ABSTRACT: Vertebrate paleontologists have proposed a model for the terrestrial end-Permian event in the Karoo Basin, South Africa. The scenario envisions vegetational collapse that resulted in a phased extinction of vertebrate taxa in the uppermost Daptocephalus Assemblage Zone and overlying Lystrosaurus Assemblage Zone. These biodiversity patterns are placed into composite stratigraphic sections at key localities, several of which are in close spatial proximity. We present a stratigraphic framework at two of these localities, Old Lootsberg Pass and Tweefontein, physically correlated over ~2 km distance into which new and previously reported fossils are placed.

Glossopterid-dominated megafloras occur in both the Daptocephalus and Lystrosaurus biozones, along with palynological assemblages. Katbergia, a burrow used by others as an indicator of the transition and post-transition interval, occurs in paleosols much lower in the upper Daptocephalus Assemblage Zone, along with various subhorizontal cylindrical structures interpreted as vertebrate burrows. New vertebrate specimens include: (1) a large skull of either Daptocephalus leoniceps or Dicynodon sp.; (2) a partial skull with large canine assignable to either Dicynodon, Daptocephalus, or Lystrosaurus mccaigi; (3) a Lystrosaurus canine in grayish-red siltstone; (4) a skull of Lystrosaurus murrayi; and (5) a non-diagnostic post-cranial skeleton of lystrosaurid affinity.

These fossils are combined with the published Karoo-vertebrate dataset to test the stratigraphic position of the Daptocephalus and Lystrosaurus Assemblage Zone boundary. We conclude that: (1) glossopterids in the Lystrosaurus Assemblage Zone indicate persistence of the clade past what is considered to be an extinction event; (2) the presence of palynomorphs known from recovery clades above the proposed vertebrate-biozone boundary indicate that these groups were present in the basin, but outside of the megafloral taphonomic window; (3) the position of the proposed vertebrate-assemblage-zone boundary is stratigraphically inconsistent and varies in its reported stratigraphic position at a minimum of 25 m, and up to 70 m, across a distance of only ~2 km; and (4) terrestrial ecosystem dynamics only can be assessed when a high resolution stratigraphic framework is developed into which biostratigraphic data are placed and, thereafter, patterns can be evaluated.

INTRODUCTION

Earth’s most severe biodiversity disruption is recorded in uppermost Permian (Changhsingian) stratigraphic sequences around the globe. This biotic crisis, the end-Permian mass extinction, is modeled as having been synchronous, affecting both the marine and terrestrial realms over a very short time frame (Ward et al. 2005; Smith et al. 2011; Chen and Benton 2012; Smith and Botha-Brink 2014), although this relationship has been questioned (Lucas 2009, 2010, in press) and new geochronologic data from various clades over variable time scales (Payne and Clapham 2011), with different extinction rates in various clades over variable time scales (Payne and Clapham 2012). In Gondwana, the terrestrial extinction model is centered around the reported demise of one plant clade, Glossopteridales (e.g., McElwain and Pumyasena 2007), and the biostratigraphic ranges of vertebrate taxa in the Karoo Basin (Ward et al. 2000, 2005; Smith and Botha-Brink 2014). The biostratigraphic utility of both groups at both the generic and species level is questioned (Lucas, personal communication 2016), and Viglietti et al. (2016) noted that their biostratigraphic scheme may not be applicable in other parts of the globe due to endemism. Tetrapod biodiversity loss at the familial level is reported to be upwards of 63% and approaches 89% at the generic level (Benton and Newell 2014), although Lucas (2009) noted that these figures are overstated. Nevertheless, this “Mother of Mass Extinctions” (Erwin 2006) is widely used as a model for ecosystem response to severe perturbation, and is considered a possible scenario for how Earth systems may react to current rapid global warming and climate extremes (Payne and Clapham 2012; Chen and Benton 2012; Benton and Newall 2014).

The Karoo Basin, South Africa, serves as one of a small number of continental successions in which the affects to, and the response of, the
terrestrial ecosystem are reported to be preserved. Currently, vertebrate biodiversity loss is envisioned as having been three phased, and occurring in response to catastrophic vegetational disturbance (Ward et al. 2005; Smith and Botha-Brink 2014). But, unlike other biotic response patterns, vertebrate loss was followed by the rapid recovery of faunas shortly following the event (Botha and Smith 2006). Only a few Permian–Triassic boundary (PTB) sections are well exposed in South Africa, and eight localities comprise the focus of most published studies (Ward et al. 2000; Smith 1995; Smith and Ward 2001; Retallack et al. 2003; Ward et al. 2005; Botha and Smith 2006; Smith and Botha-Brink 2014). These are: Bethulie and Caledon in the Free State; and Carlton Heights, Commandodrift, Wapadsberg Pass, (East) Lootsberg Pass, Tweefontein, and Old (West) Lootsberg Pass in the Eastern Cape. These latter three localities, in close geographical proximity, commonly are referred to as Lootsberg Pass (Viglietti et al. 2016). All localities are reported to display the same lithostratigraphic suite of characters that provide for a datum against which the extinction event can be recognized.

The criterion for field identification of the stratigraphic position of faunal turnover used by many workers continues to be the purported presence of a “unique” 3–5 m thick, interlaminated succession of reddish gray siltstone and mudstone couplets (Smith and Botha-Brink 2014; Botha-Brink et al. 2014; Viglietti et al. 2016). The red laminites of Ward et al. (2005) originally were described by Smith and Ward (2001, p. 1148) as comprised of “thinly bedded dark reddish-brown and olive-gray siltstone-mudstone couplets.” Yet, other studies (Gastaldo et al. 2009; Gastaldo and Neveling 2012; Neveling et al. 2016a, 2016b) demonstrated this physical datum does not exist either on a local, regional, or basin-wide scale and concluded that there is no consistent lithologic datum on which the boundary can be identified. Hence, the event as recognized by other workers (e.g., Ward et al. 2005; Smith and Botha-Brink 2014; Viglietti et al. 2016) is based strictly on a turnover in faunas, from the recently renamed Daptocephalus (Dicynodon) Assemblage Zone (AZ; Viglietti et al. 2016; Rubidge et al. 2016) to the overlying Lystrosaurus AZ (Smith and Botha-Brink 2014). That pattern is reported to be based on vertebrate occurrences that are placed into measured sections (Botha-Brink et al. 2014; Viglietti et al. 2016), some of which have been correlated lithostratigraphically between outcrops in adjacent erosional gully (donga) sections at boundary-bearing localities (Smith and Botha-Brink 2014). To date, though, single, composite stratigraphic sections of these critical sites continue to appear in the literature without any spatial or temporal framework into which fossil material has been placed.

Here, we present a stratigraphic framework based on our physical correlation and new fossil occurrences at two of the eight localities that have been the basis for interpreting patterns of faunal turnover between the Daptocephalus and Lystrosaurus AZs (Viglietti et al. 2016). We document the preservation of Glossopteris leaves, palynological assemblages, and pieces of permineralized trunks, along with new vertebrate remains, at Old Lootsberg Pass and Tweefontein. These fossils occur in the Elandsberg and Palingkloof members of the Balfour Formation, and overlying Katberg Formation. These new fossils are combined with previously published vertebrate records and placed in our physically correlated stratigraphic framework to test biodiversity trends across the Daptocephalus/Lystrosaurus biozone boundary traced over a geographic distance of ~ 2 km.

KAROO BASIN GENERAL STRATIGRAPHY

Sedimentation in the Karoo Basin, formed ahead of the rising Cape Fold Belt (Lindeque et al. 2011), began after continental deglaciation in the Late Carboniferous and continued into the Jurassic (Johnson et al. 2006). This succession, known as the Karoo Supergroup, comprises the basal Dwyka (Upper Carboniferous) and Ecca (Lower–Middle Permian) groups, representing thick diamictites overlain by a series of successions that accumulated in deep water environments. Following deglaciation, sediments record deposition in fully continental, fluvial-dominated regimes of the Beaufort (Permian–Lower Triassic) and (informal) Stormberg (Middle–Upper Triassic; Catuneau et al. 2005) groups. The Beaufort Group is subdivided into the lower Adelaide and upper Tarkastad subgroups (Fig. 1), and is reported to represent continuous sedimentation across the interval in which the vertebrate-defined PT boundary (PTB) is interpreted to be present (Ward et al. 2005; Smith and Ward 2001; Smith and Botha-Brink 2014; Viglietti et al. 2016).

The uppermost Permian (Changhsingian) strata are traditionally placed in the Elandsberg Member (Balfour Formation; Fig. 1) that consists of olive-gray silstone, in which large (dm to m) carbonate-cemented concretions may be present. These rocks may show evidence of grayish-red mottling (Smith 1995). Sandstones are fine-grained lithic or feldspathic wacke, with thick, low-angle, trough-crossbed sets attaining a total thickness of several meters. These bedload deposits are interpreted to represent high sinuosity meandering systems (e.g., Smith and Botha-Brink 2014). Stratigraphically higher, an increasing proportion of grayish-red silstone is reported to mark the transition into the Palingkloof Member wherein the vertebrate-defined PTB is placed by some workers (Ward et al. 2005; Smith and Botha-Brink 2014; Viglietti et al. 2016; Rubidge et al. 2016). A greater proportion of reddened silstone has been attributed to increasing aridification (Smith and Botha-Brink 2014) towards the
boundary event (in contrast, see Gastaldo et al. 2015; Gastaldo and Neveling 2016) wherein the Daptocephalus/Lystrosaurus biozone boundary is coincident with the age of the marine extinction event. They suggested that Lopingian rocks extend into the vertebrate-biozone boundary.

Recently, Gastaldo et al. (2015) reported the first high resolution ID-TIMS published a stratigraphic section > 160 in thickness from which a magnetostratigraphic record was obtained (see Online Supplemental Data for .kmz file). Here, we have measured sections, totaling > 800 m of section, and we have correlated them by walking bounding surfaces of laterally extensive sandstone bodies over distances of > 0.5 km. GPS coordinates were taken every 50 or 100 paces on each bounding surface and plotted using GoogleEarth to confirm the geographic relationships among sandstone units (see Online Supplemental Data for .kmz file).

The Tweefontein section, as reported by Ward et al. (2000) and used as one of their localities in the Lootsberg Pass area (Ward et al. 2005), is more of an enigma. The published GPS coordinates (Ward et al. 2001; S 31° 49.334’, E 024° 48.565’) place their Tweefontein section in an open field with no nearby exposure (Fig. 4). As these coordinates appear in more than a single paper (Ward et al. 2000, 2005), the reliability of such coordinates, when duplicated, must be taken as correct. We have examined all erosional gullies exposing outcrop across a > 3 km transect from southeast of these reported GPS coordinates to Old Lootsberg Pass. Outcrop that is closest to the published GPS coordinates is encountered in several interconnected dongas ~ 400 m to the northeast of the reported location (S 31° 49.230’, E024° 48.818’ ± 5 m, WGS84 standard). Here, three sections, totaling > 175 m, are measured and correlated using sandstone bounding surfaces with the same field technique as noted above. We have applied the superscript designation of Tweefontein1 to distinguish our locality that includes measured and physically correlated stratigraphic sections (see Online Supplemental Data for .kmz file). All sections were measured using standard field techniques and a Jacob staff with Abney level, and fresh samples were excavated to characterize lithologies. Lithologic samples from competent beds were ground into thin sections by Applied Petrographic Services Inc. and examined using a Nikon Eclipse LV100 POL microscope. Our preparations represent the earliest and first documented thin sections of mudrock in this part of the basin.

Fossils were collected from olive-gray or grayish-red siltstone, or pedogenic nodule conglomerate, under SAHRA permit 2/2/APM-PERMIT/13/08/001 to Dr. R. Prevec, and taken to The Albany Museum, Grahamstown, for preparation and curation. All macrofossil plant sites, except BUa, were collected using field equipment; site BUa was excavated with a backhoe. Macrofloral elements were examined by Dr. R. Prevec and each assigned to a preliminary morphotype scheme (Prevec et al. 2010), which is used herein, and are curated under the catalog designations using...
the collection site designation (BUa, etc.; see Online Supplemental Data Table 1 for curatorial information). Thin sections of permineralized wood were made in transverse, radial longitudinal, and tangential longitudinal orientations, ground and polished to a thickness of about 30 μm. These were studied using a Zeiss Axioskop petrographic microscope and photographed with an Olympus DP72 digital camera equipped with Stream Essentials software. Permineralized wood and thin sections are in the collections of the Evolutionary Studies Institute (formerly the Bernard Price Institute of Palaeontology), University of Witwatersrand, with acquisition numbers BP/16/1708A-G.

Lithologies preserving macrofossils (BUa and Tweefontein) were processed for palynomorphs (hydrofluoric and hydrochloric acid maceration, heavy liquid separation and sieving through a 15 μm mesh) by Global Geolab Ltd., Alberta, Canada. Palynological residues were mounted in glycerine jelly. The Old Lootsberg Pass sample (BUa) contained a relatively mature and corroded palynological assemblage; the Tweefontein assemblage was slightly less mature but had a very poor yield. The Old Lootsberg Pass sample was semi-quantitatively analyzed. Images were taken with a Nikon DS-Fi1 Digital Camera mounted on a Leica DM2500 microscope. Sample residues and slides are housed in the Paleobotanical Collections of the University of California Museum of Paleontology, Berkeley, CA, with the locality number PA1345. Curatorial information for illustrated palynomorphs is available in the appendix and figure caption.

Vertebrate fossils were prepared by staff at The Albany Museum, where they are curated (see specimen numbers below; Online Supplemental Data File Table 1 for curatorial information), and identified by Christian Kammerer (Museum für Naturkunde-Leibniz Institute for Research, Berlin). The spatial positions of vertebrate specimens used by Ward et al. (2005), Botha and Smith (2006), and Smith and Botha-Brink (2014), and subsequently incorporated into Viglietti et al.’s (2016) database, were located using GPS coordinates provided by R.H.M. Smith. GPS data augment the supplemental information published by Smith and Botha-Brink (2014). Once the collection site of each specimen was located and its elevation recorded using a Garmin 62S hand-held unit with barometric altimeter, we correlated the collection site on the same day into one or more of our measured sections using standard field methods and elevation data.

BLAAUWATER 65 AND 67 STRATIGRAPHY

The overall stratigraphic succession at Old Lootsberg Pass and Tweefontein is similar in its basic architecture, and conforms to the general pattern described above for the Balfour (Elandsberg and Palingkloof members) and Katberg formations (Fig. 5). The lowest 120 m of section is dominated by fining up sequences of basal, trough cross-bedded sandstone bedsets that are overlain by, and interbedded with, coarse-to-fine, light olive (5Y 6/1) and olive-gray (5Y 4/1) siltstone. In the field, siltstones either are well indurated or weathered fissile, with little internal structure observable. In thin section, though, these rocks show an array of primary and secondary features. Primary structures include mm- and sub-mm scale planar and ripple bedding, and micro-cross stratification. Secondary features include evidence for pedogenesis, which is found in both localities, and includes bioturbation and homogenization wherein evidence of any primary structures has been removed. Exposed only in the Tweefontein section are brownish-gray (5YR 4/1), calcite-cemented nodules which attain a long dimension > 50 cm; septarian-type concretions are common in the lowest part of this section (Fig. 5). Color mottling of olive gray (5Y 4/1) with grayish-red (10R 4/2) or brownish gray (5YR 5/1) in siltstone is evident first at the 80 m stratigraphic position at Old Lootsberg Pass, and the 110 m position at Tweefontein (Fig. 5). Upper bounding surfaces of siltstone intervals are in erosional contact with overlying sandstone bodies that attain thicknesses up to 15 m.

Sandstone units in the lower 120 m of the section are grayish yellow (5Y 7/2), fine to very fine grained wacke and organized into decimeter-scale massive (Sm; Miall 1996), planar, and lenticular beds. These may be on the order of 0.5–1.0 m in thickness and constitute barforms. Massive beds fine
of the sandstone body in the Tweefontein1 section (Fig. 5); rather a grayish-

upwards into thin-to-medium, trough cross-beds (St) and bedsets where
that fine upwards into thin-to-medium, trough cross-beds (St). Ripple

Lithologies overlying the PNC-bearing sandstone vary laterally from
east to west (Fig. 6). In the east, fossiliferous, grayish-red siltstone directly
overlies the sandstone body and is intercalated with thin-to-medium
bedded, cross-bedded sandstone without evidence of PNC lags. Siltstone
color changes to olive gray higher in this area with an increasing
proportion of channel-sandstone architectural elements (Figs. 5, 6) and an
increased frequency of thick, cross-bedded PNC channel lags, exposed
along the Old Lootsberg Pass road. In contrast, fossiliferous olive-gray
siltstone overlies sandstone bodies to the west. An increasing proportion
of grayish-red siltstone, the first occurrence of bluish-gray (5B 5/1) wacke,
and carbonate-cemented lenticular lag deposits become more common in
stratigraphically higher positions.

PALEONTOLOGY

Our collections from Old Lootsberg Pass and Tweefontein1 include
macrofloral elements, palynomorphs, burrows, and vertebrates (Figs. 3–6).
Macrofloral and palynological assemblages are preserved within the lowest
20 m of the Tweefontein1 section and both below and above the lowermost
PNC-bearing sandstone unit found (at a stratigraphically higher level) in the
Old Lootsberg Pass sections. *Kathergia* burrows (Gastaldo and Role
son 2008) commonly are associated with concretion-bearing, olive-gray
siltstone low in the Tweefontein1 section, and both olive-gray and
grayish-red siltstone above the PNC-bearing sandstone at Old Lootsberg
Pass. Four new vertebrate specimens have been collected from the Old
Lootsberg Pass area, whereas one large skull has been recovered from the
Tweefontein1 area.

Paleobotany/Palynology

Old Lootsberg Pass.—Four collection sites, two stratigraphically below
(BLC, BUa) and two above the PNC-bearing sandstone (BUB, BUc; Figs.
2, 3, 6), have yielded impressions of *Glossopteris* leaves and sphenopsids
(Fig. 7) in olive-gray siltstone. Leaves recovered from the BUa assem-
blages are the most complete, having been excavated with a backhoe, as other sites yield highly weathered shreds of rock and
fragmented fossils. Leaf morphotyping follows the conventions of Prevec
et al. (2009, 2010). The BUa assemblage is moderately diverse and
includes reproductive structures (cf. *Plumsteadia*), whorls of the
sphenophyllalean *Trizygia*, and non-diagnostic sphenopsid axes assigned
to *Paracalamites australis* (identifications of R. Prevec personal
communication 2013).

The inherent variability in leaf morphologies requires a broad
concept of shape to be included in any natural taxon. Hence, we have
used our published morphotype concept (Prevec et al. 2009, 2010),
wherein specimens that may show features of two leaf “genera” are
assigned to one that conforms most to the character states. *Glossopteris*
morphotype B1 is a very narrow microphylly with fine, gently and steeply
arched venation, equivalent to *Glossopteris* W1 from Wapadsberg Pass
(Fig. 7A; Prevec et al. 2010) and cf. *Glossopteris* C2a from Clouston Farm
(Prevec et al. 2009). Morphotype B2 is a narrowly obovate microphylly with
straight, steeply inclined veins forming trapezoid to trullate, open meshes.
It is similar to morphotype *Glossopteris* C4 from Clouston Farm (Prevec et
al. 2009). Morphotype B3a is an elongate-elliptical microphylly–notophylly
with straight, moderately to shallowly inclined venation, and open
 polygonal/trullate meshes near the midrib. Morphotype B3b is a narrowly
elliptical to obovate microphylly, with straight, moderately inclined venation
and open, polygonal/trullate to elliptical meshes that narrow only slightly
towards the margin. Morphotype B4 conforms to *Glossopteris symme-
trifolia* (Anderson and Anderson 1985; R. Prevec personal communication
FIG. 5.—Measured stratigraphic sections. A composite stratigraphic section (see Fig. 2) at Old Lootsberg Pass is correlated to Tweefontein¹ using the upper bounding surface of a thick sandstone body near the base of the section (Fig. 4). Other sandstone bodies in the Katberg Formation are physically correlated using the same methodology. The stratigraphic positions of fossils reported, herein, are shown relative to a porcellanite from which an U-Pb ID-TIMS age assignment of early Changhsingian originates (Gastaldo et al. 2015).

Glossopteris leaves occur both below and above the porcellanite, and new vertebrates were collected only above that bed. Scale in 5 m intervals.
a generalized, temporally and geographically widespread, lanceolate notophyll with fine, even, parallel meshes that arch at a moderate angle across lamina. Morphotype B5 is represented by a single leaf fragment from BUa. It is a narrow microphyll with a prominent, broad midrib, and fine venation at a shallow angle with few anastomoses. This form is similar to leaves of the Clouston Farm Glossopteris C3 morphotype (Prevec et al. 2009). Morphotype B6 is a very rare element at BUa, characterized by narrow elongated leaves with open polygonal meshes adjacent to the midrib, and small elliptical to elongate-polygonal/trullate meshes at shallow angle across the lamina. It conforms to leaves consistently associated with Rigbya arberioides fructifications (R. Prevec personal communication 2013). A full systematic treatment of this collection is forthcoming (Prevec personal communication).

The preservation of the plant macrofossils in the uppermost beds (BUc) is poor. Here, the leaves are fragmentary and sparse, found in highly weathered siltstone of outcrop limited to an area of 2 m in donga exposures (Figs. 3, 7C). Fragmentary leaves are consistent with an assignment to morphotype B1. The limited exposure and fragmentary nature of these megafloras is suggestive that these assemblages are probably only providing a glimpse of the potential plant diversity at the time of deposition.

Permineralized wood occurs at two localities on the farm. The first site is a pavement outcrop at which small to medium-sized fragments are distributed on the surface (Fig. 4). The second site is in the lowermost PNC-bearing sandstone (Figs. 3, 5, 6) and consists of parts of two trunks (55 × 43 × 30 cm and 20 × 15 × 17.5 cm) that represent transverse tree sections. Here, several additional smaller wood fragments were recovered. Growth rings are well preserved and distinct (Fig. 8A), and cellular detail is excellent. Growth bands consist of many thin-walled earlywood tracheids, 5–20 cells wide, and thick-walled latewood. Tracheids are square to rounded, and there is neither axial parenchyma nor canals (Fig. 8B). Early wood tracheids average 25 × 25 μm whereas latewood tracheids are narrower in the radial plane, measuring 25 × 17 μm. Typical gymnosperm bordered pits occur on the radial walls of the tracheids (Fig. 8C). These are uniseriate or biseriate and alternate, contiguous, and slightly compressed, ranging in size from 5 to 6 μm. Rays are uniseriate, 10-16-(20) cells high and very narrow (Fig. 8D). Cross-field pits are taxodioid to araucarioid, 5 μm in diameter, with 3–5 randomly arranged, narrowly bordered pits per field. These characters allow for the wood to be assigned to the taxon Agathoxylon africanum (Fig. 8), a biostratigraphically long-ranging taxon that occurs in the Balfour, Katberg, and Burgersdorp Formations (Bamford 1999; Bamford and Philippe 2001). The dispersed leaf genera associated with this wood anatomy are not known.

An evaluation of the growth rings of the Blaaauwater trunks provides a preliminary insight about the local growth conditions of these trees. Based on the largest, but incomplete trunk, the average width of the growth rings is 8.5 mm (range 6–14 mm; standard deviation 2.19; n = 13). The large range in ring width implies that the trees were sensitive to climatic fluctuations, producing wide rings under good growth conditions and moderately wide rings under less favorable conditions (Chaloner and Creber 1990). The bands of latewood cells are very narrow (averaging 12 cells when compared with over 100 earlywood cells, 1:8–1:10) indicating that the growing season was long and conditions were favorable. Growth rings in the thin section show some anomalies that include incomplete rings, traumatic rings, and shear zones (Fig. 8), but it is not known what the latter features represent.

The palynological assemblage from BUa is consistent with macrofloral observations of a low-diversity glossopterid woodland with an understory....
of sphenophytes (Fig. 9; see Online Supplemental Data File). Sphenophyllalean spores (*Columinisporites ovalis*, *Laevigatosporites* sp., and cf. *Laevigatosporites* combined) dominate (~90 %) the assemblage and likely represent contributions from *Trizygia speciosa*. *Columinisporites* monolete spores with a ridged perispore are known in situ from several Paleozoic sphenopsid cone taxa (e.g., Riggs and Rothwell 1985; Taylor 1986). If the perispore was not preserved, the spores would be assigned to the dispersed spore genus *Laevigatosporites* (Balme 1995; Playford and Dino 2000). In Gondwana, several morphospecies of multi-taeniate dispersed pollen genera are associated with glossopterids (Balme 1995; Lindström et al. 1997). Species of *Protohaploxypinus* and *Striatopodocarpites* are reported in situ from pollen sacs morphologically identical to those found in attachment to glossopterid pollen organs (Surange and Chandra 1975; Zavada 1991; Lindström et al. 1997). *Weylandites* is known

Fig. 7.—Common *Glossopteris* leaf morphotypes from Old Lootsberg Pass and Tweefontein1. A) *Glossopteris* morphotype B3a from the Blaauwater locality Bua. Scale = 1 cm. B) *Glossopteris* morphotype B1 (equivalent to *Glossopteris* W1 from Wapadsberg Pass; Prevec et al. 2010) from the Blaauwater locality BUc. Scale in mm. C) *Glossopteris* morphotype 1 (equivalent to *Glossopteris* W1 from Wapadsberg Pass; Prevec et al. 2010) collected at 17.6 m in the Tweefontein1 section. Scale in mm. D) A whorl of *Trizygia speciosa* recovered at 17.6 m in the Tweefontein1 section. Scale in mm. All images courtesy of R. Prevec.
from a pollen organ with a potential glossopterid affinity (Balme 1995). In this assemblage, pollen taxa of glossopterid affinity (Protohaploxyphinus sp., P. limpidus, P. diagonalis, Striatopodocarpites cancellatus, and W. lucifer) were relatively common (1–5%).

The palynological assemblage includes various other gymnosperms (peltasperms, corystosperms, and conifers) that are not represented in the coeval macrofossil records in Gondwana, but are reported from Euramerican Permian and Gondwanan Triassic floras (Fig. 9; Anderson and Anderson 1985). The likely parent plants of some rare taeniate bisaccate pollen in the assemblage—Lueckisporites virkkiae, Guttulapolpitenes hannonicus, and the common Lunatisporites—are peltasperm seed ferns and conifers (e.g., Clement-Westerhof 1987). Falcisporites and Alisporites are rare in the palynoflora. These bisaccate alete pollen genera are known to represent corystosperm and peltasperm seed ferns (Zavada and Crepet 1985; Balme 1995; Lindström et al. 1997). Falcisporites australis is reported from the Early Triassic peltasperm Lepidopteris (Retallack 2002; Lindström et al. 1997), whereas Alisporites was produced both by Autunia, a Euramerican Permian peltasperm, and voltzian conifers and Gondwanan corystosperms (Balme 1995). To date, no conclusive macrofossil evidence is reported for either peltasperms, corystosperms, or conifers, components of well-drained soil (seasonally dry) conditions, in the Lopingian of the Karoo Basin. Pollen types associated with these groups could either represent parautochthonous or allochthonous elements, or plant groups known from the basin but with which they have hitherto not been associated.

**Twefontein**

One stratigraphic interval low in the section preserves a Glossopteris-dominated assemblage similar to that found at Old Lootsberg Pass and elsewhere in the area at Wapadberg Pass (Fig. 2; Prevec et al. 2010). Leaves are fragmentary as recovery is from limited outcrop of a highly weathered olive-gray siltstone in which these are preserved. Whorls of the sphenophyll Trzygia speciosa and non-diagnostic sphenopsid axes of Paracalamites australis are common. Lower in the section, non-diagnostic sphenopsid axes are found associated with an interval in which carbonate-cemented concretions occur (Fig. 5).

**Ichnotology**

*Katbergia carltonensis* is an ornamented cylindrical decapod-crustacean burrow oriented at various angles depending on the level of exposure in a paleosol (Gaswal et al. 2008). The lowest occurrence of the genus is found in olive-gray siltstone at Twefontein (Fig. 5) where burrows attain widths of one cm and exposed lengths of 30 cm. In contrast, these burrows are not encountered in olive-gray siltstone in the Old Lootsberg Pass section and first appear as common elements in both olive-gray and thick intervals of grayish-red siltstone at Old Lootsberg Pass above, or laterally equivalent to, the PNC-bearing sandstone (Li et al. in press; Fig. 10A). Additionally, larger diameter casts occur.

Larger, cylindrical to elliptical, very fine sandstone or coarse siltstone casts occur primarily in olive-gray siltstone (Fig. 10B). These are oriented subhorizontal, vary in diameter from 10 cm to a few decimeters, and may attain lengths of > 0.5 m. They commonly are compressed elliptically indicating an incomplete fill of the void before burial and compression. To date, no skeletal material has been found preserved within any cast. The size, shape, and orientation of these structures are consistent with other vertebrate burrows reported from the Karoo Basin (e.g., Groenewald 1991; Bordy et al. 2011), several of which have been ascribed to Lystrosaurus (Modesto and Botha-Brink 2010) and Thraxodon (Damiani et al. 2003).

**Vertebrate Paleontology**

**Old Lootsberg Pass.**—The following specimens are the first to be reported from the critical interval where taxonomic turnover is reported by other workers. Three new vertebrate fossils have been recovered from within and above the lowermost PNC-bearing sandstone (Gastaldo et al. 2015; Figs. 5, 6, 11A, 11C). We provide our observational data, along with the possible systematic affinities of the partial skull as determined by Christian Kammerer. The first is a dicynodontoid skull fragment (AM 3659) that originated from the pedogenic conglomerate-nodule lag in the western part of the transect (GPS coordinates available upon request). It is poorly preserved and only can be assigned to an indeterminate Dicyonodontoididea based on its size, particularly large-diameter canines, labial fossa, and absence of a postcaniniform crest (Fig. 11A, 11B; C. Kammerer personal communication 2013). These features also are found in Aulacephalodon, but that taxon generally has more massive caniniform processes than what is found in our material. When compared with the suite of uppermost Daptocephalus AZ and overlying Lystrosaurus AZ taxa, the skull has features typical of taxa of the former assemblage zone (C. Kammerer personal communication 2016). Several taxa possess this suite of characters and overall general morphology, and possible affinities include Dicyodon, Daptocephalus, and *Lystrosaurus maccaii* (Kammerer et al. 2011). However, other taxa to which the specimen might belong also include Dinanomodon and Lystrosaurus curvatus, as the latter grew to similar sizes and are more similar to *L. maccaii* than is appreciated (C. Kammerer personal communication 2016). Considering all
morphological features, the skull exhibits features more similar to forms in the *Daptocephalus* AZ rather than those found in the overlying *Lystrosaurus* AZ (Kammerer to Prevec personal communication 2013).

The other specimens are assignable to *Lystrosaurus*. One is a maxilla with canine preserved in a nodular concretion from a grayish-red siltstone interval in the eastern part of the transect (AM3657; Fig. 6). The other is a skull of *Lystrosaurus murrayi* (C. Kammerer to R. Prevec personal communication 12/2015; AM3658), collected from an isolated, boulder-sized float block of sandstone originating from above the PNC-bearing sandstone (Figs. 6, 11C). Skull characters include the: presence of prefrontal bosses, of which such ornamentation is absent in *L. curvatus*; presence of a median premaxillary ridge that expands into a prefrontal boss; a relatively short maxilla in proportion to the skull length, as compared with one that is long and thin in *L. declivis* and *L. mccaigi*; and a triplanar cranial profile, when compared with a biplanar profile in *L. declivis* and *L. mccaigi*, and a curved profile in *L. curvatus*. *Lystrosaurus murrayi* is used by other workers as a biostratigraphic indicator of the earliest Triassic (Botha and Smith 2007; Smith and Botha-Brink 2014; Viglietti et al. 2016).

**Twefontein**.—An isolated skull (Fig. 12) was recovered from a nodule-bearing olive-gray siltstone (GPS coordinates available upon request), high in the section (Fig. 5). AM4757, curated at The Albany Museum, Grahamstown, initially was identified as *Dicynodon lacerticeps* (C. Kammerer personal communication 9/2013; Kammerer et al. 2011) but Kammerer (personal communication 2/2016) noted that it is similar to the holotype of *Dicynodon leontocephalus* (a junior synonym of *Daptocephalus leoniceps*; Kammerer et al. 2011). This taxon, though, displays “a problematic mixture of *Dicynodon* and *Daptocephalus* characters” as does specimen AM4757 (Kammerer personal communication 2/2016). Currently, the specimen is interpreted to be *Daptocephalus*, but there is the possibility that this specimen could be an extremely large *Dicynodon* (Kammerer personal communication 2/2016). Both the interorbital region is obscured and the palate is worn off in AM4757, leaving critical diagnostic characters unavailable.

**DISCUSSION**

The bountiful vertebrate-fossil record of the Permian–Triassic Beaufort Group, with nearly 20,000 specimens catalogued and databased (e.g., van der Walt et al. 2010, 2015), has allowed for the refinement of a biostratigraphic paradigm in the absence of any unique lithologic marker beds. The prevalence of monotonous olive-gray and grayish-red siltstone successions, in which yellowish gray channel-sandstone bodies are enveloped, leave few distinguishing lithologic features on which to subdivide this succession based on biostratigraphic criteria. As a consequence, a multi-parted biostratigraphic strategy was devised on which to separate time-equivalent sequences using vertebrate assemblages (Rubidge 1995). This was necessary due to the absence of any robust magnetic polarity stratigraphy or chronostratigraphy, and a reported dearth...
of paleobotanic data for the basin on which a palynological zonation could be based (Gastaldo et al. 2005). The assignment of vertebrate faunas to either the Permian or Triassic initially followed the proposal by Broom (1906, 1911), wherein the Cistecephalus-bearing rocks (incorporating the Dicynodon [Keyser and Smith 1979] ≈ Daptocephalus Assemblage Zone) were considered as Permian and the overlying Lystrosaurus beds considered Triassic (e.g., Viglietti et al. 2016). Broom’s biostratigraphic scheme has been modified as new paleontological data were acquired, and temporal patterns from other disciplines developed, into which vertebrate occurrences could be placed (e.g., Rubidge et al. 2013, 2016; Gastaldo et al. 2015).

The latest Permian and earliest Triassic vertebrate assemblages are reported to be the Daptocephalus (formerly Dicynodon; see Viglietti et al. 2016) and Lystrosaurus AZs, respectively. Many workers (Ward et al. 2005; Smith and Botha 2005; Smith and Botha-Brink 2014; Viglietti et al. 2016) have equated the end-Permian extinction event in the marine realm with the vertebrate-biozone boundary and faunal turnover. Viglietti et al. (2016) report that the FAD of Lystrosaurus occurs ~150 m below the Daptocephalus/Lystrosaurus AZ boundary in and around Nieu Bethesda (Fig. 1; Botha and Smith 2007). Yet, Viglietti et al. (2016) also state that

![Fig. 10.—Ichnology.](image1)

![Fig. 11.—Vertebrate paleontology at Old Lootsberg Pass. A) Partial skull (AM3659) recovered from the pedogenic-nodule conglomerate lag deposit of the thick sandstone at the base of Old Lootsberg Pass (Figs. 3, 5, 6; image courtesy of R. Prevec). It consists of a maxilla with large diameter canine that is assigned to Dicynodontidea indeterminate. See text for possible systematic affinities. Scale in cm. B) Line illustration of dicynodontid skull showing the recovered part in gray (mx = maxilla, v = vomer, pt = pterygoid, q = quadrate). C) Lystrosaurus murrayi (AM3658) skull recovered from a sandstone-float block (Figs. 3, 5, 6) above the sandstone body in which the partial dicynodontid skull was recovered. Scale in cm.)
the latter the only species of the taxon not to extend above the reported biozone boundary, and overlying fauna to witness the loss of \textit{L. curvatus}.

The loss of this taxon is accompanied by the appearance of \textit{L. murrayi} and \textit{L. declivis} without the presence of \textit{Prolocophon} in the assemblage at this level (Smith and Botha-Brink 2014 and Online Supplemental Data; although see Rubidge et al. 2016, their fig. 14.3).

The new fossil collections we report, herein, mainly come from the uppermost part of Viglietti et al.’s (2016) \textit{Daptocephalus} Assemblage Zone. This part of the biozone is delimited by the presence of \textit{D. leonticeps} and \textit{L. maccaigi}, and the absence (presumed extinction) of \textit{Dicynodon lacerticeps}. Hence, vertebrates previously reported by Smith and Botha-Brink (2014) as \textit{D. lacerticeps} in the area (Fig. 4; RS 18, RS 80) are reconsidered in the recent circumscription of the genus (Kammerer et al. 2011), and regarded in our analysis as reports of \textit{D. leonticeps} until a detailed systematic study indicates otherwise. Therefore, the co-occurrence of \textit{D. sp. cf. D. leonticeps} (AM4757) and \textit{L. maccaigi} (RS 17, RS 81), along with the presence of \textit{L. murrayi} (Figs. 5, 6, 11C) higher in Old Lootsberg Pass, place our collections in the upper part of the \textit{Daptocephalus} and lower part of the \textit{Lystrosaurus} biozones, transitioning the reported turnover event.

\textbf{Paleobotanical Significance}

The preservation of \textit{Glossopteris} morphotypes, along with sphenopsids and a nearly identical palynoflora in correlative successions demonstrates the presence of a consistent vegetation in the Lootsberg area. Local biodiversity does not vary systematically, and is similar to that reported by Prevec et al. (2010) at Wapadsberg Pass (Fig. 2). Hence, a uniform vegetation existed over the timeframe encompassed by these successions. Narrow microphylls of morphotype B1 are most common. In other South African localities, these narrow microphylls are typical elements that tend either to dominate (= C2 from Clouston Farm; Prevec et al. 2009) or are the sole glossopterid morphotype (= W1 from Wapadsberg Pass; Prevec et al. 2010; Anderson and Anderson 1985). This macrofloral assemblage occurs stratigraphically low at Tweefontein\(^1\) (Fig. 5), below the porcellanite bed that yielded a U-Pb ID-TIMS zircon age that is early Changhsingian (253.48 ± 0.15 Ma; Gastaldo et al. 2015). At Old Lootsberg Pass, these morphotypes are found higher in the section (Fig. 6). They occur both subjacent to the PNC-bearing sandstone, and in olive-gray siltstone that is laterally correlative with grayish-red siltstone in which vertebrate remains of the \textit{Lystrosaurus} AZ were collected. The predominance of these narrow microphylls and notophylls with fine, gently arching, elongated meshes in this part of the stratigraphy, may be reason for the interpretation that broad-meshed glossopterid leaves became extinct at the end of the Guadalupian (259.8 ± 0.4 Ma; Retallack 2013).

Recovered palynofloras are consistent with macrofloral observations of a low-diversity glossopterid woodland (\textit{Protohaploxypinus limidus}, \textit{Striatopodocarpites cancellatus}, and \textit{Weylandites lucifer}) with an understory of trizygoid sphenophytes (\textit{Columnisporites} sp. cf. \textit{C. peppersii}). In addition, the assemblage also includes various other gymnosperm, peltasperm, corystosperm, and conifer pollen that are not represented in coeval macrofossil records. These clades are reported from younger South African macrofloras assigned to the Triassic (Anderson and Anderson 1985). The Blauwater Farm palynoflora includes both taeniate and alete bisaccate pollen. Taeniate bisaccate pollen are represented by \textit{Lueckisporites virkii}, \textit{Guttulapollenites hannonicus}, and \textit{Lunatisporites novialensis}, and originate from peltasperm seed ferns and conifers (e.g., Clement-Westhof 1987). Bisaccate alete pollen of the genera, \textit{Falci spirites} and \textit{Alisporites}, were produced by corystosperm and peltasperm seed ferns (Balme 1995; Lindström et al. 1997). The presence of \textit{Falci spirites australis}, here and in the Wapadsberg Pass palynoflora (Prevec et al. 2010), is reported elsewhere as a rare Lopingian element (Foster 1979; Lindström et al. 1997) and also an Early Triassic indicator, identified as the
reproductive propagule of the peltasperm Lepidopteris (Retallack 2002). Alisporites, in contrast, was produced both by a Euramerican Permian peltasperm, Autunia, and various volkziant conifers (Balme 1995).

To date, no conclusive upper Permian macrofossil evidence from the Karoo Basin is reported for either peltasperms, coryostperms, or conifers, all of which are considered to have been components of better drained soil (seasonally dry) conditions at the time. This is not true elsewhere, as the genus Dicrodium—once considered the poster child of the Triassic recovery flora (Retallack 1995; McElwain and Punyasena 2007)—occurs in Lopingian deposits of Jordan (Abu Hamad et al. 2008), Oman (Kerp et al. 2006), and Pakistan (Schneebeli-Hermann et al. 2015). Pollen types associated with these groups in the Loostboar Pass area represent either parautochthonous or allochthonous elements, or plant groups previously identified in the basin but with which they have yet to be associated. Their presence indicates that the parent plants grew outside of the latest Permian taphonomic window (Gastaldo et al. 2005; DiMichele and Gastaldo 2008). Although these clades eventually replaced the Glossopteris flora, they were members of the extrabasinal vegetation in the Changhsingian of South Africa. Their rise to dominance in the Karoo Basin most likely was due to an overall shift in climate, from seasonally wet to more seasonally dry conditions, a vegetational response documented elsewhere (DiMichele et al. 2008 Looy et al. 2014). As rainfall patterns, soil moisture conditions, and temperature parameters shifted over time, coryostperm, peltasperm, conifer, and other gymnosperm taxa already present in the Karoo Basin expanded their range and came to dominate the landscape. Their occurrence in the palynoflora indicates that these taxa neither evolved in response to the extinction event nor “migrated” from outside of Gondwana (Retallack 2002) to fill an ecological void. Rather, the coexistence of wetland and dryland biomes in the Karoo, and the eventual replacement of the former by the latter, parallels ecological dynamics documented in the Cisuralian–Guadalupian of the western United States (e.g., Montañez et al. 2007; DiMichele et al. 2008). The presence of both biomes reinforces Rees’ (2002) view that long-term climate change, if not the main culprit is, at least, an important accomplice, and adds support for the conclusion of Benton and Newell (2014) that a unidirectional shift towards hotter and more seasonally dry conditions in the Lystrosaurus zone is an oversimplification.

The presence of glossopterid taxa in the Lystrosaurus AZ, along with permineralized trunk remains with well-developed growth rings (see discussion, below, on the vertebrate biozone boundary) is evidence that contradicts the currently accepted, long-term aridification scenario envisioned to be responsible for vertebrate turnover (Smith and Ward 2001; Ward et al. 2005; Smith and Botha-Brink 2014; Viglietti et al. 2016; Rubidge et al. 2016). Plant preservation, and particularly soft parts including leaves, can become part of the fossil record only within a circumscribed taphonomic window (DiMichele and Gastaldo 2008). This taphonomic window requires burial accompanied by pore-water geochemistry of saturated sediments that prevented or retarded bacterial degradation, which can be controlled by some combination of Eh and pH. Once buried under conditions promoting preservation, plant parts must remain in the taphonomic window on both short and long temporal scales to end up as a recognizable entity in the fossil record. Once regional or local groundwater conditions change, and water tables drop to below the burial level, as is the case under seasonally dry or semi-arid climates, organic matter is, again, accessible to bacterial activity and is removed from the potential fossil record (Gastaldo and Demko 2011). The fact that Glossopteris leaves are recovered from the Lystrosaurus AZ along with woody trunks of 0.5 m diameter, in which complacent growth is recorded, not only is evidence for seasonally wet conditions under which these plants grew (Greif et al. 2006), but also that groundwater tables remained high across the landscape promoting and insuring preservation of the most labile tissues (DiMichele and Gastaldo 2008; Gastaldo and Demko 2011). Hence, an interpretation of that vegetational “die off” is associated with vertebrate turnover (Smith and Botha-Brink 2014) cannot be supported by the evidence in this region.

**Significance of Katbergia Occurrences**

Smith and Ward (2001) proposed the occurrence of a unique lithofacies of interlaminated couplets of green-and-red mudrock interpreted as the physical expression of effects associated with the end-Permian terrestrial extinction event. This unique and purportedly mappable unit was equated with the PTB and reported to be found elsewhere in the Southern Hemisphere (Retallack et al. 2003; see Gastaldo et al. 2009 and Gastaldo and Neveling 2012 for empirical field relationships). This interpretation, though, has been contradicted by Ward et al. (2012) who stated that the facies can be found both above and below their vertebrate-defined PTB, without quantification as to the number of occurrences or localities in which this phenomenon occurs. One reported characteristic feature of the interval is the presence of “subhorizontal silstone-filled cylinders, resembling calliannispid shrimp burrow casts, [which] make their first appearance in this facies” (Smith and Ward 2001, p. 1148). Subsequently, Gastaldo and Rolerson (2008) characterized these burrows, assigned them to the ichnogenus Katbergia, and demonstrated their occurrence in other lithologies at several stratigraphic positions in the Palingkloof Member and Katberg Formation. More recently, the occurrence of Katbergia has been used as an indicator for the uppermost Permian and is reported to first appear in massive mottled maroon/gray mudrock facies that directly underlie the “laminated reddish-brown silstone/mudstone couplets”, which continue to be equated to the PTB “event” beds (Smith and Botha-Brink 2014, p. 103). Yet, Katbergia burrows first occur near the base of our Tweefontein1 measured section, physically correlated (Figs. 4, 5, 13) with the interval below the porcellanite that yielded a U-Pb ID-TIMS early Changhsingian age date. Hence, this burrow cannot be associated only with rocks either in close proximity to the biozone transition or in the overlying Lystrosaurus biozone. It is a component of early Changhsingian terrestrial ecosystems in the Karoo Basin.

**A Test of the Daptocephalus/Lystrosaurus Biozone Boundary**

Vertebrate fossils recovered from the Blaauwater Farms account for part of the data set on which the Karoo Basin extinction model has been developed and interpreted to represent ecosystem response to the End-Permian event (Ward et al. 2005; Smith and Botha-Brink 2014; Rubidge et al. 2016). Specimens used by Smith and Botha-Brink (2014) were vetted by Viglietti et al. (2016) to identify the highest quality specimens before their incorporation into a revision of the Daptocephalus biozone. Viglietti et al. (2016) recognized that collections prior to 1976 were catalogued using only farm names and elevations, resulting in a generalized set of coordinates for recovered specimens. Such records often were entered into collection catalogs only as a “farm centroid” set of coordinates; Smith and Botha-Brink (2014) and Viglietti et al. (2016) have omitted such records in their recent analyses. More accurate locality and biostratigraphic data have been generated since the 1970s. These data place vertebrates into: (1) measured stratigraphic sections and, more recently; (2) measured stratigraphic sections along with GPS coordinates accompanying specimens (Viglietti et al. 2016). The three-phased extinction model of Smith and Botha-Brink (2014) across the biozone boundary is based on the stratigraphic position of taxa relative to their PTB datum. This is possible because Smith and Botha-Brink (2014, p. 100) and Viglietti et al. (2016, p. 4) remarked that the GPS coordinates of vertebrate specimens used in their database are “much more accurate” in their locality position than locality data found in earlier literature. Such data have allowed specimens to be positioned on measured sections from which reliable FAD and LAD are determined, and the stratigraphic distance of any vertebrate fossil provided relative to the biozone (PTB) boundary. Hence, the relative stratigraphic
FIG. 13.—Physically correlated stratigraphic sections at Lootsberg Pass and Tweefontein' using upper bounding surfaces of thick sandstone bodies into which the stratigraphic position of RS vertebrates reported by Smith and Botha-Brink (2014) have been placed (Fig. 4; see Online Supplemental Data for .kmz file for correlative...
positions of vertebrates on the Blaauwater Farm traced into our stratigraphic framework are considered as accurate in the following analysis, with some acknowledged variance (+/- 5 m) due to problems associated with GPS replication (Fig. 13).

Thirteen vertebrates, all with RS designations (reported to represent the most accurate data by Vigilietti et al. 2016), are reported from the area between Old Loootsberg Pass and Tweefontein. Nine of these specimens were collected from pavement exposures in fields of gentle topographic relief (Fig. 4). Four specimens occur close to, or above, the 1700 m contour, which places them in the thick sandstone interval of the resistant Katberg Formation that tops escarpments. One additional IZIKO Museum specimen—SAM-K08626 D. lacerticeps—is reported in the museum’s digital database but not used in the Smith and Botha-Brink (2014) analysis. It is neither found as part of the monographic revision of Kammerer et al. (2011). All RS vertebrates and specimen SAM-K08626 are placed into our correlative stratigraphy along with the newly recovered vertebrates (Fig. 13), resulting in a myriad of incompatibilities.

The first apparent inconsistency in the RS data is in the position at which vertebrate specimens are placed relative to the Daptocephalus AZ boundary. For example, specimen RS 81 (L. maccaini) is reported as having been collected 57 m below the boundary at Tweefontein. Yet, the stratigraphic position where it was collected is above, and of inverted stratigraphic order to, three specimens that cluster around a position reported by Smith and Botha-Brink (2014) to be ~30 m below their PTB. It should be noted that two of these vertebrates—RS 15 and RS 17—all are in close stratigraphic proximity to the conglomerate with zecolane bed that yielded a U-Pb ID-TIMS zircon early Changhsingian (253.48 ± 0.15 Ma; Gastaldo et al. 2015) age assignment in this part of the section (Fig. 13). In contrast, although the stratigraphic positions of RS vertebrates in the Old Loootsberg Pass section maintain a logical ordering, at least 50 m of stratigraphic section separate RS 80 (~50 m) and RS 25 (~49 m), when these specimens are reported to have been collected within 19 m of each other (Smith and Botha-Brink 2014, Online Supplemental Data). Due to such inconsistencies, it is necessary, then, to evaluate the stratigraphic position of the boundary between the assemblage zones in each section to determine whether it is as tightly constrained as indicated by Smith and Botha-Brink (2014, fig. 12).

Six vertebrate specimens were reported by Smith and Botha-Brink (2014) in the uppermost 30 m of the Daptocephalus (= Dicyonodon) AZ from the Blaauwater Farm (Fig. 13). Two of these, RS 17 and RS 19, were considered by Vigilietti et al. (2016, supplemental data) as diagnostic of their uppermost faunal assemblage. Hence, when the stratigraphic position of each specimen is measured upsection to the position of the vertebrate-defined boundary, these data should converge in a short interval that defines the assemblage zone boundary. This, though, is not the case (Fig. 13). We choose to demonstrate the incoherence by comparing where that boundary is placed in the Old Loootsberg Pass section, using three specimens (RS 18, RS 19, RS 20), versus where three vertebrates (RS 15, RS 16, RS 17) reported from essentially the same distance below the boundary occur in the Tweefontein section that has been physically correlated less than 2 km away.

At Old Loootsberg Pass, the position of the biozone boundary that is compatible with the vertebrate data falls in a succession of olive gray coarse-to-fine siltstone without evidence for any laminated reddish-brown siltstone/mudstone couplets (Neveling et al. 2016a). This observation also holds for the PTB position in the Tweefontein section of Smith and Botha-Brink (2014) based on the reported distance of vertebrates below the turnover in assemblages. In fact, no laminated red-mudrock interval conforming to their Facies C occurs here. The first appearance of mottled olive gray and grayish-red siltstone in our Tweefontein section occurs ~30 m higher at the top of the section (115 m stratigraphic position in Fig. 13; Li et al. in press). When a comparison is made between the reported stratigraphic position of vertebrate specimens in the Old Loootsberg Pass and Tweefontein sections, the placement of the biozone boundary differs by ~25 m over this short, physically correlated distance (Fig. 13). This difference exceeds the stratigraphic resolution reported by Smith and Botha-Brink (2014) for the LAD of taxa deemed critical to delineating the faunal turnover between assemblage zones.

Vertebrates collected and reported by Smith and Botha-Brink (2014) near the top of Old Loootsberg Pass pose an additional riddle. Once again, two specimens—RS 21, RS 22—come from an area with little topographic relief, but are reported to differ by 20 m in their stratigraphic placement above the biozone boundary. When physically traced into our measured section, they occur in the same stratigraphic interval. But, when their reported positions are used to pinpoint the boundary in subjacent rocks, the biozone transition of Smith and Botha-Brink (2014) is located in the Lystrosaurus AZ at the Katberg Formation (Fig. 13). This is consistent with where Ward et al. (2000, 2005) mark the base of their Old Loootsberg section (Fig. 3). Hence, the proposed position of the boundary between the Daptocephalus (Vigilietti et al. 2016) and Lystrosaurus AZs, when field tested, is highly variable and suspect. In fact, it can be seen that the biozone boundary of Smith and Botha-Brink (2014) falls at four different levels in our physiically correlated stratigraphic framework, separated by up to 70 m of section.

Gastaldo et al. (2015) argued for an upward extension of the, then, Dicyonodon (now Daptocephalus) biozone to the incised base of a thick sandstone body that lies ~15 m stratigraphically higher than where the data of Smith and Botha-Brink (2014) indicate its placement at Old Loootsberg Pass. Our suggested placement of the biozone boundary is based on the stratigraphic position of the dicynodontid skull fragment of Permian aspect (AM3659, Fig. 11A, 11B). That specimen was preserved in the lag deposit of a pedogenic nodule conglomerate (Fig. 13), which represents the result of landscape erosion and degradation, and concentration of cemented clasts in the base of fluvial channels (Pace et al. 2009). We acknowledge that the occurrence of a single specimen of Permian aspect at this horizon only demonstrates that an undetermined thickness of section was eroded during landscape incision in response to a change in fluvial gradient (Gastaldo and Demko 2011) in the area. The exact placement of the assemblage zone boundary will require an understanding of lateral lithofacies relationships over a wider spatial area and the relative position of vertebrate specimens within that larger stratigraphic framework.

Our results from the Blaauwater Farm leave questions about the credibility of a phased extinction model that is dependent on the accurate placement of vertebrate specimens in stratigraphic context relative to a datum that cannot be located at two critical boundary localities. Smith and Botha-Brink (2014) contended that the vertebrate record of the upper Balfour Formation exhibits a pattern wherein three distinct phases of vertebrate extinction, and two phases of rapid recovery (Smith and Botha 2005), occurred over a stratigraphic interval of only ~75 m (the surface). Vigilietti et al. (2016, their supplemental data) use specimens RS19 at Old Loootsberg Pass and RS 17 (yellow highlighted) at Tweefontein to circumscribe the uppermost Daptocephalus zone. Reported vertebrate positions relative to the Daptocephalus (Dicyodon)/Lystrosaurus biozone boundary show both discrepancies in distances from the boundary and inverted stratigraphic relationships. When the biozone boundary is determined using published relationships of RS vertebrates either below or above the turnover, four potential stratigraphic positions of the event result. The two situations that fall in the upper Daptocephalus biozone, though, are offset by ~25 m of section, which is greater than the stratigraphic resolution over which each phased extinction proposed by Smith and Botha-Brink (2014) is to have occurred. These relationships cast doubt on the utility of the vertebrate biozonation and its reliability to circumscribe extinction. See Figure 5 for additional symbol information.
differential between where a boundary can be placed at Tweefontein\(^1\) and the highest possible boundary at Old Looitseberg Pass; Fig. 13). In contrast, Marshall (2005) explained the same pattern in vertebrate occurrences as the consequence of the Signor-Lipps effect (Signor and Lipps 1982). The interval over which the vertebrate fauna is reported to have experienced turnover is manifest at Old Looitseberg Pass and our Tweefontein\(^1\) sections. Yet, the irregularities in the reported vertebrate positions relative to the biozone boundary and, as a consequence, the current Karoo end-Permian model envisioned by other workers (Roopnarine and Angielczyk 2015; Viglietti et al. 2016; Rubidge et al. 2016), only lead to the conclusion that fundamental problems exist in the data set. As such, the probability is low that the published vertebrate data from the Blauwater Farm (Old Looitseberg Pass and Tweefontein\(^1\); Smith and Botha-Brink 2014), in conjunction with our new paleontological data, can accurately circumscribe the base of the *Lystrosaurus* biozone. These problems can be resolved only when vertebrate collections are undertaken within comprehensive stratigraphic frameworks, an ongoing project, rather than when presented in one or more composite stratigraphic sections in which lateral variation remains unaccounted.

CONCLUSIONS

New paleontologic data from two localities on the Blauwater 65 and 67 farms in the Eastern Cape Province, South Africa, are used in conjunction with previously published records of vertebrate fossils in a field test of the widely accepted phased extinction and recovery of vertebrates over the *Daptocephalus* (formerly *Dicynodon*)/*Lystrosaurus* biozone boundary, a boundary equated by many workers to the end-Permian terrestrial extinction event (Ward et al. 2005; Smith and Botha-Brink 2014). A local framework is developed using sections measured over a ~2 km distance in which two, long stratigraphic sections, augmented by interspersed shorter measured intervals, are physically correlated using laterally contiguous sandstone bodies as datums. This framework includes a porcellanite bed from which a U-Pb ID-TIMS age of early Changhsingian age has been reported (Gastaldo et al. 2015). The new paleontologic data include several intervals, below and above the porcellanite, in which: (1) a megafauna of *Glossopteris* and *Trizygia* are preserved; (2) palynologic assemblages are recovered in which both pre-extinction and “post-extinction” taxa coexist, a feature reported in other Gondwanan assemblages (e.g., Foster 1979; McLoughlin et al. 1997; Lindström and McLoughlin 2007; Prevec et al. 2010); (3) the ichnogenus, *Kathergia*, is found to be a component of the early Changhsingian landscape; and (4) vertebrates assignable to both the *Daptocephalus* and *Lystrosaurus* assemblage zones occur.

Contrary to the proposal that the Karoo Basin experienced a vegetational die-off in the upper *Daptocephalus* biozone that was responsible for a phased extinction of vertebrates, our collections indicate that glossopterids and sphenophytes continued to colonize landscapes of the *Lystrosaurus* AZ. These plants, along with evidence from permineralized tree trunks and the taphonomic conditions necessary for their preservation, indicate that seasonally wet regimes were essentially uninterrupted over the biozone transition. The presence of this wetland flora at several stratigraphic horizons in the *Lystrosaurus* AZ contradicts the assertion that severe aridification drove vertebrate turnover. Additionally, the occurrence of parautchothous or allochthonous palynomorphs with corystoospores, peltasperm, conifer and other gymnosperms indicates that these floral elements can neither be considered as having “migrated” into the basin after biozone turnover nor be considered the “recovery” flora. These clades already were present somewhere in the landscape, but outside of the megafossil taphonomic wetland window. The presence of *Kathergia*-burrowed, olive-gray and grayish-red siltstone, some of early Changhsingian age, also points to a landscape in which seasonally wet conditions prevailed (Gastaldo and Rolerson 2008).

Characteristic vertebrate taxa of both the *Daptocephalus* and *Lystrosaurus* AZs have been collected and identified, demonstrating that the measured sections encompass the uppermost units of the former and lowermost units of the latter. Somewhere in this stratigraphy lies the biozone boundary horizon which, according to the current paradigm, should be able to be identified either lithologically or biostratigraphically. Yet, we find no evidence for anything more than olive-gray siltstone without lamination, motting, or interbeds with grayish-red siltstone in these stratigraphic intervals in which the purported boundary occurs. When testing the stratigraphic position of the assemblage-zone boundary with previously published vertebrate records, wherein distances below or above the boundary are reported (Smith and Botha-Brink 2014, supplementary data), four different horizons in our physically correlated sections are identified as the “unique” datum. Over the ~2 km distance on the Blauwater farms, these occur anywhere from ~25 m to ~70 m apart stratigraphically. The inferred biozone boundary in our Tweefontein\(^1\) section is lower than that at Old Looitseberg Pass, and considerably closer to the geochronologically defined interval with an early Changhsingian age assignment. We conclude that such observations raise serious questions about the reliability of the data set used to construct what many have, over several decades, considered to be the terrestrial response to the end-Permian extinction event. We also contend that these data support our previous conclusion (Gastaldo et al. 2015) that the base of the *Lystrosaurus* AZ has a very low probability of having been coeval with the end-Permian events in the marine realm.

ACKNOWLEDGMENTS

The authors appreciate the hospitality and kindness shown to them over past decade by: Justin and Liesl Kingwill, Blauwater Farm; and JP and Hester Steynberg, Ganora Guest Farm. Field assistance by E.H. Gastaldo, A. Ndhukwani (Council for Geoscience), M. Langwena ‘14, K. Spencer ‘14, and T. Chiizinski ‘14 (Colby College); the majority of fossil discoveries, as well as field-specimen identification and morphotype characterization of plant material by R. Prevec (The Albany Museum), supported financially under the auspices of the grants and agencies listed below; and vertebrate identification by K.D. Angielczyk (Chicago Field Museum), C. Kammerer (American Museum of Natural History), and J. Fröbisch (Museum für Naturkunde, Berlin) are acknowledged. Student participation was supported by the Selover Family student-research endowment and Barrett T. Dixon Geology Research and Internship Fund for undergraduate experiences in the Department of Geology, Colby College. Pls research efforts were supported, in part, by: the Council for Geoscience (South Africa); JWG startup funds at the University of Texas–Dallas; and NSF EAR 0749895, 0934077, and 1123570 to RAG; and a Fulbright Scholar Award from the U.S. Department of State to RAG in the Department of Geology, Rhodes University, Grahamstown. Comments by two anonymous reviewers strengthened the final manuscript draft.

SUPPLEMENTAL MATERIAL


REFERENCES


