Is the vertebrate-defined Permian-Triassic boundary in the Karoo Basin, South Africa, the terrestrial expression of the end-Permian marine event?

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ABSTRACT

The end-Permian extinction records the greatest ecological catastrophe in Earth history. The vertebrate fossil record in the Karoo Basin, South Africa, has been used for more than a century as the standard for understanding turnover in terrestrial ecosystems, recently claimed to be in synchrony with the marine crisis. Workers assumed that systematic turnover at the *Dicynodon* assemblage zone boundary, followed by the appearance of new taxa directly above the base of the *Lystrosaurus* assemblage zone, is the continental expression of the end-Permian event and recovery. To test this hypothesis, we present the first high-precision age on strata close to the inferred Permian-Triassic boundary. A U-Pb isotope dilution–thermal ionization mass spectrometry zircon age of 253.48 ± 0.15 Ma (early Changhsingian) is from a silicified ash layer ~60 m below the current vertebrate-defined boundary at Old Lootsberg Pass (southern South Africa). This section yields newly discovered plants and vertebrates, and is dominated by a normal polarity signature. Our collective data suggest that the *Dicynodon-Lystrosaurus* assemblage zone boundary is stratigraphically higher than currently reported, and older than the marine extinction event. Therefore, the turnover in vertebrate taxa at this biozone boundary probably does not represent the biological expression of the terrestrial end-Permian mass extinction. The actual Permian-Triassic boundary in the Karoo Basin is either higher in the Katberg Formation or is not preserved. The currently accepted model of the terrestrial ecosystem response to the crisis, both in this basin and its extension globally, requires reevaluation.

INTRODUCTION

The Permian vertebrate biostratigraphy of the Karoo Basin, South Africa, forms the basis of a global model to explain the terrestrial ecosystem response to the end-Permian crisis as recognized in the marine record (Ward et al., 2005; Smith and Botha-Brink, 2014). Here (and elsewhere; Lucas, 2010) the terrestrial Permian-Triassic boundary (PTB) currently is associated with the Last Appearance Datum of the therapsid *Dicynodon*, and three other taxa of the *Dicynodon* assemblage zone (AZ), and their replacement by an array of taxa with their first appearance in the *Lystrosaurus* AZ (Smith and Botha-Brink, 2014). Estimates of as much as 89% of tetrapod generic biodiversity loss (Benton and Newell, 2014) are reported across this boundary. Vertebrate turnover is interpreted as coincident with the marine mass extinction event (Ward et al., 2005), which was dated as 251.9 Ma (Burgess et al., 2014).

The extinction of *Dicynodon* AZ taxa is interpreted as a consequence of dramatic climate change affecting the Karoo Basin (Ward et al., 2005), although others (e.g., Gastaldo et al., 2014; Gastaldo and Neveling, 2014) have demonstrated inconsistencies in the lithologic and chemostratigraphic data on which this model was based. Latest Permian floodplains were colonized by the gymnosperm *Glossopteris* and ground-creeping horsetails (e.g., *Trizygia*), which grew on immature olive-green paleosols with poorly developed soil horizons (Gastaldo et al., 2014). Landscape devegetation (Smith and Ward, 2001) is thought to be the consequence of increasing drought that took a toll on the food chain, ultimately leading to vertebrate extinction. The first appearance of paleosol color mottling associated with a shift in siltstone color to grayish-red (Smith and Ward, 2001), found below the vertebrate-defined PTB, is interpreted to reflect a rapid change in seasonality (Smith and Botha-Brink, 2014) that affected the *Glossopteris* flora. An increasing proportion of massive, grayish-red siltstone above the vertebrate-defined PTB is believed to be of earliest Triassic age, reflecting an overall drying trend, a view supported by the appearance of intraformational pedogenic conglomeratic facies concentrated in channel-lag deposits (Ward et al., 2005; Smith and Botha-Brink, 2014).

We present new paleontologic, geochronometric, and magnetostratigraphic data and observations from Old Lootsberg Pass (southern South Africa, ~31.5°S, 24.5°E; Fig. 1), a critical South African locality on which the current continental extinction model is based (Ward et al., 2005; Smith and Botha-Brink, 2014). These data and observations are used in conjunction with the original biostratigraphic database of Smith and Botha-Brink (2014) and their global positioning system (GPS) specimen coordinates to extend the stratigraphic range of both Permian plants and vertebrates in the basin. From beds above the vertebrate-defined PTB, we have discovered *Glossopteris*-dominated megafloral assemblages and a typical Permian palynoflora in olive-gray siltstone; and a dicynodontoid skull of characteristically Permian aspect and woody trunk segments of *Agathoxylon africanum* from the stratigraphically lowest intraformational conglomerate facies (Fig. 2), currently considered as indicative of the lower Triassic in the Karoo Basin (Botha and Smith, 2006). The stratigraphy at Old Lootsberg Pass is dominated by normal magnetic polarity, with a short reverse polarity magnetozone in sandstone and siltstone exposed ~3 m above a silicified volcaniclastic bed (Figs. 1B and 2) located beneath the vertebrate-defined PTB. This silicified volcaniclastic unit has a U-Pb isotope dilution–thermal ionization mass spectrometry (ID-TIMS) age of 253.48 ± 0.15 Ma, determined from single, chemically abraded zircon grains, that places our studied section in the early Changhsingian.

GEOLOGIC SETTING

Karoo Supergroup deposition began in the late Carboniferous and ended in the Jurassic, filling a basin fronting the Cape Fold Belt (Johnson et al., 2006). Rocks of the Beaufort Group record fully continental deposits. Meandering fluvial architectures, typical of the Elandsberg Member of the uppermost Permian Balfour Formation, incised into widespread olive-gray paleosols. These were replaced by fluvial architectures interpreted to represent low-sinuosity regimes, and grayish-red mottled siltstone associated with the Palingkloof Member (Smith and Botha-Brink, 2014), in which the vertebrate-defined PTB is placed (Fig. 2). A transition to

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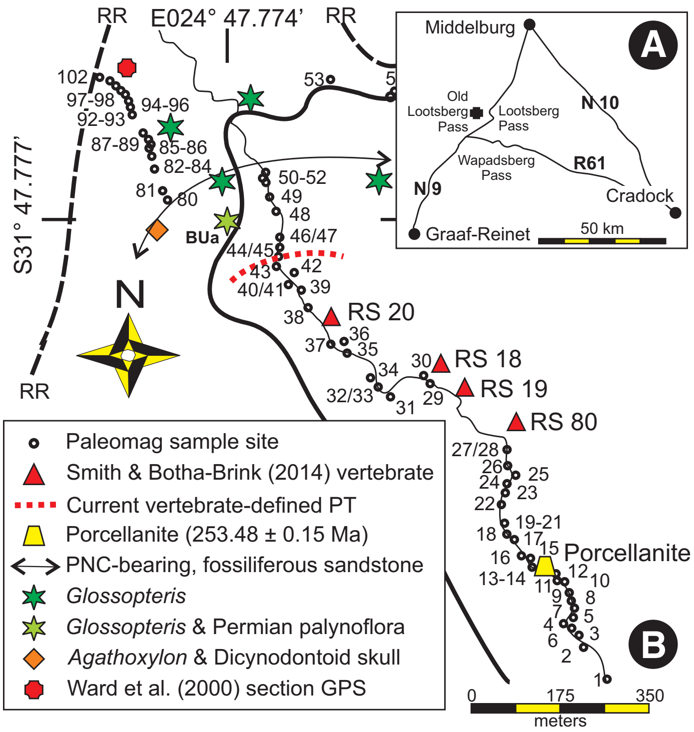

Figure 1. A: Old Lootsberg Pass in South Africa. B: Measured-section transect showing paleomagnetic (Paleomag) sample sites and porcellanite location on the Blaauwater 87 farm, Eastern Cape Province. Global positioning system (GPS) located positions and Smith and Botha-Brink (2014) vertebrate samples and the vertebrate-defined Permian-Triassic boundary (PTB) (dotted line) relative to our section are shown. New paleontological collections are marked. Drill sites for magnetostratigraphy are shown by closed circles. RR—railroad; PNC—pedogenic nodule conglomerate. All GPS coordinates are World Geodetic System 1984 (WGS 84) standard; base map is 3124DD Lootsberg 1:50,000 South Africa, Council for Geoscience, Pretoria.

braidplain architectures and maroon paleosols is reported in the overlying sandstone-dominated Katberg Formation (Ward et al., 2005).

PALEONTOLOGY

Smith and Botha-Brink (2014) reported four *Dicynodon* AZ vertebrate sites below their PTB at Old Lootsberg Pass, all of which are above our porcellanite (Figs. 1B and 2); they also reported three vertebrates in the *Lystrosaurus* AZ above the top of the section we describe here (see the GSA Data Repository[1]). Vertebrate fossils we collected include a partial dicynodontoid skull enveloped in the most basal conglomerate lag deposit (Fig. 2; see the Data Repository). The void of the skull is filled with intraformational conglomerate; its presence in, and preservation by, this carbonate-cemented facies is interpreted to indicate that the animal and river system were contemporaneous and the skull was not reworked. The large skull (>20 cm) displays particularly large diameter (3 cm) canines and, although preservation precludes assignment to a specific taxon, its overall size and anatomy suggests systematic affinities including *Dicynodon*, *Daptocephalus*, or *Lystrosaurus maccaigi* of the *Dicynodon* AZ (Kammerer et al., 2011; B. de Klerk and C. Kammerer, 2013, personal commun.).

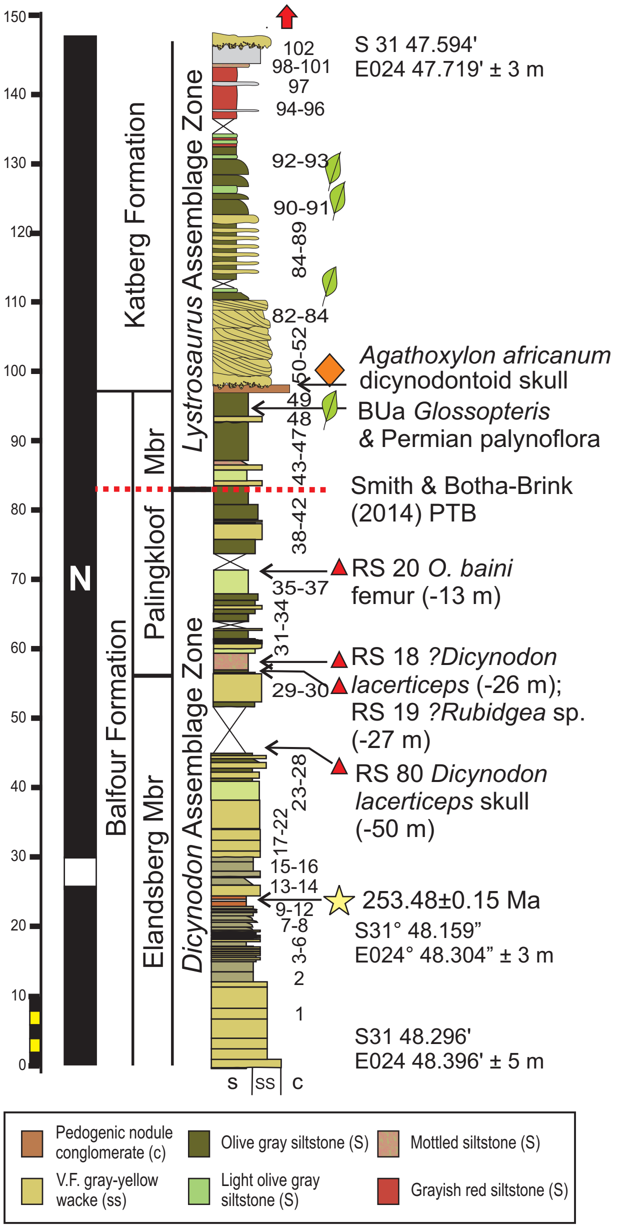

Figure 2. Lithostratigraphy, magnetostratigraphy (numbered sites; N—normal polarity), and paleontology of the Old Lootsberg Pass section; global positioning system coordinates for the base and top of our section are provided (for details, see the Data Repository [see footnote 1]). Vertebrate collection number, systematic identification, and stratigraphic position of Smith and Botha-Brink (2014) specimens below their Permian-Triassic boundary (PTB) (dotted red line) are marked. Question marks represent specimens of postcranial material where systematic identification is uncertain. Mbr—member; *O. baini*—*Oudenodon baini*; ss—sandstone; V.F.—very fine.

We collected fossil plants from six sites in strata above the vertebrate-defined PTB (see Smith and Botha-Brink, 2014). Of these sites, 4 are within 10 m below the laterally traceable, intraformational conglomerate-bearing sandstone that conforms to post-extinction lithologies, and 2 occur >20 m above it (Figs. 1B and 2). All collections are *Glossopteris* dominated and several occur with the typical Permian sphenophyll *Trizygia speciosa*. There is no taphonomic evidence indicating any reworking of leaves (DiMichele and Gastaldo, 2008). A characteristic Permian palynoflora of moderate diversity (BUa in Fig. 1B) is consistent with

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[1] GSA Data Repository item 2015313, vertebrate paleontology; Blaauwater palynology; U-Pb ID-TIMS geochronology methodology; magnetic polarity stratigraphy, methods, and results; and additional references and figures, is available online at www.geosociety.org/pubs/ft2015.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

the macroflora record (glossopterids: *Protohaploxypinus limpidus*, *Striatopodocarpites cancellatus*, and *Weylandites lucifer*; trizygioid sphenophytes: *Columnisporites*). The palynoflora also includes an array of other gymnosperm, peltasperm, corystosperm, and conifer pollen not found in regional, time-equivalent macrofloral records, but that appear in Karoo floras considered to be of Triassic age (Anderson and Anderson, 1985; see the Data Repository). Woody trunk segments (>0.5 m diameter) with well-preserved growth rings of the long-ranging Permian–Triassic gymnosperm wood, *Agathoxylon africanum* (Bamford, 1999), also occur in the intraformational conglomerate-bearing sandstone (Fig. 2).

U-Pb GEOCHRONOLOGY AND MAGNETIC POLARITY STRATIGRAPHY

The porcellanite, or silicified ash layer (Figs. 1B and 2), contains abundant unaltered, euhedral, elongate, equant, and multifaceted zircon grains. U-Pb analyses of 11 single grains yielded data for 4 that are interpreted as antecrysts, or inherited due to postdepositional sedimentary recycling or inclusion during magmatic ascent and/or emplacement. Data for the remaining 7 grains have overlapping $^{206}Pb/^{238}U$ ages that together have a weighted mean age of 253.48 ± 0.15 Ma (2σ; mean square of weighted deviates, MSWD = 0.47), interpreted as the best age estimate of the main zircon population. This maximum depositional age estimate places the porcellanite in the early Changhsingian (254.2–251.9 Ma; for methods and analyses, see the Data Repository).

Intensities of the natural remanent magnetization (NRM) for Old Lootsberg Pass rocks range from ~5.0 to 0.1 mA/m. In most samples, the magnetization component isolated beyond a few demagnetization steps is of northwest to north-northwest declination and moderate negative inclination; it is interpreted to be of normal polarity. This normal polarity remanence persists up to the maximum laboratory unblocking temperature of low-Ti magnetite (~580 °C) in thermal demagnetization, and to peak fields of >70 mT. This principal component of the NRM is interpreted to be a composite of a first-unblocked secondary magnetization, associated with Early Jurassic Karoo magmatism, superimposed on an earlier acquired remanence. Over a narrow interval defined by data from three sites, and best defined at P17 (Figs. 1B and 2), demagnetization trajectories at laboratory unblocking temperatures >450 °C indicate the preservation of a south-directed magnetization component of moderate positive inclination. These data are interpreted as reverse polarity. Other than this thin stratigraphic interval (Fig. 2), all other data indicate a sequence dominated by normal polarity. Rock magnetic and anisotropy of magnetic susceptibility data indicate, respectively, that the principal magnetic phase is moderate-coercivity magnetite, and that the rocks display a well-developed depositional fabric. Detrital magnetite is identified in petrographic inspection (for methods, results, and analysis, see the Data Repository).

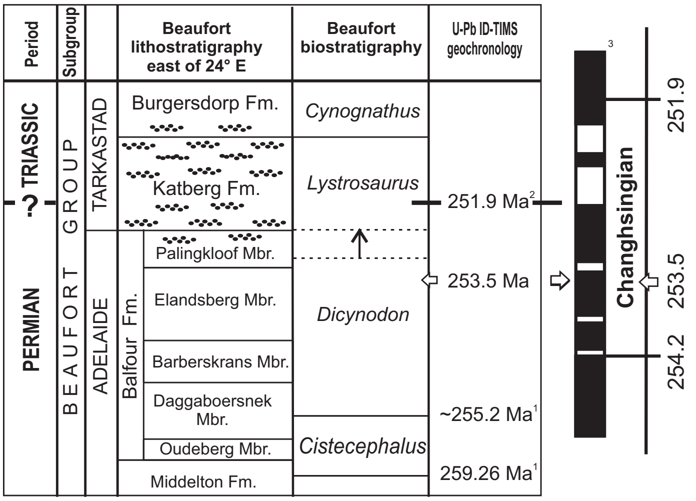
DISCUSSION AND CONCLUSIONS

The current understanding of the terrestrial response to the end-Permian mass extinction is that the *Glossopteris* flora disappeared in northern Gondwana (Hermann et al., 2011), eastern Australia (Metcalfe et al., 2015), and across the Southern Hemisphere coincident with the PTB ca. 251.9 Ma as a consequence of ecosystem instabilities. In turn, vegetational loss reduced vertebrate biodiversity (Ward et al., 2005), as evidenced by a turnover from a complex, latest Permian tetrapod fauna of the *Dicynodon* AZ, to rapidly appearing earliest Triassic taxa in the *Lystrosaurus* AZ (Lucas, 2010). The tetrapod pattern, based originally on the South Africa record (Smith and Ward, 2001) and extrapolated globally, is interpreted to be accompanied by a shift in climate-sensitive sediments indicative of increased aridification and evidenced by the appearance of reddish siltstone and intraformational conglomerate (Benton and Newell, 2014). These Karoo Basin patterns are reported in a normal polarity magnetozone ~10 m above the boundary of a reversed polarity zone (Ward et al., 2005). Our new data require a reassessment of this Karoo Basin model and its applicability elsewhere.

The presence of *Glossopteris* preserved over a stratigraphic distance of ~45 m above the current vertebrate-defined PTB, in strata that can be assigned either to the upper Palingkloof Member or Katberg Formation at Old Lootsberg Pass (Figs. 1B and 2), indicates that neither the taxon's demise nor vegetational collapse was coincident with the reported tetrapod turnover (Smith and Ward, 2001). Typical wetland plants (Prevec et al., 2010) and woody trunks with well-developed tree rings in the *Lystrosaurus* biozone (Fig. 2) are evidence that contradicts an interpretation of post-extinction aridification (Smith and Botha-Brink, 2014). Rather, a prevailing amenable climate in which wetland vegetation persisted must have been maintained beyond the current upper *Dicynodon* biozone boundary. If the *Lystrosaurus* biozone is Triassic, the Karoo Basin should be considered a *Glossopteris* refugium with recovery clades (Anderson and Anderson, 1985) already present in the palynological spectrum, but outside of the megafloral taphonomic window (DiMichele and Gastaldo, 2008).

The preservation of a characteristic Permian dicynodontoid skull coeval with a channel deposit exhibiting lithofacies and facies associations characteristic of post-extinction deposits has several ramifications. Our dicynodontoid skull extends the upper boundary of the *Dicynodon* biozone into what has long been considered the Early Triassic *Lystrosaurus* biozone, requiring a biozone-boundary shift upsection in accord with its present definition (Fig. 3; Rubidge, 1995). This supports previous concerns (Gastaldo et al., 2009) about the correspondence between a supposed facies change and faunal turnover (Ward et al., 2005; Smith and Botha-Brink, 2014). The occurrence of our specimen in a sandstone body of post-extinction architecture, along with the paleobotanical data, supports the attribution of a late Permian age assignment and, as a consequence, placement in the pre-extinction Lootsbergian A land-vertebrate faunachron (Lucas, 2010).

Our magnetostratigraphic data augment those previously published for Old (West) Lootsberg Pass (Ward et al., 2005) and establish a different polarity record for these rocks. Our magnetic polarity stratigraphy shows a section dominated by normal polarity, with one thin reverse polarity magnetozone ~55 m below the vertebrate-defined PTB (Fig. 2).



[1]Rubidge et al. (2013); [2]Burgess et al. (2014); [3]Szurlies (2013)

Figure 3. Karoo Basin lithostratigraphy and biostratigraphy, and biozone boundary dates for the base of the *Cistecephalus* and *Dicynodon* assemblage zones (Rubidge et al., 2013). The relative position of our isotope dilution–thermal ionization mass spectrometry (ID-TIMS) porcellanite age near the top of the *Dicynodon* zone (arrows) is placed against the global composite magnetic polarity time scale of Szurlies (2013) based on the magnetostratigraphy of the Old Lootsberg Pass, South Africa, section. The hypothesized stratigraphic position of the Permian-Triassic boundary is manifest somewhere in the *Lystrosaurus* assemblage zone in the Katberg Formation. Lithostratigraphic units and biozones are not drawn to scale. Mbr.—member; Fm.—formation.

These data indicate that the uppermost part of the *Dicynodon* AZ is in an interval dominated by normal polarity chrons. This differs from a reported reverse magnetozone within ~10 m of the vertebrate-defined PTB for the area, as well as at Commando Drift dam near Cradock (Fig. 1; Ward et al., 2005). When our data are compared with the global Permian magnetostratigraphy, they are more consistent with the early, rather than latest, Changhsingian polarity record (Fig. 3), in accord with with our U-Pb ID-TIMS age estimate.

The silicified porcellanite from which we obtained a high-precision early Changhsingian age (253.48 ± 0.15 Ma) is ~60 m below the vertebrate-defined PTB (Smith and Botha-Brink, 2014) and <75 m below a facies assemblage traditionally used to characterize the Early Triassic in the Karoo Basin. Rubidge et al. (2013) provided high-resolution U-Pb ID-TIMS zircon dates from underlying Permian vertebrate biozones and placed the lower boundary of the *Dicynodon* AZ at ca. 255.2 Ma (Fig. 3); the *Dicynodon* AZ attains a maximum thickness of 500 m in the area (Rubidge, 1995). Approximately 440 m of section and 1.69 m.y. separate our porcellanite from the base of this biozone. Geologic data do not support a change in average depositional rate above this bed, which means that it is improbable that the PTB, which is >1.6 m.y. younger, is situated 60–75 m higher in the section. Conservatively, we argue that the data from Old Lootsberg Pass preclude the turnover between the *Dicynodon* and *Lystrosaurus* AZs in South Africa as the terrestrial expression of the marine mass extinction event. The actual stratigraphic placement of the PTB in this basin is in the Katberg Formation, which is well documented to be riddled with diastems and nonconformities of long duration.

In summary, new multidisciplinary data from the Karoo Basin call into question our current understanding of the terrestrial response to the end-Permian mass extinction. Paleoecological evidence does not support the reported coincidence of climate aridification, floral collapse, and tetrapod turnover. Similarly, magnetostratigraphic and geochronometric data, when conservatively interpreted, indicate that the turnover between the *Dicynodon* and *Lystrosaurus* biozones, as currently defined, occurred in the early Changhsingian and was not coeval with the marine mass extinction event.

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REFERENCES CITED

Anderson, J.M., and Anderson, H.M., 1985, Palaeoflora of southern Africa. Prodomus of South African megafloras Devonian to Lower Cretaceous: Rotterdam, Netherlands, Balkema, 416 p.

Bamford, M.K., 1999, Permo-Triassic fossil woods from the South African Karoo Basin: Palaeontologica Africana, v. 35, p. 25–40.

Benton, M.J., and Newell, A.J., 2014, Impacts of global warming on Permo-Triassic terrestrial ecosystems: Gondwana Research, v. 25, p. 1308–1337, doi:10.1016/j.gr.2012.12.010.

Botha, J., and Smith, R.M.H., 2006, Rapid vertebrate recuperation in the Karoo Basin of South Africa following the End-Permian extinction: Journal of African Earth Sciences, v. 45, p. 502–514, doi:10.1016/j.jafrearsci.2006.04.006.

Burgess, S.D., Bowring, S., and Shen, S.Z., 2014, High-precision timeline for Earth's most severe extinction: National Academy of Sciences Proceedings, v. 111, p. 3316–3321, doi:10.1073/pnas.1317692111.

DiMichele, W.A., and Gastaldo, R.A., 2008, Plant paleoecology in deep time: Missouri Botanical Garden Annals, v. 95, p. 144–198, doi:10.3417/2007016.

Gastaldo, R.A., and Neveling, J., 2014, Anatomy of a mass extinction: Sedimentological and taphonomic evidence for drought-induced die-offs at the Permo-Triassic boundary in the main Karoo Basin, South Africa: Comment: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 396, p. 99–118, doi:10.1016/j.palaeo.2014.01.002.

Gastaldo, R.A., Neveling, J., Clark, C.K., and Newbury, S.S., 2009, The terrestrial Permian-Triassic boundary event bed is a non-event: Geology, v. 37, p. 199–202, doi:10.1130/G25255A.1.

Gastaldo, R.A., Knight, C.L., Neveling, J., and Tabor, N.J., 2014, Latest Permian paleosols from Wapadsberg Pass, South Africa: Implications for Changhsingian climate: Geological Society of America Bulletin, v. 126, p. 665–679, doi:10.1130/B30887.1.

Hermann, E., Hochuli, P.A., Bucher, H., Brühwiler, T., Hautmann, M., Ware, D., and Roohi, G., 2011, Terrestrial ecosystems on North Gondwana following the end-Permian mass extinction: Gondwana Research, v. 20, p. 630–637, doi:10.1016/j.gr.2011.01.008.

Johnson, M.R., Anhaeusser, C.R., and Thomas, R.J., eds., 2006, The geology of South Africa (second edition): Johannesburg, Geological Society of South Africa, 691 p.

Kammerer, C.F., Angielczyk, K.D., and Fröbisch, J., 2011, A comprehensive taxonomic revision of *Dicynodon* (Therapsida, Anomodontia) and its implications for dicynodont phylogeny, biogeography, and biostratigraphy: Journal of Vertebrate Paleontology, v. 31, p. 1–158, doi:10.1080/02724634.2011.627074.

Lucas, S.G., 2010, The Triassic timescale based on nonmarine tetrapod biostratigraphy and biochronology, *in* Lucas, S.G., ed., The Triassic timescale: Geological Society of London Special Publication 334, p. 447–500, doi:10.1144/SP334.15.

Metcalfe, I., Crowley, J.L., Nicoll, R.S., and Schmitz, M., 2015, High-precision U-Pb CA-TIMS calibration of middle Permian to lower Triassic sequences, mass extinction and extreme climate-change in eastern Australian Gondwana: Gondwana Research, v. 28, p. 61–81, doi:10.1016/j.gr.2014.09.002.

Prevec, R., Gastaldo, R.A., Neveling, J., Reid, S.B., and Looy, C.V., 2010, An autochthonous glossoperid flora with Latest Permian palynomorphs from the *Dicynodon* Assemblage Zone of the southern Karoo Basin, South Africa: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 292, p. 391–408, doi:10.1016/j.palaeo.2010.03.052.

Rubidge, B.S., ed., 1995, Biostratigraphy of the Beaufort Group (Karoo Supergroup): South African Commission on Stratigraphy Biostratigraphic Series, Volume 1, 46 p.

Rubidge, B.S., Erwin, D.H., Ramezani, J., Bowring, S.A., and de Klerk, W.J., 2013, High-precision temporal calibration of Late Permian vertebrate biostratigraphy: U-Pb zircon constraints from the Karoo Supergroup, South Africa: Geology, v. 41, p. 363–366, doi:10.1130/G33622.1.

Smith, R.H.M., and Botha-Brink, J., 2014, Anatomy of a mass extinction: Sedimentological and taphonomic evidence for drought-induced die-offs at the Permo-Triassic boundary in the main Karoo Basin, South Africa: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 396, p. 99–118, doi:10.1016/j.palaeo.2014.01.002

Smith, R.M.H., and Ward, P.D., 2001, Pattern of vertebrate extinctions across an event bed at the Permian-Triassic boundary in the Karoo Basin of South Africa: Geology, v. 28, p. 227–230.

Szurlies, M., 2013, Late Permian (Zechstein) magnetostratigraphy in western and central Europe, *in* Gąsiewicz, A., and Słowakiewicz, M., eds., Palaeozoic climate cycles: Their evolutionary and sedimentological impact: Geological Society of London Special Publication 376, p. 73–85, doi:10.1144/SP376.7.

Ward, P.D., Botha, J., Buick, R., Dekock, M.O., Erwin, D.H., Garrison, G., Kirschvink, J., and Smith, R.H.M., 2005, Abrupt and gradual extinction among Late Permian land vertebrates in the Karoo Basin, South Africa: Science, v. 307, p. 709–714, doi:10.1126/science.1107068.

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