by bisaccates, indicating a wet 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–C) and ferns (Fig. 8D). Such taxa originate from vegetation 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 pollen with Voltzian conifer, 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., 2020b). Many of these taxa were once considered indicative of Triassic vegetation 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).

4. Spatial and Temporal Distribution of Karoo Plant Assemblages

The majority of the Karoo bedrock is covered either in dwarf succulent shrubby vegetation, talus comprised of resistant sandstone and/or dolerite boulders, or both which may be up to depths of several meters. 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 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 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 incompetent matrix has weathered around calcified skeletons and skeletal elements.

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 of Gastaldo et al. (2018, 2021; -31.824033°, 24.812067°; to 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: Old Lootsberg Pass is 9.5 km to the NW, Wapadsberg Pass is 9.5 km to the SE, Carlton Heights is 45 km to the NW, and Kommandodrif Dam is 115 km to the ESE. 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 reported vertebrate-defined extinction event, equated to the PTB extinction (Ward et al., 2005; Smith and Botha-Brink, 2014; Viglietti et al., 2021), were recovered from ~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 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 koppie. 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 (including unpublished observations), their total stratigraphic thickness, the number and type of plant-bearing intervals for each locality, and pertinent citations.

4.2.1 Eastern Cape Province

The easternmost set of classic localities centers in-and-around Wapadsberg Pass. Here, sections are published for Old and New Wapadsberg Pass, and for donga exposures on farm Quaggasfontein; two measured sections have been described on farm Pienaarsbaaken (unpublished). A total of 1,130 m of section are detailed from these 12 successions. Glossopterid-dominated assemblages are preserved as bedded litters in the basal intervals of the Old and New Wapadsberg sections (Prevec et al., 2010), whereas isolated aerial debris is rare higher in the section. Here, only nine 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 horizons preserve them in fine-grained laminated siltstone higher in these sections. In contrast to megafloral assemblages, glossopterid pollen grains are often admixed with those of other gymnosperm groups for which there is no evidence in the megafloral record (Gastaldo et al., 2018). 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 including, and west of, 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 Tweefontein (sensu latu) and Blaauwater. Over this expansive area we have reported >1650 m in 23 measured sections; there are several, shorter measured-and-described intervals that remain unpublished. Similar to Wapadsberg Pass sites, glossopterids dominate the megaflora and microflora in seven and two localities, respectively (Table 1). All fossils are preserved in olive-gray siltstone.

Megafloral preservation in olive-gray siltstone is also the case at Kommandodrif Dam (N=2) and Carlton Heights (N=2) where isolated aerial debris is reported (Gastaldo et al., 2005). A single horizon of isolated debris occurs in the Palingkloof Member at Carlton Heights in a bedded 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 plant debris is rarely encountered in the Katberg Formation, where we have measured 380 m of stratigraphy in eight sections. Here, plant hash is scattered atop bedding in very fine sandstone and we have found identifiable debris on only a single horizon (Gastaldo et al., 2005). Additional, scattered megafloral elements (Retallack et al., 2003; Fig. 6) and 22 horizons have been reported to yield microfloral assemblages, spread over an interval of 59 m (Steiner et al., 2003). The succession from which these palynological assemblages were 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 (N. Tabor, pers. comm. 2019) 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/Fairydate (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). Although isolated resistant equisetalean or unidentifiable 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). Rocks on farm Nooitgedacht have been more productive.

Nooitgedacht outcrops occur around two koppies on the farm: 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-meter section from Loskop (Gastaldo et al., 2020a; unpublished field notes 08/2022). Botha et al. (2020) report five intervals in which megafloral remains are preserved, and figure specimens assigned to *Paracalamites*, *Glossopteris* and its reproductive propagules, and an indeterminate fern genus. Gastaldo et al. (2020a) report two horizons 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 is preserved ~10 m higher, above an erosional surface at the base of a down-cutting fluvial regime, that is assigned to the *Playfordiaspora crenulata* zone (Fig. 2).

4.2.3 Lesson 1: Proportional representation of paleobotanical assemblages

In total, 29 horizons macrofossil assemblages, excluding beds on which isolated axes or

mesofossil organic drapes occur, and four beds from which permineralized woods have been encountered and described spanning the uppermost Permian and lower Triassic succession. In contrast, at least 48 beds (Table 1) have been 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 %). Although spore-and-pollen assemblages are encountered more frequently in the literature (1.3%; Table 2), 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., in press). 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 4,709 m (Gastaldo et al., in press). In reality, identifiable macrofloral remains generally are limited to intervals of centimeters to decimeters reducing their proportionality in the rock record.

4.3 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 riverine processes prior to either avulsion,

abandonment, or a resetting of the land surface in response to landscape degradation or a basinward shift in depocenters. Continued erosion and reworking of unconsolidated 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 and Demko, 2011). Erosional bounding surfaces, often incised into underlying deposits and found at the base of fluvial sandstone bodies, are evidence of an interval of landscape 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, terrestrial 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., in press). Yet, without any geochronologic or rock magnetic data with which to place 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.

4.3.1 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 (silcification, 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.

4.3.1.1 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., 2018) or, more often, as a devitrified claystone (tuffite; Gastaldo et al., 2014, 2021, unpublished). Analytical results of all horizons 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 occur as trough fills in fluvial crossbed sets situated stratigraphically above these airfall horizons (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).

4.3.1.2 Free State Province

In contrast to volcanogenic beds in the Eastern Cape, only devitrified claystone 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 low in the Spitskop section 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) ~3 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 either in their text or supplemental data. 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 is dated to begin at 252.31 ± 0.07 Ma and lasted ~100 ka (Mays et al., 2020; and others).

4.3.2 Magnetostratigraphy

Rock magnetic properties, if not reset by younger intrusive activity, can provide insight into the broad timing of when landscapes developed. When attempting to discern time, magnetic polarity data obtained from closely spaced stratigraphic horizons, either by drilling or oriented sampling of siltstone (Gastaldo et al., 2018, 2021), 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). 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.

4.3.2.1 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, fig. 19), where the latter occurs in a stratigraphic position that is below that of the Old Lootsberg Pass reverse magnetozone. The interval in which the upper reverse polarity magnetozone may occur, if not eroded away, was not sampled due to logistics. Only a single normal polarity magnetozone is documents 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). 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., 2018).

4.3.2.2 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, 2020). 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, 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 from these sites. In contrast, the magnetostratigraphy reported from the Loskop section on farm Nooitgedacht, constrained by a U-Pb age date (see 4.3.2.1; Gastaldo et al., 2020), occurs in a normal polarity magnetozone (see: 4.3.1.2). The upper bounding surface of the magnetozone is erosional and overlain by a fluvial sandstone body with a basal pedogenic conglomerate-lag deposit.

4.4 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 paleosol leaf-litter horizon exposed along New Wapadsberg Pass (Prevec et al., 2010; Gastaldo et al., 2014). This is because tuffite in close association with this plant bed yielded only a few detrital zircon grains and rock magnetic properties are reset by dolerite intrusions. Gastaldo et al. (2018; unpublished) note that the three youngest grains yielded ages of 253.6 ± 0.7 Ma, 253.2 ± 0.3 Ma, and 252.03 ± 0.4 Ma. But, 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 an age of 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, 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., 2020). The upper boundary of this palynozone in Eastern Australia recently has been extended from the PTB (Mays et al. 2020) to the Griesbachian–Dinerian boundary (250.4 Ma; Mays et al., 2021). To date, we have neither geochronometric nor paleomagnetic data for this part of the Nooitgedacht section to better constrain the age of the *P. crenulata* microfloral assemblage. The same is 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, 2014; Smith et al., 2022). The palynoassemblage is assigned to the *Protohaplopinus 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 *Reduviasporites* (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–Dinerian boundary in the mid-Induan at ~251.5 Ma, limited to a temporal range of ~ 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.

4.4.1 Lesson 2: Geochronometric and rock magnetic data, developed in a sequence stratigraphic context, constrain time and biological trends in continental successions

Lesson 1 taught us 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 has taught us that stratigraphic successions touted as “continuous” continental records are not 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). 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 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 horizons from which interpretations can be made (Gastaldo and Demko, 2011). Hence, it is not parsimonious to accept a stratigraphy on 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 Earth Systems perturbation and ecosystem response of 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 sequence stratigraphic

framework from which invertebrate assemblages are collected and assessed (Patkowsky and Holland, 2012). In the marine record, turnover-and-extinction patterns 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 Patkowsky, 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 Paleobotanical assemblages in space and time

5.1.2 Spatial relationships of plant-fossil assemblages

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 within 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 pedotypes. Pedogenic 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, 2013). 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 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 equivalents 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 constitute 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 palynology are preserved in other depositional environments, and preservation in these settings account for a higher percentage of paleobotanical assemblages in the Balfour and Katberg formations.

Rivers dissect the floodplain landscape on which soils develop. Sediment accumulation

during times of pedogenesis occurs as bedload deposits that include channel lags and overlying barforms of various configuration where plant debris, transported as suspension load, may settle on bedding planes of low-velocity bedforms (lamination, trough fills, planar and trough cross beds and bedsets). If grain size is small (very fine sand [125–62.5 μm] and silt [62.5–3.9 μm]), sediment supply is periodically high, and sediment accumulation is coincident at the time of phytoclast 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. In most instances, decay of these organic drapes results in an organic lamination in which only the most recalcitrant axes may be identifiable. Such phytoclast fields (e.g., comminuted or dispersed plant detritus) are a common feature of many, but not all, fluvial deposits. Their presence or absence is a function of fluvial discharge rates 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 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. Beaufort Group (Fig. 2) river deposits are dominated by trough cross beds of various scale in which there are few examples of phytoclast fields draping bedding (Gastaldo et al., 2021). 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 (Gastaldo et al., in press). 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 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 lakes, the OMZ is 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 in the past, 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.

5.1.2 Lesson 3: Spatial distribution of paleobotanical assemblages

Plant-fossil assemblages are neither distributed equally within or across correlative sections. Soft-tissue preservation 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., in press), 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 are biased toward plant debris sourced from vegetation growing in soils marginal to depositional settings. This is true in all fully continental basins.

5.2 Temporal relationships of plant-fossil assemblages

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, 11) and disregard the geographical distribution of potential depositional settings across that landscape (see 5.1.2). Gastaldo and Demko (2011) proposed that plant preservation has a higher probability to be incorporated and preserved in the stratigraphic record during the initial phases of landscape build up, or aggradation, in an active depocenter following a resetting of local and/or regional base level (see full discussion in Gastaldo et al., 2020c). This is because sediment-accumulation rates are highest during this initial phase of transport and 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 (Figs. 4A, 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 prevent invertebrate colonization. During the initial aggradational phase, overbank deposition is common, interfluvial paleosols increase in thickness, and there is an overall rise of the regional water table. Climate is one factor that controls aggradation wherein poorly drained interfluvial soils are maintained 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 aggradation. As floodplain aggradation slows or ceases, pedogenesis results in more mature soil profiles. Under these mature conditions (landscape stasis), a prevailing low sediment-accumulation rate precludes the burial and isolation of phytodebris 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 mega- and microfloras are likely all Changhsingian in age. The Tweefontein[1] floras (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 span at least four magnetozones in a succession of at least 18 aggradational and degradational cycles of sedimentation (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, 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 floras ranged into the latest Permian (Fig. 11). An unconformity occurs a few meters above the horizon from which we have obtained our U-Pb 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 252.3–251.5 Ma (Mays and McLoughlin, 2022). Preliminary geochronometric data from Nooitgedacht indicates an early Triassic age assignment to the palynoflora where 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 floristic turnover as a consequence of the terrestrial end-Permian extinction event (Fielding et al., 2019), and Mays et al. (2020, fig. 1) placed its upper boundary coincident with the marine event. Since then, new U-Pb ages in Eastern Australia have constrained the *P. microcorpus* palynozone to the Dienarian (latest Induan; Mays and McLoughlin, 2022). 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). We note that global analysis of mega- 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 in the Early Triassic, from the Griesbachian to the Dinerian, is reported (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.

5.2.1 Lesson 4: Temporal distribution of paleobotanical assemblages

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 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. Rather, the rocks of the Elandsberg through Katberg interval represent highly

condensed successions (Figs. 10, 11), of variable thickness, 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 temporal 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* flora that dominated the southern paleohemisphere landscape 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 which 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 equisetalean 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., 2020b), where soils have the lowest potential for plant-part preservation, as floodplain aggradation slowed in response to changes in prevailing climate and rainfall. Microfloras evidence shifts from predominantly wetland glossopterid-dominated assemblages, with little evidence for the presence of other gymnosperm taxa, to assemblages in which peltasperms, corystosperms, voltzialean conifers and other gymnosperm pollen are found in higher proportions associated with calcic Vertisols (Gastaldo et al., 2018).

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, 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. 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. Megafloral assemblages serve as windows into colonized landscapes in-and-around depositional settings, whereas microfloral assemblages represent ecologies 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.

The accepted paradigm of the stratigraphy spanning the uppermost Permian and lowermost Triassic Karoo rocks is one of a continuous 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.

Declaration of competing interest

None

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Table Captions

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, megafloras, and microfloras have been either reported or observed; and references for published fossil-plant assemblages. Note that data on measured sections published by earlier workers are not included because of uncertainy 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 farm 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).

Table 2 – Number of horizons and percentage of stratigraphic record from which permineralized wood, adpression megafloras, paleosols with subaerial litters and subsurface rooting have been recovered, and productive-and-figured palynological assemblages per locality (see Table 1). In addition, numbers of individual samples from which palynological assemblages have been reported in the literature are separated.

Figure Captions

Figure 1. Map of the main Karoo Basin, South Africa, showing the geographical distribution of the Dwyka and Ecca Groups (Carboniferous–Permian), the Permian-and-Triassic vertebrate biozones and the Jurassic Drakensberg Group. Vertebrate Assemblage Zones follow Smith et al.

(2020) with the exception of the *Daptocephalus* and *Lystrosaurus* Assemblage Zones as demonstrated to be coeval by Gastaldo et al. (2021).

Figure 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, 2018, 2019, 2020a, 2021). U-Pb ages are from [1]Rubidge et al. (2013), [2]Gastaldo et al. (2015), [3]Gastaldo et al. (2020a), and [4]unpublished (white arrow). The biostratigraphic overlap of the Last Appearance Datum of the diagnostic taxa used to define the *Daptocephalus* Assemblage Zone and First Appearance Datum of the diagnostic taxa used to define the base of the *Lystrosaurus declivis* AZ are depicted. 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).

Figure 3. Maps of classic localities where the Permian–Triassic transition and 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.

Figure 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. Scales in mm and cm.

Figure 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.

Figure 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.

Figure 7. Karoo Fossil Wood, where generic identification is best discriminated in Radial Longitudinal Section (RLS). Anatomical features in neither Transverse (TS) nor Transverse Longitudinal (TLS) section are useful for generic identification. (A) TS of a typical Permian pycnoxylic gymnosperm wood with uniform rows of round to square tracheids. Magnification 40x. (B) TLS of a typical Permian pycnoxylic gymnosperm wood with longitudinal tracheids and uniseriate, homocellular rays (R). (C) RLS of Early Permian *Prototaxoxylon uniseriale* with spiral thickenings on the tracheids. Bordered pits (bp) are uniseriate and cross-field pits (cf) are cupressoid or taxodioid. (D) RLS of *Australoxylon teixeirae* (Permian) with clusters of borders pits on the tracheid walls. (E) RLS of *Agathoxylon africanum*, the most common woody spanning late Permian–Triassic, with biseriate alternate bordered pitting. (F) RLS of late Permian

Agathoxylon karooensis with bi-to-triseriate alternate bordered pitting. Scale: all tracheids are 35-40 μm in diameter.

Figure 8. Representative Beaufort Group palynomorphs. Algae: (A) *Mehlisphaeridium* sp., Quaggasfontein farm, Eastern Cape. Equisetales: (B) *Calamospora* sp., Quaggasfontein farm, Eastern Cape; (C) *Columinsiporites* cf. *peppersii*, Wapadsberg Pass, Eastern Cape (Prevec et al., 2010; UCMP 398617, SA-NWP2.A, E37-1). Pteridophytales: (D) *Horriditriletes teretangulatus*, Clouston Farm, Kwazulu Natal (Prevec et al., 2009; UCMP 398623, SA-CA0.5-9, H37-4.). Glossopteridales: (E) *Protohaploxypinus* sp., (F) *Striatiopodocarpites* sp., Quaggasfontein farm, Eastern Cape, (G) *Striatiopodocarpites cancellatus,* Clouston Farm, Kwazulu Natal (Prevec et al., 2009; UCMP 398628, SA-CA0.5-5, C44-3); Peltaspermales and Voltzialeas: (H) *Scheuringipollenites* sp., (I) *Alisporites* sp., Quaggasfontein farm, Eastern Cape; Voltzialeas: (J) *Guttulapollenites* sp., Quaggasfontein farm, Eastern Cape. Gymnospermales (?Peltaspermales): (K) *Falcisporites australis*, Quaggasfontein farm, Eastern Cape. Fungal/algal: (L) *Reduviasporonites* sp., Donald 207 farm (Gastaldo et al., 2019; UCMP PA1351.1, 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.

Figure 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., 2018).

The landscape was reset by the erosion of sediments deposited during a reverse-polarity chron with the emplacement of a 11-m thick fluvial deposit at the onset of a degradational 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.

Figure 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., 2018, 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 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 incompetent lithologies. GPS coordinates (WGS84 standard) are presented for the top of measured sections; see Gastaldo et al. (2018, 2021) for detailed sections and their correlation across Blaauwater–Tweefontein–Lootsberg Pass.

Figure 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. Gray bar indicates that no rock magnetic data are available for this part of the composite section; text of preliminary, unpublished U-Pb age estimate appears in gray.

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)
	Katberg Fm.	Carlton Heights					22[4]	Steiner et al. (2003)
Upper Permian		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, 2018); Prevec et al. (2010); unpublished
	Elandsberg Mbr. ?	Tweefontein				1	1	Gastaldo et al. (2017)

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 uncertainy about where mega- or microfloras were recovered. [1] Thickness of measured sections is based only

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

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.

Figure 1

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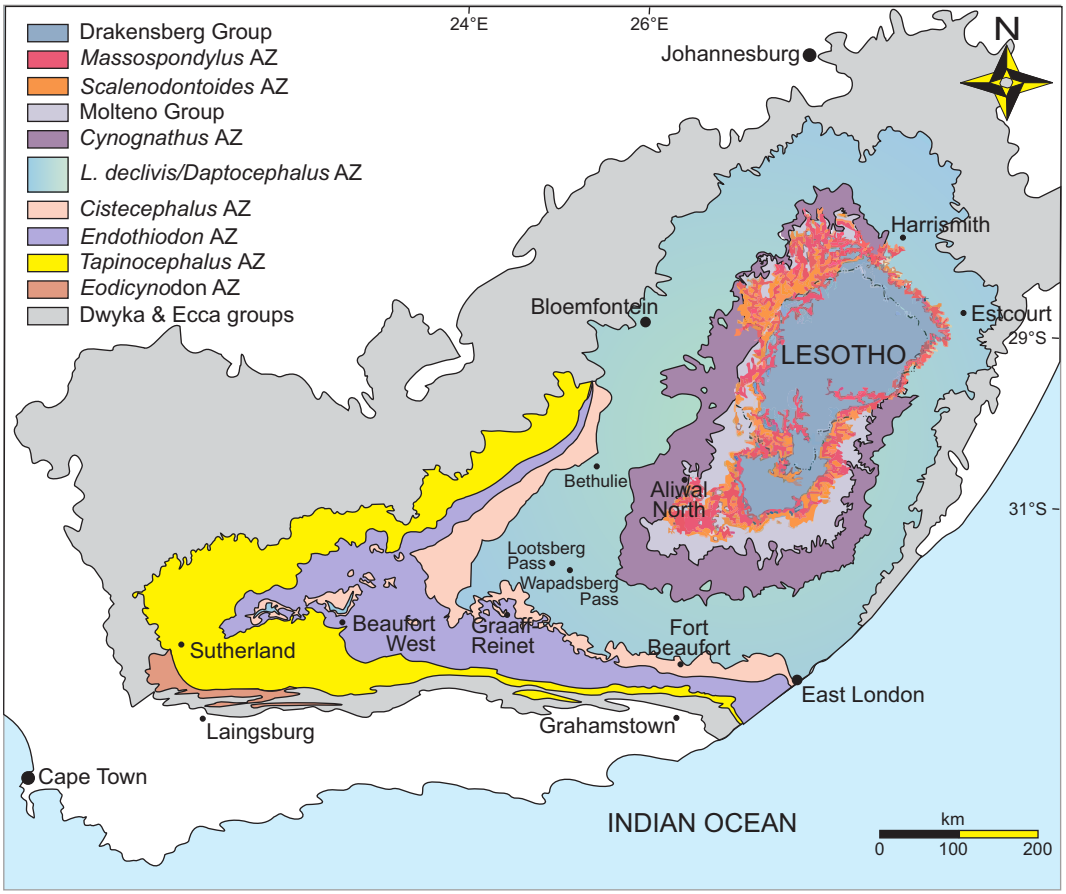

Figure 2

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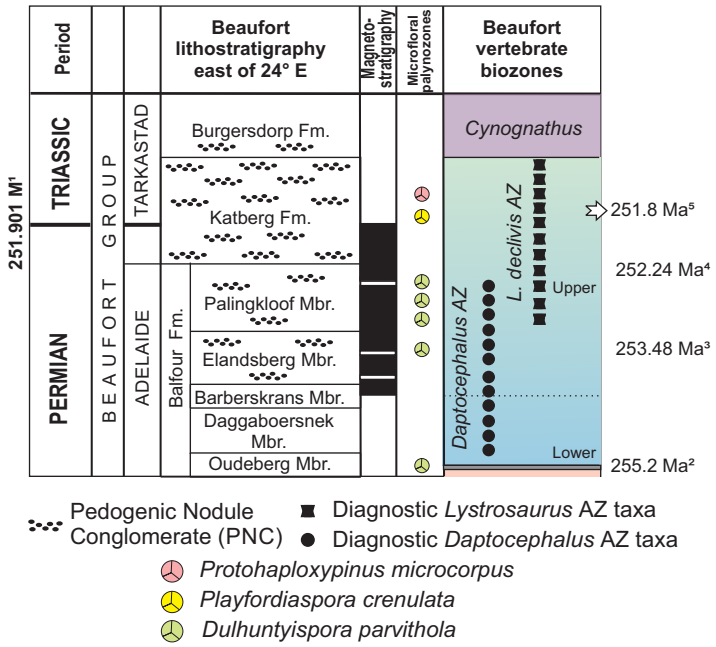

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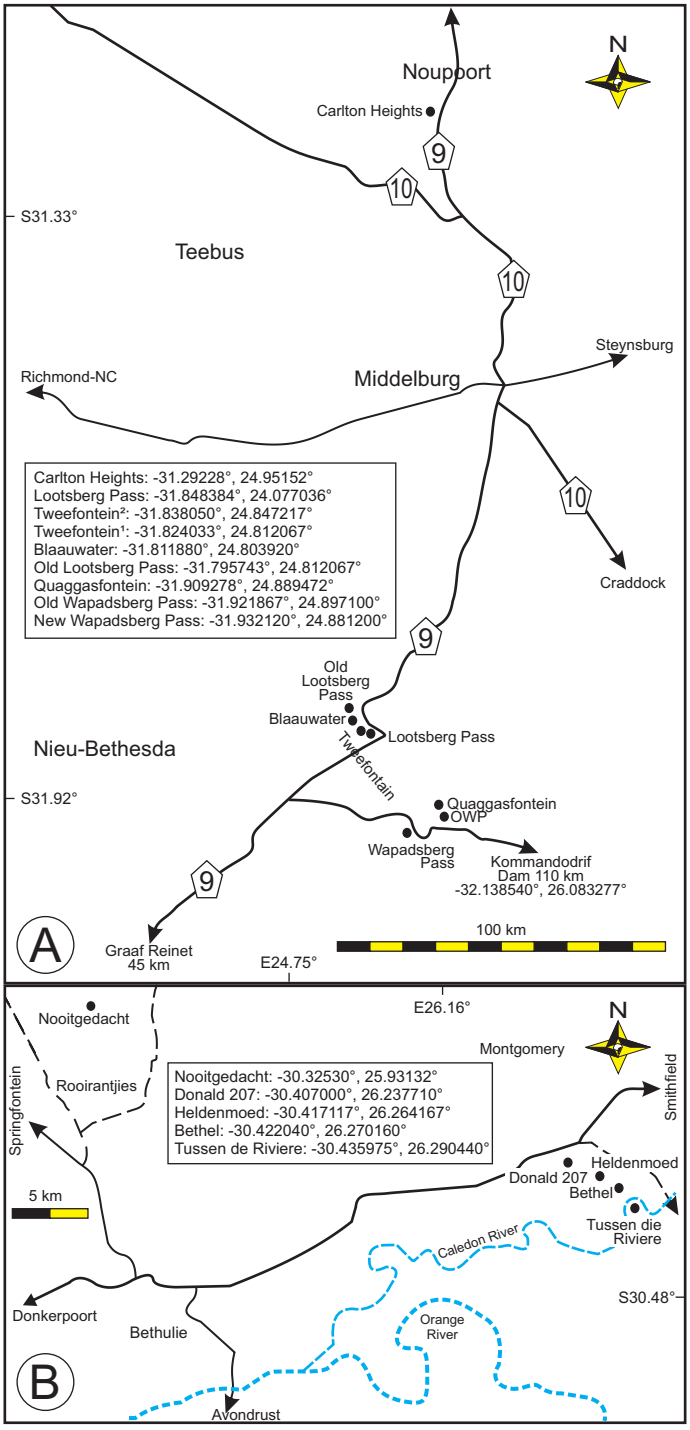

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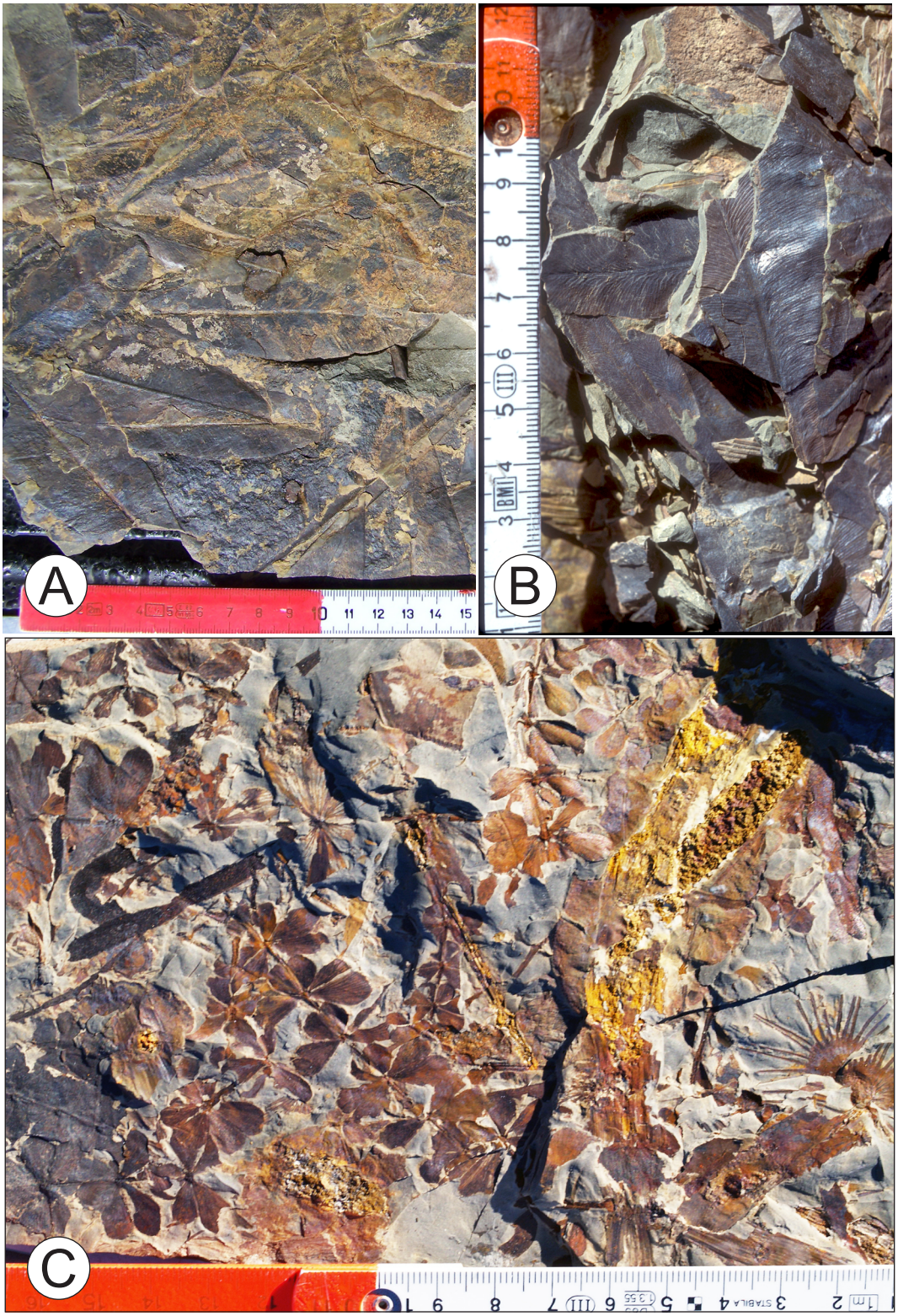

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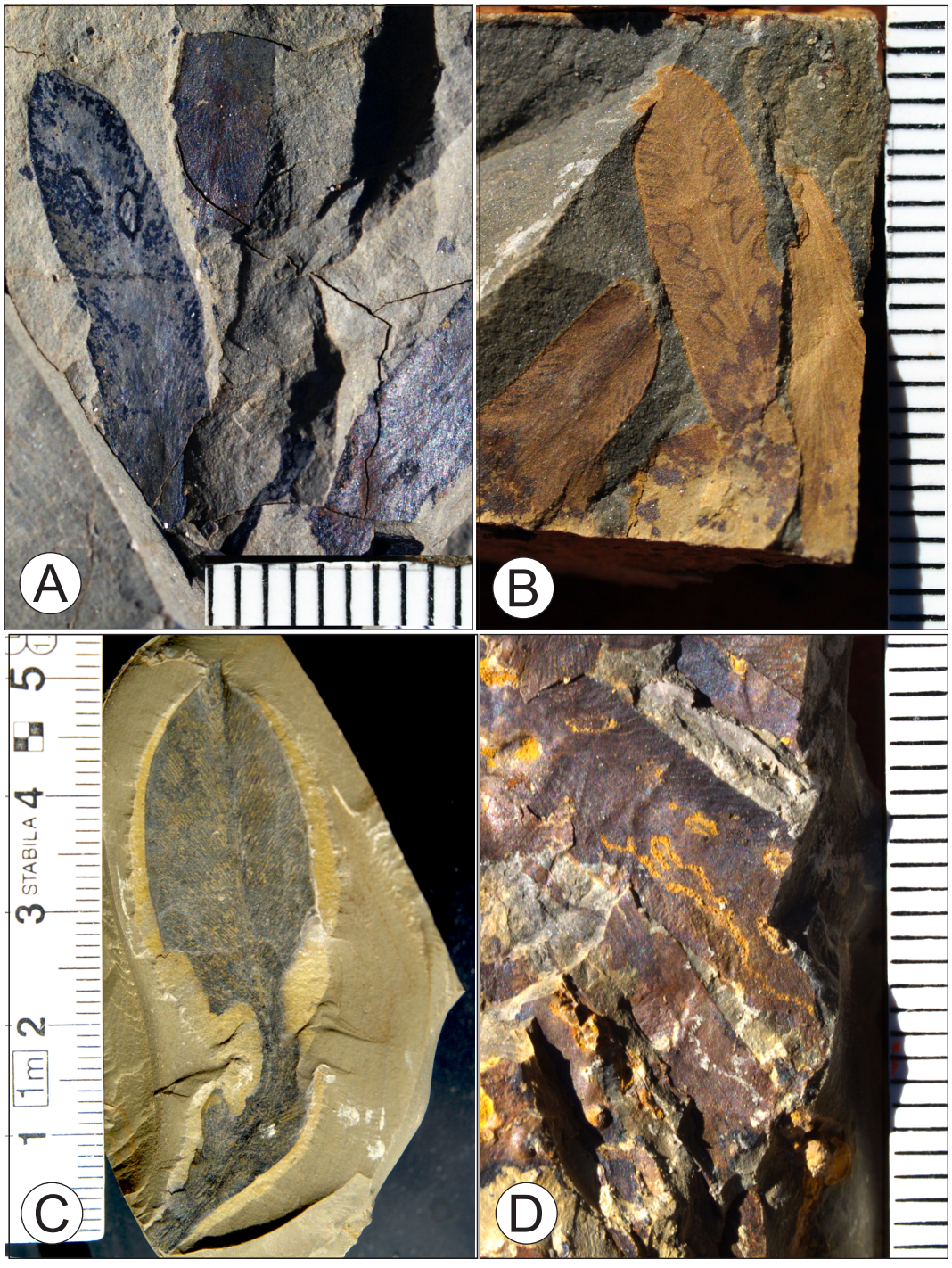

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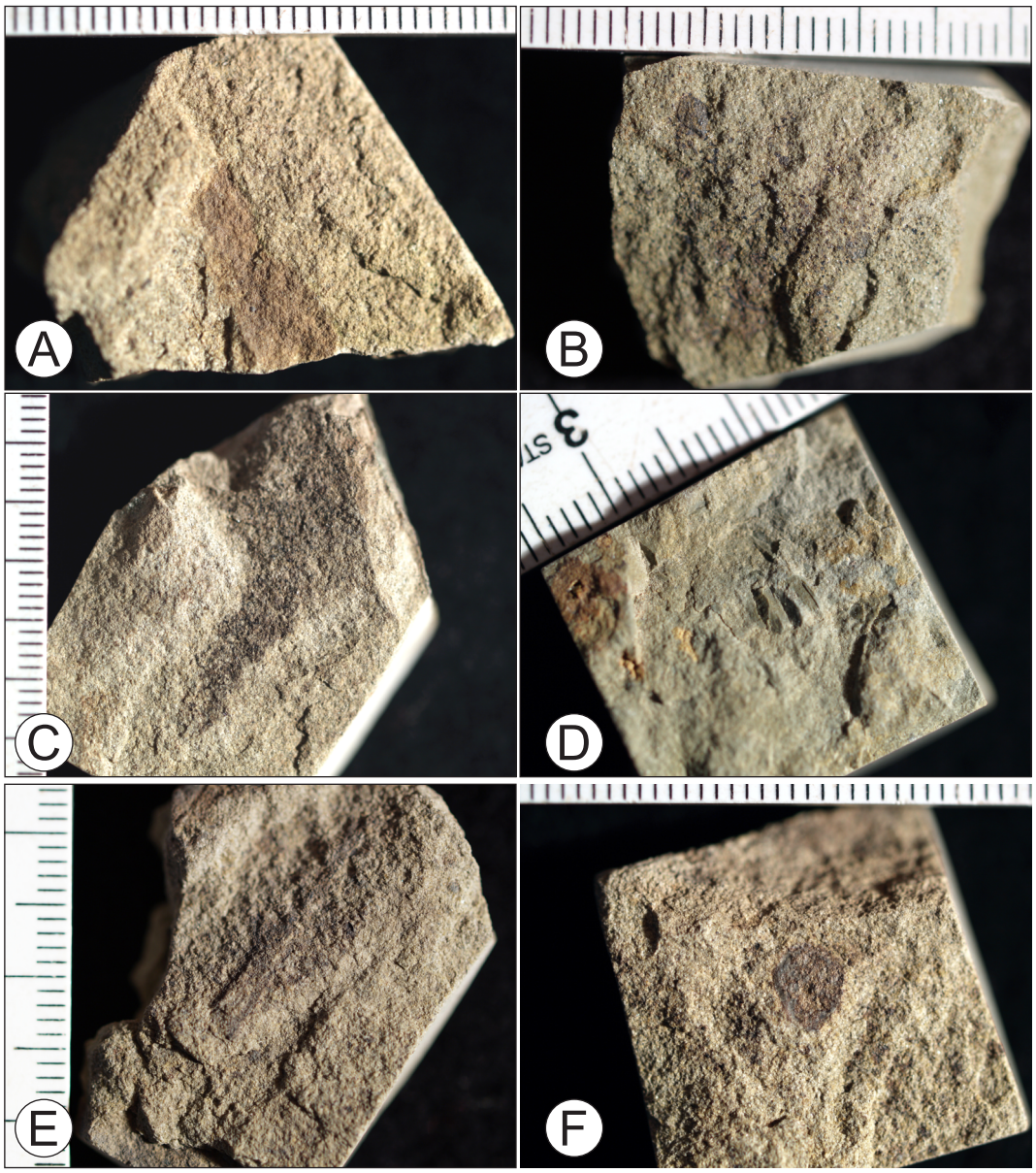

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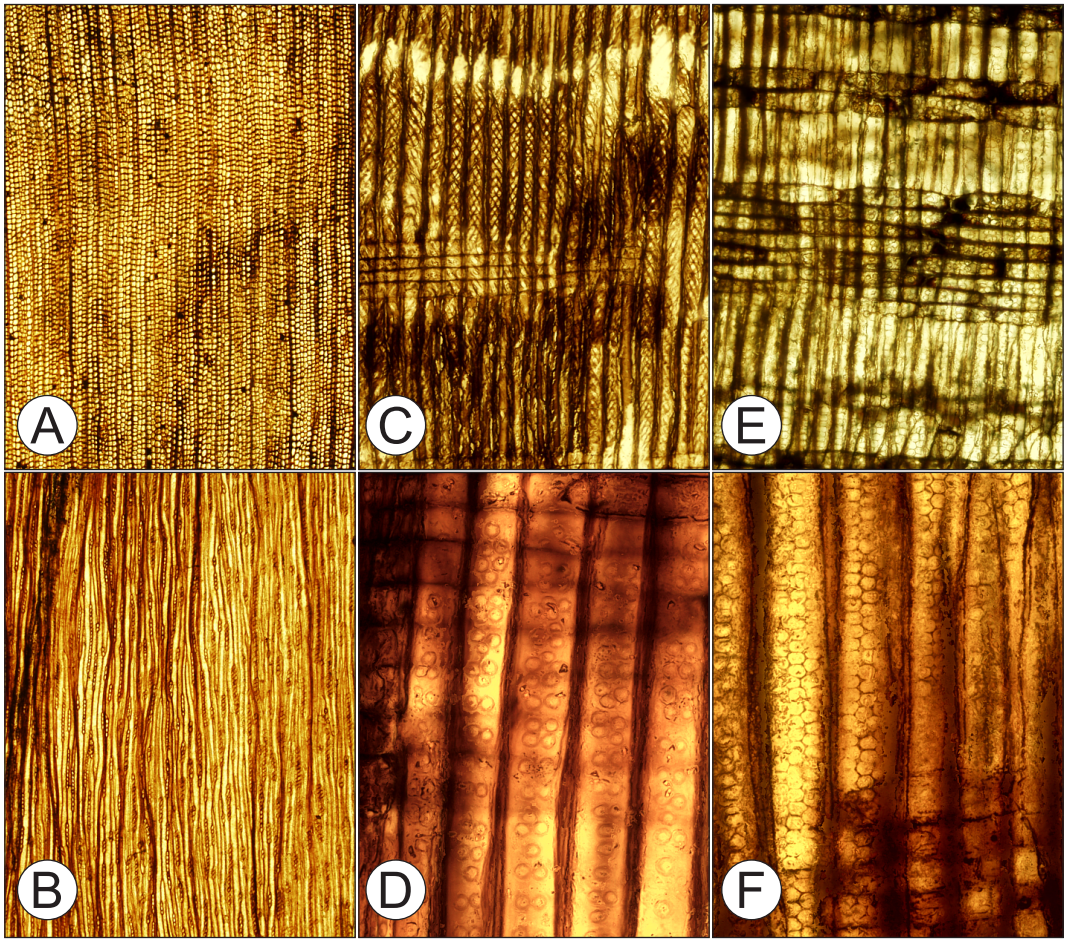

Figure 8

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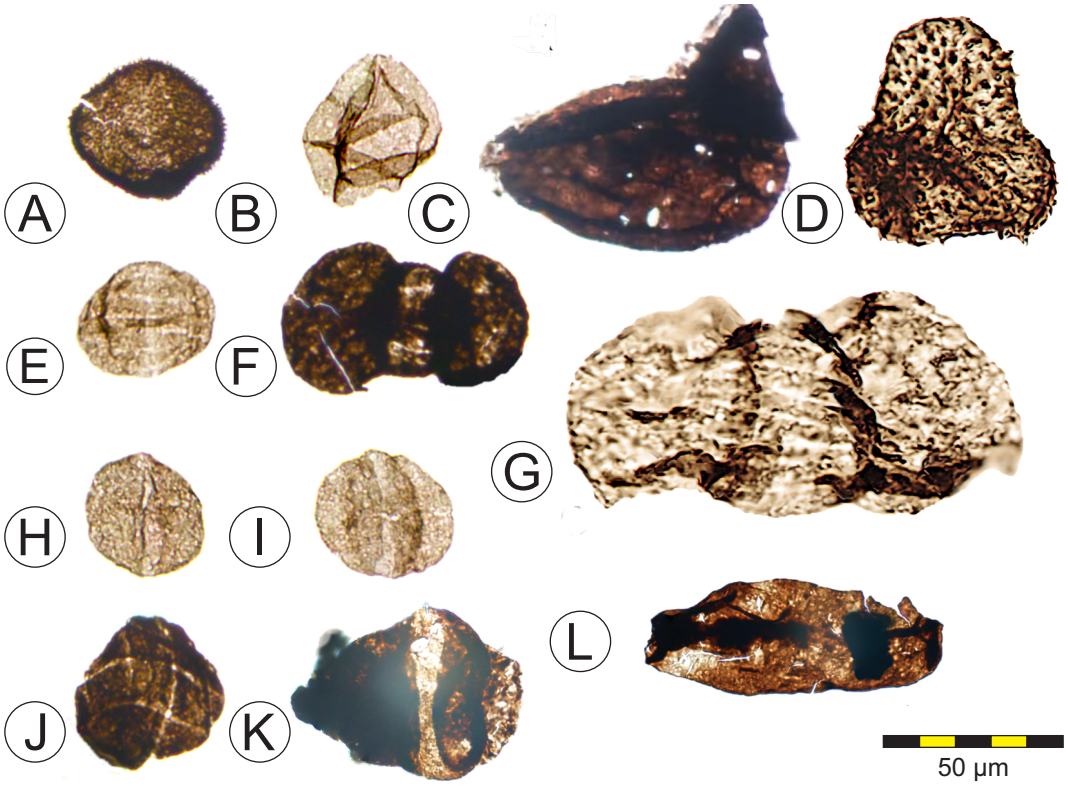

Figure 9

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Figure 10

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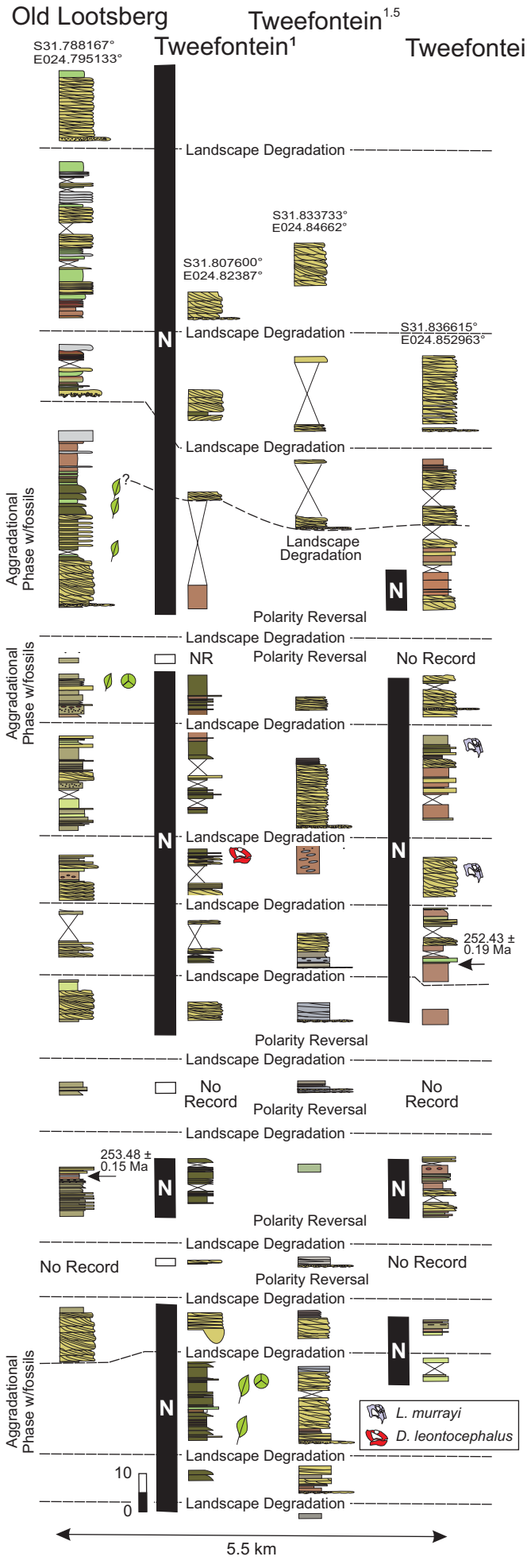

Figure 11

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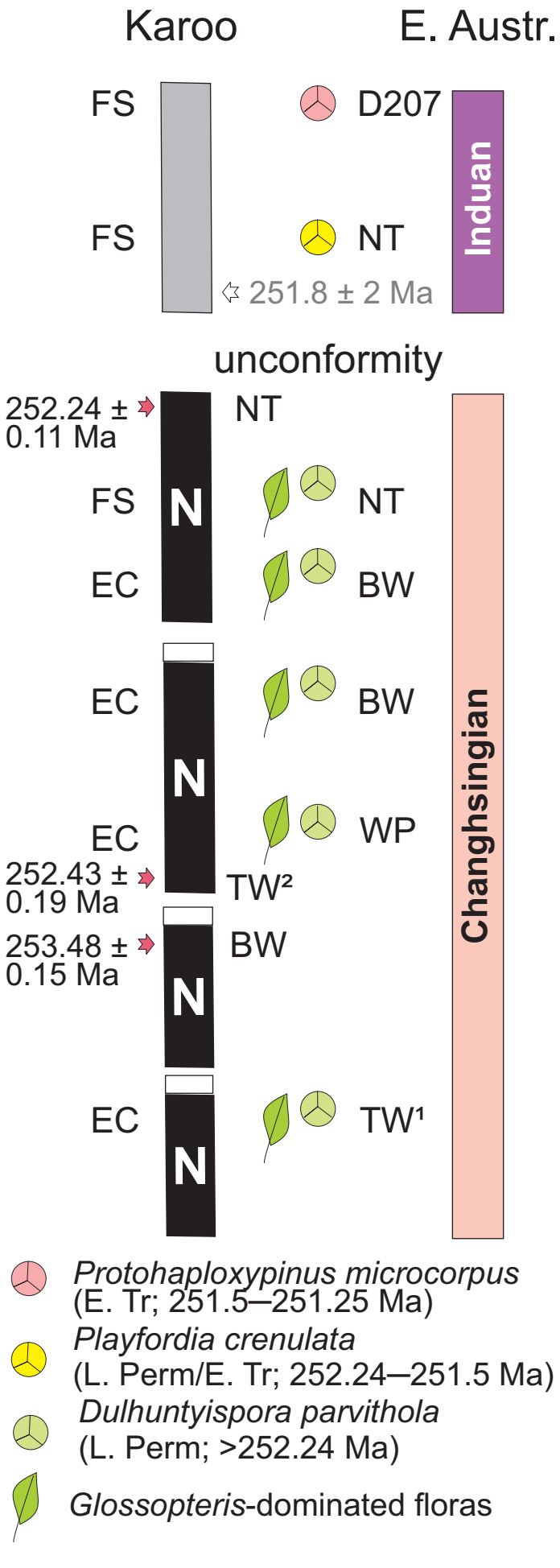

Title page (with author information)

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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Declaration of interests

☒The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: