

PALEONTOLOGY OF THE BLAAUWATER 67 AND 65 FARMS, SOUTH AFRICA: TESTING THE *DAPTOCEPHALUS/LYSTROSAURUS* BIOZONE BOUNDARY IN A STRATIGRAPHIC FRAMEWORK

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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 megaflores 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 megaflores 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; Shen 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 the Karoo Basin (Gastaldo et al. 2015) suggest a very low probability of coincidence. In the marine record at Meishan, China, the onset and end of the extinction event are dated as having occurred between 251.941 ± 0.037 and 251.880 ± 0.031 Ma (Burgess et al. 2014), with an estimated duration of 60 ± 48 ka. Marine systematic loss is reported to approach 85% (Shen et al. 2011; Clapham and Payne 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 Punyasena 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 Newell 2014).

The Karoo Basin, South Africa, serves as one of a small number of continental successions in which the effects 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 lithologic 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,

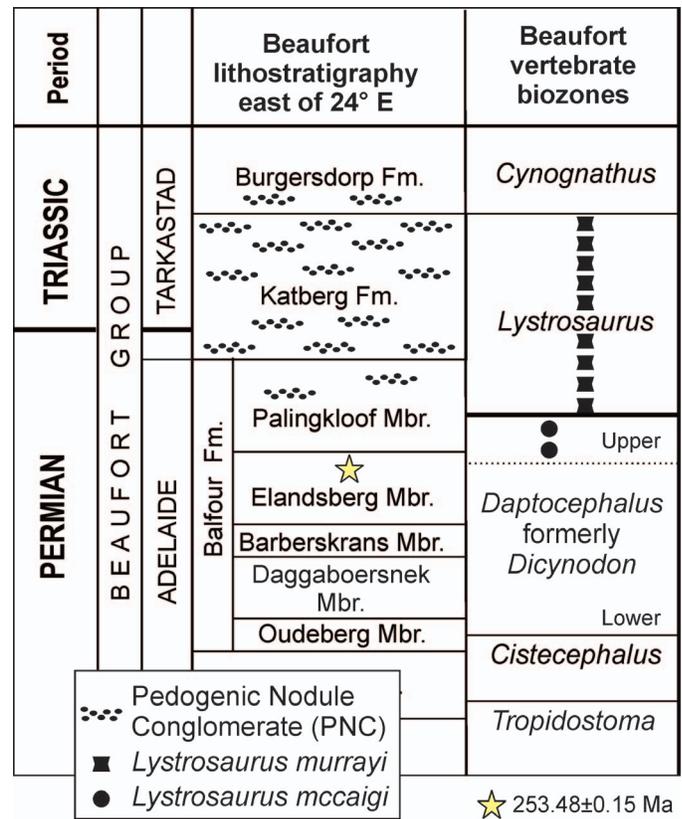


FIG. 1.—Litho- and vertebrate biostratigraphy of the Beaufort Group in the Karoo Basin, South Africa. Biostratigraphic ranges of *L. mccaigi* and *L. murrayi* follow Botha and Smith (2007), which are used by Viglietti et al. (2016) to delimit the Upper *Daptocephalus* Assemblage Zone from the overlying *Lystrosaurus* Assemblage Zone. The biozone boundary is considered by several workers (Ward et al. 2005; Smith and Botha-Brink 2014; Rubidge et al. 2016) as coincident with the Permian–Triassic Boundary (PTB) as recognized in the marine record. The placement of the PTB in the Katberg Formation follows the conclusion of Gastaldo et al. (2015) based on a U-Pb ID-TIMS age date of 253.48 ± 0.15 in the Elandsberg Member of the Balfour Formation.

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 siltstone, 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 siltstone 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 siltstone has been attributed to increasing aridification (Smith and Botha-Brink 2014) towards the

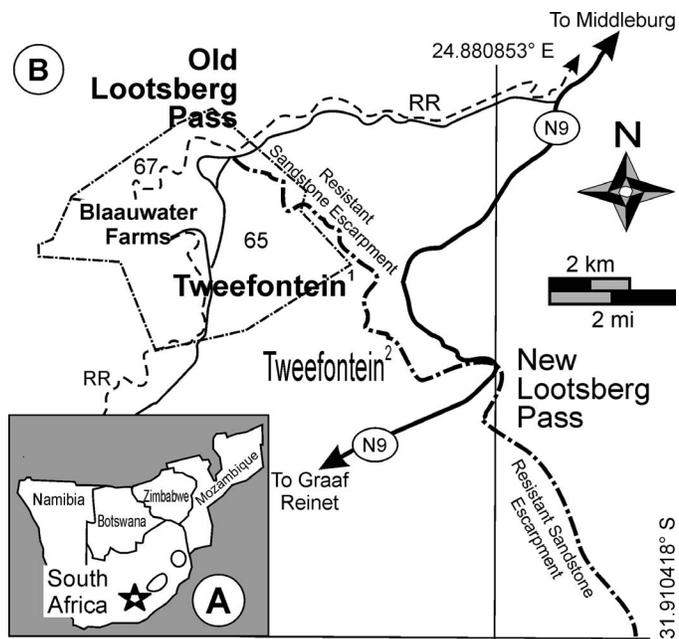


FIG. 2.—Locality maps. A) Generalized map of southern Africa on which Old Lootsberg Pass is located with a star. B) Map showing the geographic relationship between several of the localities—Old (West) Lootsberg Pass, Tweefontein, and (East) Lootsberg Pass—on which the current model of ecosystem response to the End-Permian event is based (Ward et al. 2000, 2005; Smith and Botha-Brink 2014). Localities used in the current study are in bold text. The current study reports on materials from the Blaauwater 65 and 67 farms.

boundary event (in contrast, see Gastaldo et al. 2015; Gastaldo and Neveling 2016) wherein the *Daptocephalus* (*Dicynodon*; Rubidge 1995) AZ (Viglietti et al. 2016) is replaced by the overlying *Lystrosaurus* AZ (LAZ; Ward et al. 2005; Lucas 2010). Siltstones in the LAZ, currently considered to be of Triassic age (Botha and Smith 2007; Lucas 2010; Smith and Botha-Brink 2014; Viglietti et al. 2016), are characterized as being reddened, although Smith and Botha-Brink (2014) acknowledged the occurrence of olive-gray siltstones in the biozone. Grayish-red siltstone is reported to be accompanied by a changeover in sandstone architectural elements to thin, trough cross-bedded units, interpreted to represent anabranching fluvial regimes (Ward et al. 2000). This changeover is purportedly in response to vegetational “die off” and the extinction of the *Glossopteris* flora (Ward et al. 2000, 2005; Smith and Ward 2001). Recently, Gastaldo et al. (2015) reported the first high resolution ID-TIMS age on zircons from a porcellanite cropping out in the Elandsberg Member and positioned ~ 60 m below the purported vertebrate-defined boundary at Old Lootsberg Pass. This bed has an early Changhsingian age (253.48 ± 0.15 Ma) and Gastaldo et al. (2015) concluded that it is improbable that the vertebrate-biozone boundary is coincident with the age of the marine extinction event. They suggested that Lopingian rocks extend into the Katberg Formation of the Tarkastad Group (Fig. 1).

Currently, the overlying Katberg Formation is assigned to the Triassic (Ward et al. 2005) and the LAZ is recognized as part of the Lootsbergian Land-Vertebrate Faunachron (Lucas 2010). Sandstone character of this predominantly arenaceous unit (Visser and Dukas 1979; Hiller and Stavrakis 1980) is variable across the basin, but can be generalized as being a fine to very-fine grained feldspathic wacke organized into meter-scale, trough-cross beds representing barforms in anabranching fluvial systems (Pace et al. 2009). A lithology closely associated with the lowermost Katberg Formation and uppermost Palingkloof Member—pedogenic nodular conglomerate (PNC; Visser and Dukas 1979)—has been used to

categorize these as Induan-aged deposits (Smith and Botha 2005; Botha and Smith 2006; Smith and Botha-Brink 2014). Intraformational PNC conglomerates occur either as basal channel lags (Pace et al. 2009) or isolated lenticular beds enveloped in grayish-red siltstone (Smith 1995), and may include mudclast aggregates (Gastaldo et al. 2013).

LOCALITIES AND METHODS

The Blaauwater 65 and Blaauwater 67 farms in the Eastern Cape Province are the location of two of eight cornerstone stratigraphic sections used to support the terrestrial end-Permian extinction paradigm (Ward et al. 2000, 2005). These are Old Lootsberg Pass (S31° 47.771', E24° 47.861', WGS84 datum; Fig. 2) and Tweefontein¹ (see below). Rocks exposed from Old Lootsberg Pass to Lootsberg Pass, and eastward, are essentially flat lying, with a strike that runs northwest-southeast and a gentle dip of one degree to the northeast. There is no obvious evidence of faulting or fault displacement in the area, and sandstone bodies can be traced laterally for several kilometers of distance. These conditions allow for beds or exposure surfaces to be traced physically either to outcrop or to a donga section. A Garmin Map62S with barometric altimeter served to assist in maintaining elevational relationships.

Exposures at Old Lootsberg Pass are easy to locate, and are either in erosional gullies (dongas) or outcrop parallel to the dirt roadway and railroad once used to traverse this mountain (Fig. 3). Gastaldo et al. (2015) published a stratigraphic section > 160 m in thickness from which a magnetostratigraphic record was obtained (see Online Supplemental Data for .kmz file). Here, we have 11 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', (W) E024° 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

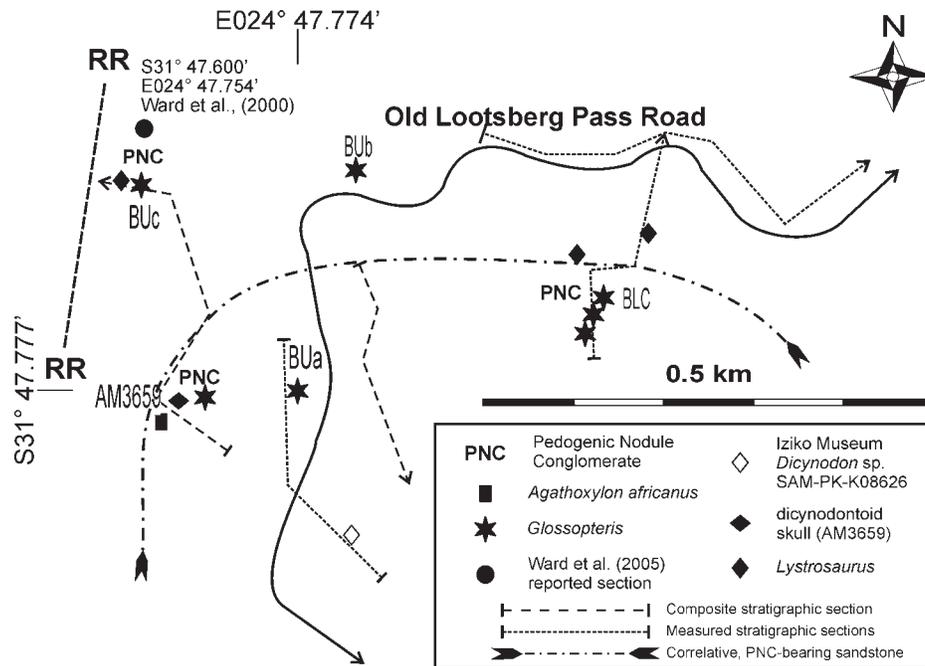


FIG. 3.—Old (West) Lootsberg Pass wherein megafloras (Albany Museum collections BUa, BUb, BUc, BLC), vertebrate remains, and pedogenic nodule conglomerate (PNC) localities, and stratigraphic sections measured (short dashed lines) are plotted. Double tailed dotted-and-dashed line illustrates the bedding outcrop of the sandstone body used by Gastaldo et al. (2015) as a correlation datum. The GPS position of the measured section reported by Ward et al. (2000, 2005) is shown as a solid circle, and occurs below the railroad tracks in the Katberg Formation. Scale = 0.5 km.

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 Tweefontein¹ 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 Tweefontein¹ 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 Tweefontein¹ (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

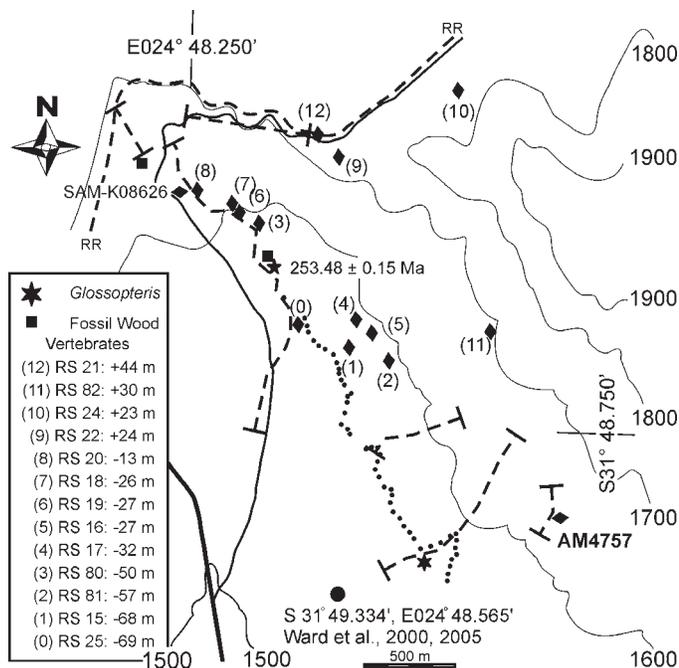


FIG. 4.—Expanded map showing the relationships between several measured sections (dashed lines) at Old Lootsberg Pass and Tweefontein¹ that are physically correlated based on walking the upper bounding surface of a thick sandstone body (solid circles; .kmz file in Online Supplemental Data File). The published GPS coordinates of Ward et al. (2000, 2005) for their Tweefontein locality is shown as a solid circle, and occurs in a field with little topographic relief. The positions of vertebrates from the data set of Smith and Botha-Brink (2014) used to develop their three-phased extinction model for the basin are shown. Each specimen's relative position reported by these workers, either below or above their biozone boundary, is provided. Abbreviation: RR = railroad. Scale = 0.5 km.

upwards into thin-to-medium, trough cross-beds (St) and bedsets where ripple lamination (Sr) commonly occurs on laminar bedform surfaces. Troughs in barforms commonly are filled with a succession of low angle, mm-thick cross-beds. The upper bounding surface of a thick sandstone body at the 20–30 m interval in the Old Lootsberg Pass section can be traced for ~ 2 km to Tweefontein¹ (Figs. 4, 5; see Online Supplemental Data for .kmz file). A change in sandstone color to light bluish gray (5B 7/1) occurs high in the section, although there is no change in grain size associated with it. Evidence in these two sections for the presence of a basal, intraformational PNC lag is found first in a thick sandstone at a stratigraphic height of ~ 125 m (Fig. 5).

The thick, upper sandstone in which a pedogenic nodule conglomerate is found can be traced across exposures at Old Lootsberg Pass for a distance of > 0.5 km (Figs. 3, 6). It attains a maximum thickness > 11 m, thins to the east and west to < 0.5 m, after which it pinches out laterally into grayish-red (east) or olive-gray (west) siltstone. There is no evidence of the sandstone body in the Tweefontein¹ section (Fig. 5); rather a grayish-red siltstone is its lateral equivalent. The Tweefontein¹ siltstone succession represents either overbank floodplain deposits that underwent pedogenic alteration, or abandoned channel-fill fines that experienced early diagenesis with clay minerals coated by finely dispersed hematite (Li et al. in press). Pedogenic Nodule Conglomerate lag deposits (PNC; Pace et al. 2009) overlie the basal contact in two exposures at Old Lootsberg Pass, represent less than 0.1% of total exposure, and consist of small, cm-scale carbonate-cemented nodules and mudclasts, as well as skull-and-bone fragments. Clasts are set in a matrix of very fine-grained sandstone and coarse siltstone. The lags are carbonate cemented and weather moderate yellowish brown (10YR 5/4). The fine to very fine sandstone is organized

into decimeter-scale massive (Sm; Miall 1996), planar, and lenticular beds that fine upwards into thin-to-medium, trough cross-beds (St). Ripple lamination (Sr) occurs on laminar bedform surfaces.

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. *Katbergia* burrows (Gastaldo and Rolerson 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 assemblages are the most complete, having been excavated with a backhoe, as other sites yield highly weathered shards 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 conspectus 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 microphyll 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 microphyll 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 microphyll–notophyll with straight, moderately to shallowly inclined venation, and open polygonal/trullate meshes near the midrib. Morphotype B3b is a narrowly elliptical to obovate microphyll, with straight, moderately inclined venation and open, polygonal/trullate to elliptical meshes that narrow only slightly towards the margin. Morphotype B4 conforms to *Glossopteris symmetrifolia* (Anderson and Anderson 1985; R. Prevec personal communication

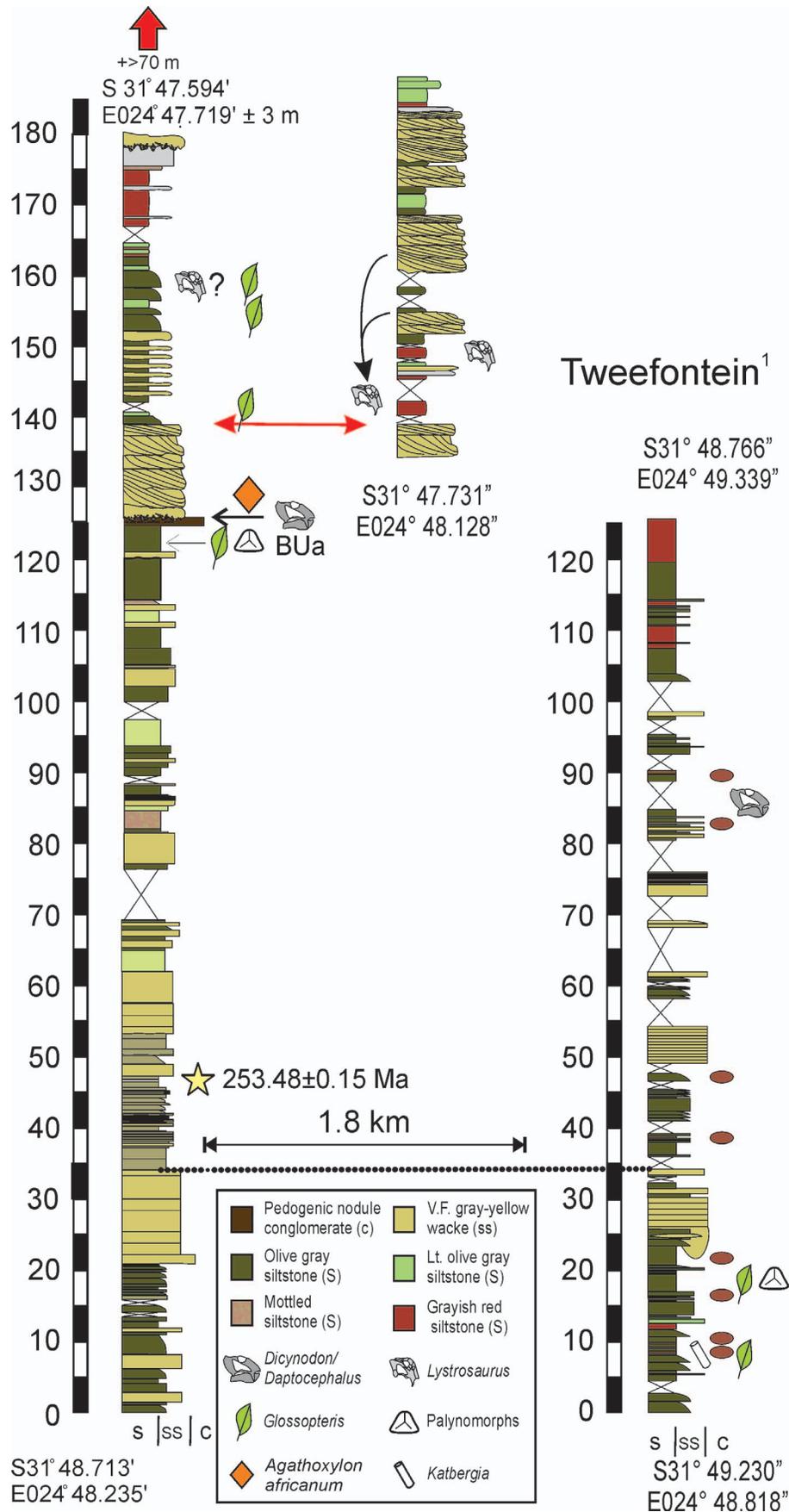


FIG. 5.—Measured stratigraphic sections. A composite stratigraphic section (see Fig. 2) at Old Lootsberg Pass is correlated to Tweefontein¹ using the upper bounding surface of a thick sandstone body near the base of the section (Fig. 4). Other sandstone bodies in the Katberg Formation are physically 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.

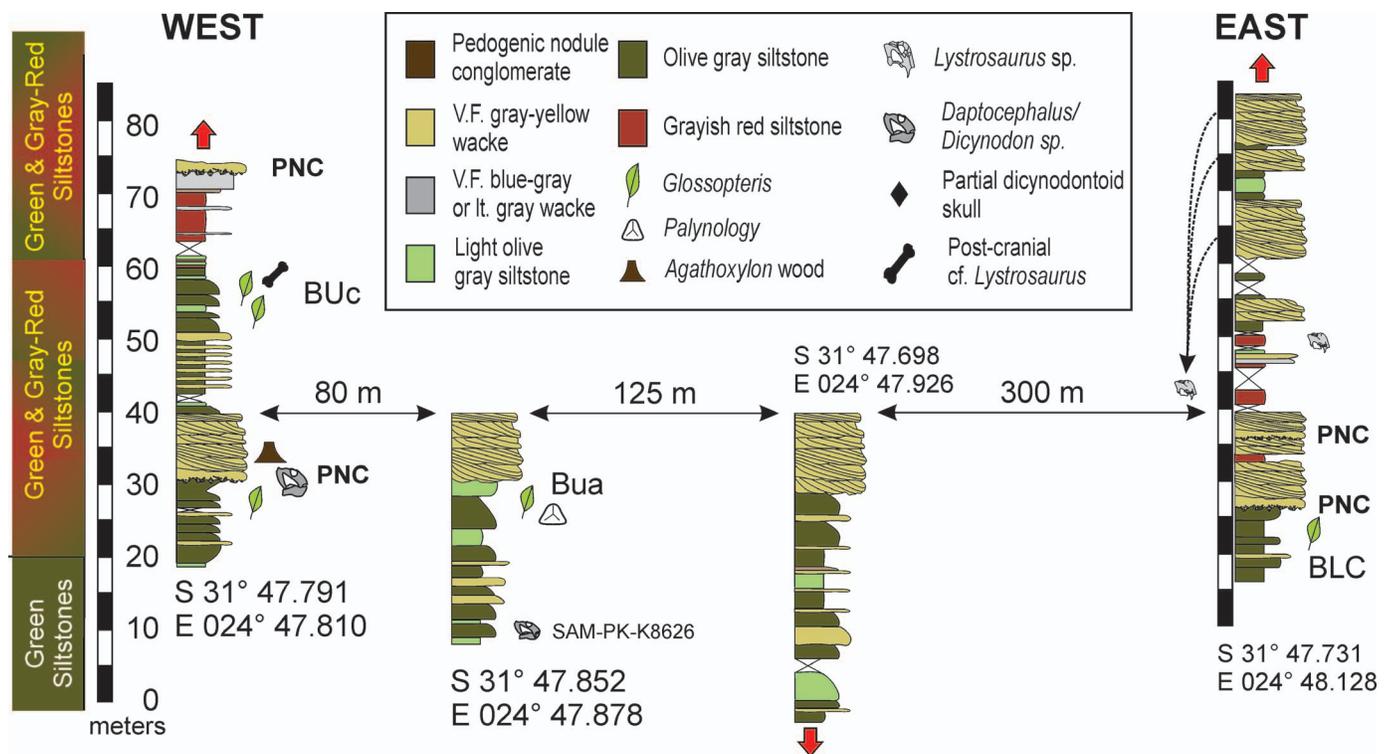


FIG. 6.—Correlation of parts of four of eleven measured sections at Old Lootsberg Pass in which a transition from olive-gray to mottled olive-gray and grayish-red, and grayish-red siltstone intervals is seen both vertically and laterally over a distance of < 0.5 km. Locations of megafossil collections (BUa, BUc, BLC; Fig. 3) and our *Lystrosaurus* are shown relative to a thick sandstone in which pedogenic nodule conglomerate lag deposits occur. Red arrows indicate that there is additional measured section either above or below the datum (Neveling et al. 2016a). The stratigraphic position of the Iziko Museum's cf. *Daptocephalus* (*Dicynodon*) specimen (SAM-PK-K8626) is shown. Scale in 5 m intervals.

2013), 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 Cloustone 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 megafossils 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 ($55 \times 43 \times 30$ cm and $20 \times 15 \times 17.5$ 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 rounded, and there is neither axial parenchyma nor canals (Fig. 8B). Early wood tracheids average 25×25 μ m whereas latewood tracheids are narrower in the radial plane, measuring 25×17 μ m. 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 μ m. Rays are uniseriate, 10–16–(20) cells high and very narrow (Fig. 8D). Cross-field pits are taxodioid to araucarioid, 5 μ m 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 Blaauwater 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

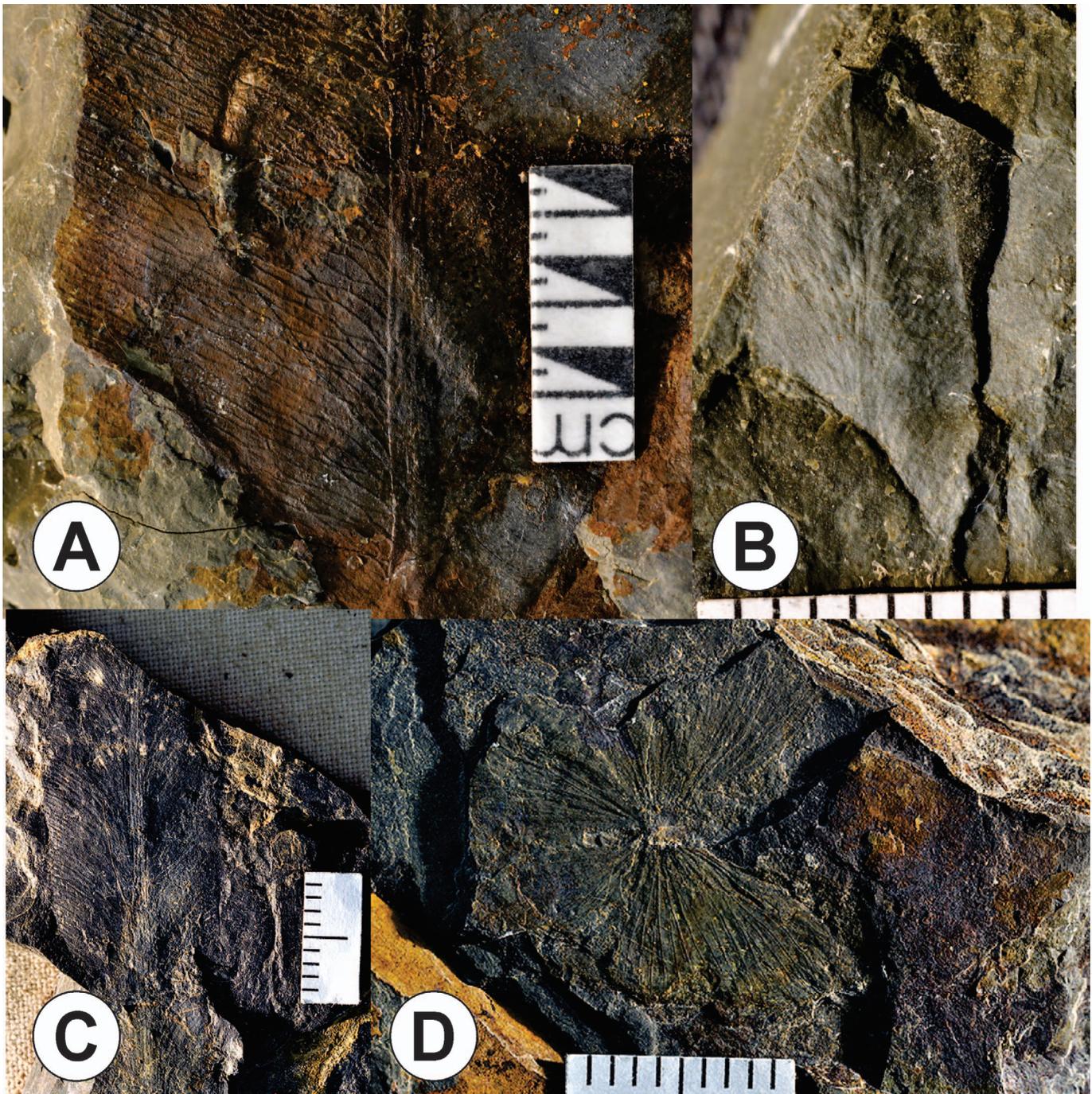


FIG. 7.—Common *Glossopteris* leaf morphotypes from Old Lootsberg Pass and Tweefontein¹. **A)** *Glossopteris* morphotype B3a from the Blaauwater locality Bua. Scale = 1 cm. **B)** *Glossopteris* morphotype B1 (equivalent to *Glossopteris* W1 from Wapadsberg Pass; Prevec et al. 2010) from the Blaauwater 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.

of sphenophytes (Fig. 9; see Online Supplemental Data File). Sphenophyllalean spores (*Columnisporites ovalis*, *Laevigatosporites* sp., and cf. *Laevigatosporites* combined) dominate (~ 90 %) the assemblage and likely represent contributions from *Trizygia speciosa*. *Columinisporites* monolet 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 *Protohaploxyipinus* 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

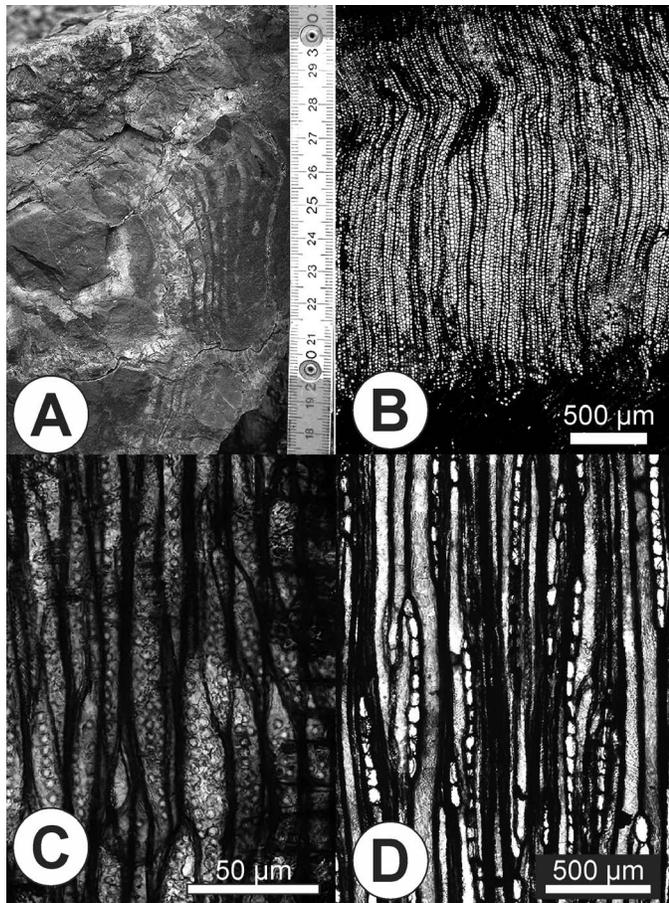


FIG. 8.—*Agathoxylon africanum*. **A**) Image of *in situ* trunk of permineralized fossil wood showing distinct growth rings. **B**) Photomicrograph of transverse section of *Agathoxylon africanum* showing almost square earlywood tracheids. The dark, cells to the top and base are the thick-walled latewood tracheids. **C**) Radial longitudinal section showing araucarian bordered pits that are biseriate, alternate, and slightly compressed. **D**) Tangential longitudinal section showing narrow and uniseriate rays are narrow and uniseriate. Scales as indicated on images.

from a pollen organ with a potential glossopterid affinity (Balme 1995). In this assemblage, pollen taxa of glossopterid affinity (*Protohaploxylinus* 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 taeniata bisaccate pollen in the assemblage—*Lueckisporites virkkiae*, *Guttulapol-lenites hannonicus*, and the common *Lunatisporites*—are peltasperm seedferns 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 seedferns (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.

Tweefontein¹.—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 Wapadsberg 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 *Trizygia 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).

Ichnology

Katbergia carltonensis is an ornamented cylindrical decapod-crustacean burrow oriented at various angles depending on the level of exposure in a paleosol (Gastaldo and Rolerson 2008). The lowest occurrence of the genus is found in olive-gray siltstone at Tweefontein¹ (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 *Lystroraptor* (Modesto and Botha-Brink 2010) and *Thrinaxodon* (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 Dicynodontoidea based on its size, particularly large-diameter canines, labial fossa, and absence of a postcaniniform crest (Fig. 11A, 11B; C. Kammerer personal communication 9/2013). 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 *Lystroraptor* 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 *Dicynodon*, *Daptocephalus*, and *Lystroraptor maccaigi* (Kammerer et al. 2011). However, other taxa to which the specimen might belong also include *Dinanomodon* and *Lystroraptor curvatus*, as the latter grew to similar sizes and are more similar to *L. maccaigi* than is appreciated (C. Kammerer personal communication 2016). Considering all

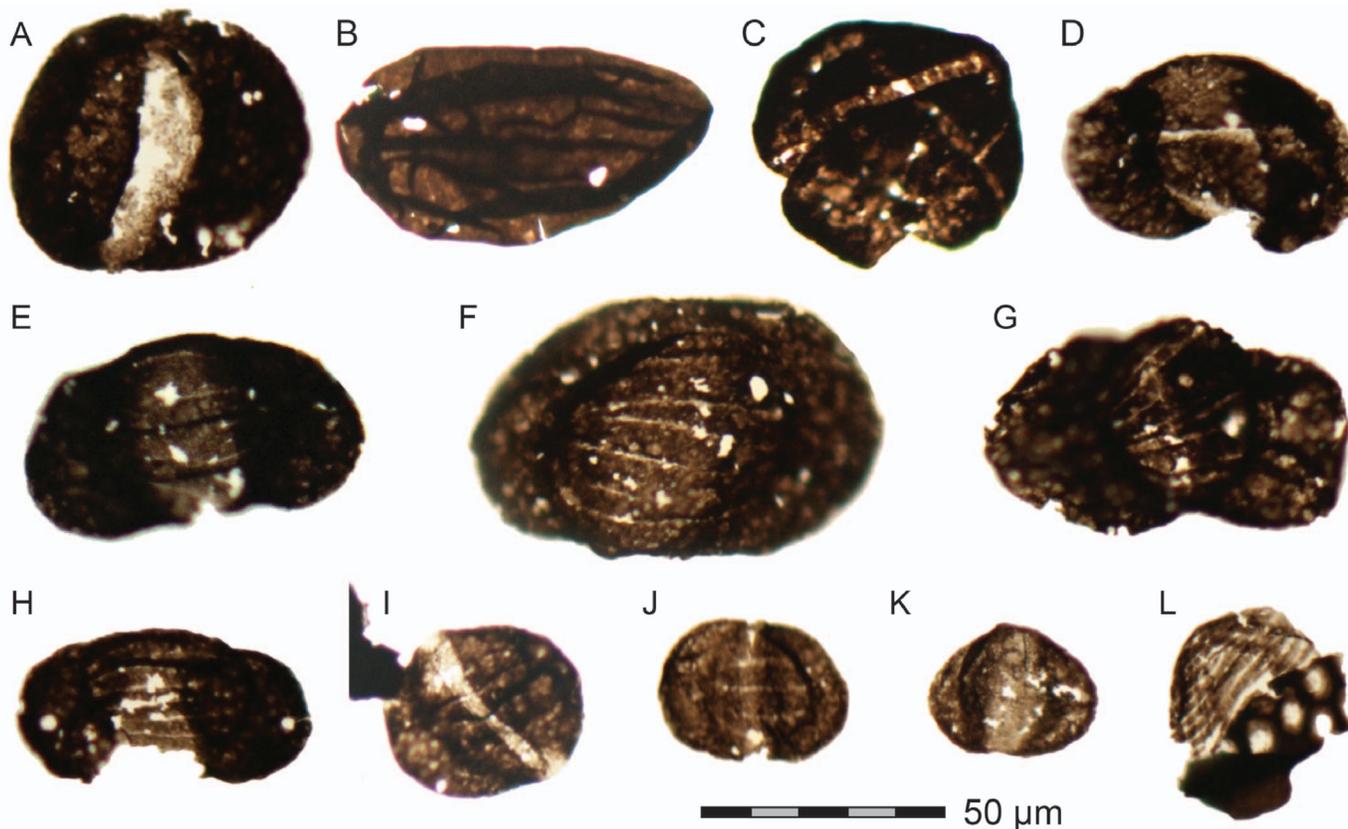


Fig. 9.—Selected pollen and spores from Old Lootsberg Pass locality BUa. Scale bar = 50 μm . Specimen names are followed by slide code and England Finder graticule coordinates in UCMF collection locality number PA1345. **A**) *Alisporites* sp. cf. *A. potonie* (U37-3; specimen 400000). **B**) *Columnisporites* sp. cf. *C. peppersii* (H34-4; specimen 400001). **C**) *Guttulapollenites hannonicus* (K43-1; specimen 400002). **D**) *Lueckisporites virkkiae* (J47-3; specimen 400003). **E**) *Lunatisporites noviaulensis* (D22-2; specimen 400004). **F**) *Protohaploxypinus* sp. (U18-3; specimen 400005). **G**) *Protohaploxypinus diagonalis* (O41-1; specimen 400006). **H**) *Striatoabieites multistriatus* (U37-1; specimen 400007). **I**) *Protohaploxypinus rugatus* (M12-3; specimen 400008). **J**) *Protohaploxypinus limpidus* (R22-1; specimen 400009). **K**) *Alisporites tenuicarpus* (M36-1; specimen 400010). **L**) *Weylandites lucifer* (U42-1; specimen 400011).

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).

Twefontein¹.—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 lithostratigraphic criteria. As a consequence, a multi-partied 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

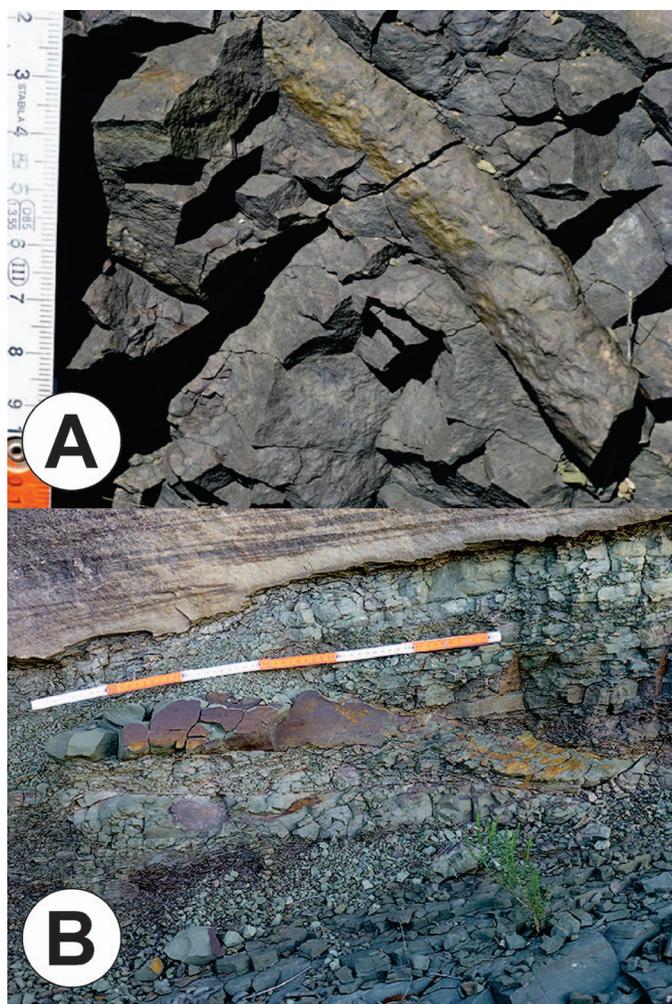


FIG. 10.—Ichnology. **A**) Subvertical *Katbergia* siltstone-cast burrow, showing surficial scratch marks (Gastaldo and Rolerson 2008) in grayish-red siltstone. Scale in cm. **B**) Subhorizontal and inclined sandstone cast of burrow in olive-gray siltstone from exposure in the Katberg Formation along Old Lootsberg Pass roadway. Scale in decimeters.

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

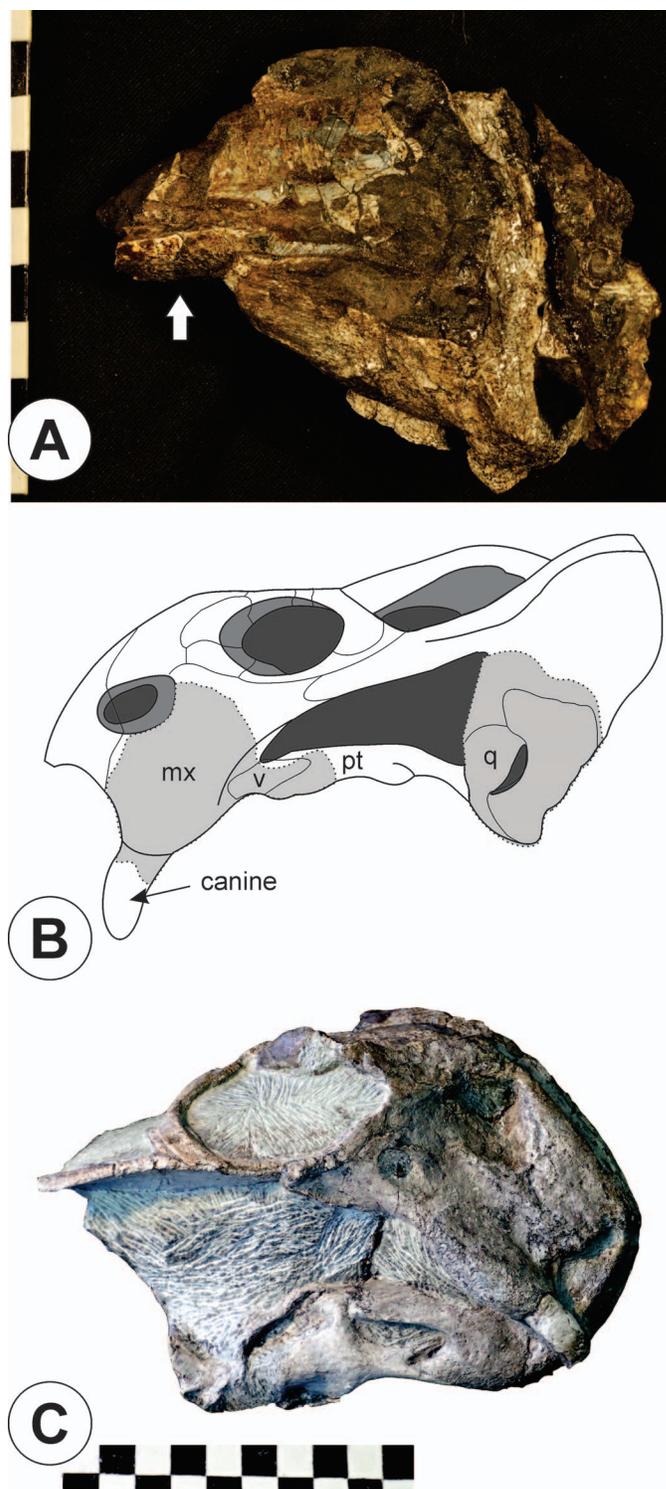


FIG. 11.—Vertebrate paleontology at Old Lootsberg Pass. **A**) Partial skull (AM3659) recovered from the pedogenic-nodule conglomerate lag deposit of the thick sandstone at the base of Old Lootsberg Pass (Figs. 3, 5, 6; image courtesy of R. Prevec). It consists of a maxilla with large diameter canine that is assigned to Dicynodontoida indeterminate. See text for possible systematic affinities. Scale in cm. **B**) Line illustration of dicynodontoid 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 dicynodontoid skull was recovered. Scale in cm.



FIG. 12.—Prepared specimen of cf. *Dicynodon leontocephalus* (AM4757) collected from olive gray siltstone at Tweefontein¹. See text for details. Scale in cm and dm.

their subdivision of the *Daptocephalus* AZ into a lower and upper interval is based on the database of Smith and Botha-Brink (2014) in which the lowest occurrence of *L. maccaigi* is reported only to be 32 m below their vertebrate-defined boundary. That specimen (RS161) originates from Tussen Die Rivier in the Free State. The specimen of *L. maccaigi* (SAM-PK-10920; Viglietti et al. 2016, table 1) from the Nieu Bethesda area used by them to signal the FAD of the taxon more than 100 m lower in the section is not part of the Smith and Botha-Brink (2014) database. Smith and Botha-Brink (2014, supplemental data) do report a specimen with a similar number (SAM-PK-K10920), but assigned that fossil to *D. lacerticeps* and is placed at 12 m below their vertebrate-defined boundary. Hence, the base of the *Lystrosaurus* Assemblage Zone (Groenewald and Kitching 1995) has yet to be redefined with confidence, but conventions applied by South African workers (Smith 1995; Smith and Ward 2001; Ward et al. 2005; Smith and Botha 2005; Botha and Smith 2006; Smith and Botha-Brink 2014; Viglietti et al. 2016; Rubidge et al. 2016, and others) differ from those defined in Rubidge's (1995) biostratigraphic compilation of the basin.

Groenewald and Kitching (1995) note that *Lystrosaurus* is the dominant vertebrate taxon, comprising up to 95% of specimens collected in the *Lystrosaurus* AZ, and they placed its base at the bottom of the Palingkloof Member. Here, they noted a dramatic change in siltstone color, from greenish gray to red, accompanies the first occurrence of *Lystrosaurus* sp. At the time, Groenewald and Kitching (1995) included five species in the biozone, one of which, *L. oviceps*, is now a synonym of *L. curvatus* (Grine et al. 2006). They further reported the first appearance datum of the captorhinid *Prolocophon* to be coincident with *Lystrosaurus*. Since then, the ranges of two species of *Lystrosaurus* (*L. maccaigi* and *L. curvatus*) are reported to have initiated in the upper *Daptocephalus* AZ fauna (Smith and Botha 2005; Botha and Smith 2006; Smith and Botha-Brink 2014) with replacement of these taxa in the lowermost *Lystrosaurus* AZ strata by two new taxa, *L. murrayi* and *L. declivis* (Botha and Smith 2007) in the upper Palingkloof Member. Current workers now report the first appearance of *Prolocophon* to be 60 m above the biozone boundary (Ward et al. 2005; Smith and Botha-Brink 2014). Hence, recent convention holds that the uppermost *Daptocephalus* AZ fauna includes *L. curvatus* and *L. maccaigi*,

the latter the only species of the taxon not to extend above the reported biozone boundary, and overlying fauna to witness the loss of *L. curvatus*. The loss of this taxon is accompanied by the appearance of *L. murrayi* and *L. declivis* without the presence of *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) *Daptocephalus* Assemblage Zone. This part of the biozone is delimited by the presence of *D. leoniceps* and *L. maccaigi*, and the absence (presumed extinction) of *Dicynodon lacerticeps*. Hence, vertebrates previously reported by Smith and Botha-Brink (2014) as *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 *D. leoniceps* until a detailed systematic study indicates otherwise. Therefore, the co-occurrence of *D. sp. cf. D. leoniceps* (AM4757) and *L. maccaigi* (RS 17, RS 81), along with the presence of *L. murrayi* (Figs. 5, 6, 11C) higher in Old Lootsberg Pass, place our collections in the upper part of the *Daptocephalus* and lower part of the *Lystrosaurus* biozones, transitioning the reported turnover event.

Paleobotanical Significance

The preservation of *Glossopteris* morphotypes, along with sphenopsids and a nearly identical palynoflora in correlative sections 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 Tweefontein¹ (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 *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 (*Protohaploxylinus limidus*, *Striatopodocarpites cancellatus*, and *Weylandites lucifer*) with an understory of trizygoid sphenophytes (*Columnisporites* sp. cf. *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 Blaauwater Farm palynoflora includes both taeniate and aleate bisaccate pollen. Taeniate bisaccate pollen are represented by *Lueckisporites virkkiaae*, *Guttulapollenites hannonicus*, and *Lunatisporites noviaulensis*, and originate from peltasperm seed ferns and conifers (e.g., Clement-Westerhof 1987). Bisaccate aleate pollen of the genera, *Falcisporites* and *Alisporites*, were produced by corystosperm and peltasperm seed ferns (Balme 1995; Lindström et al. 1997). The presence of *Falcisporites 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 voltzian conifers (Balme 1995).

To date, no conclusive upper Permian macrofossil evidence from the Karoo Basin is reported for either peltasperms, corystosperms, 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 *Dicroidium*—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 (Schneebeil-Hermann et al. 2015). Pollen types associated with these groups in the Lootsberg 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, corystosperm, 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 glossopterids 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 (Greb 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 siltstone-filled cylinders, resembling callianassid 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 siltstone/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 older 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

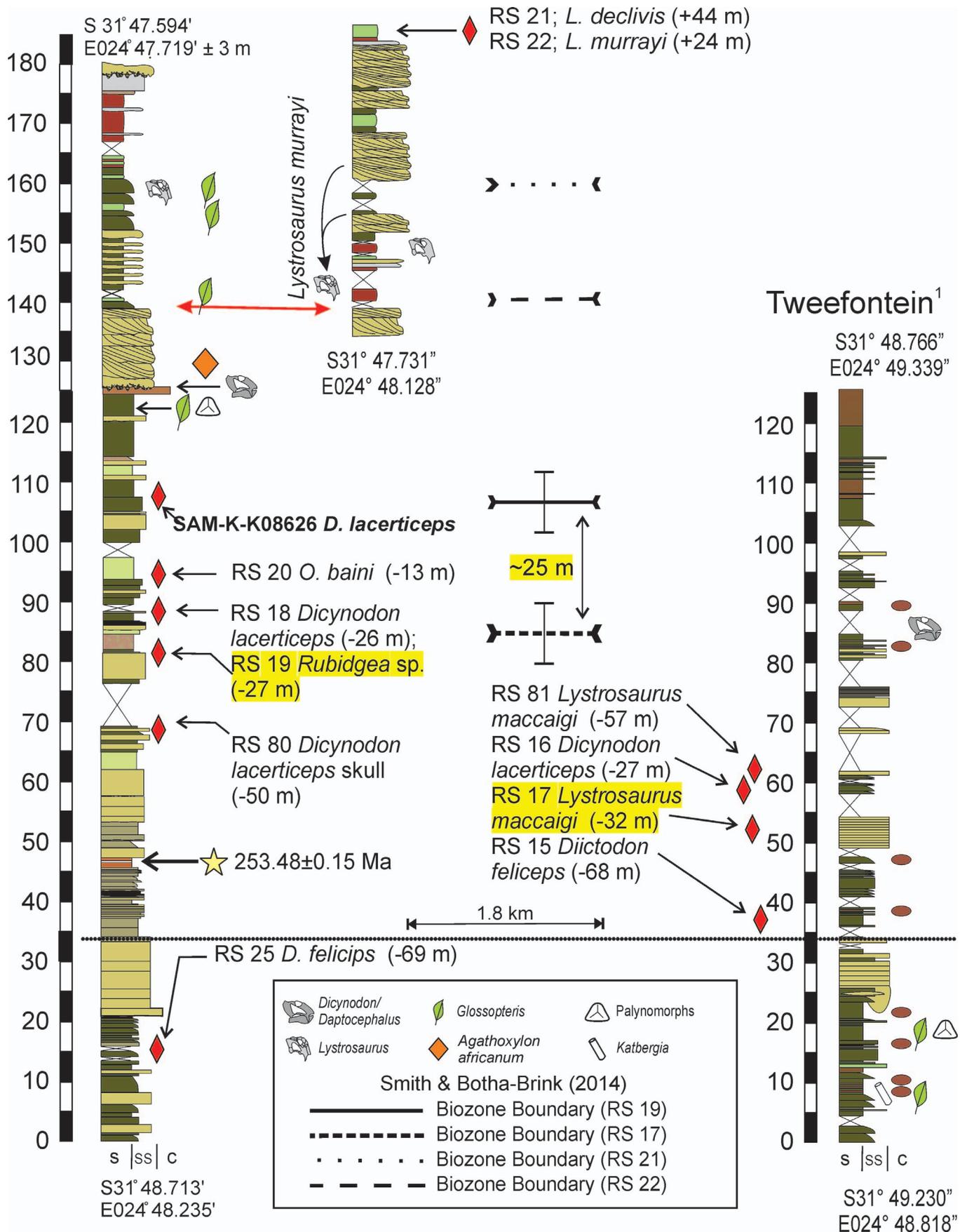


FIG. 13.—Physically correlated stratigraphic sections at Lootsberg Pass and Tweefontein¹ using upper bounding surfaces of thick sandstone bodies into which the stratigraphic position of RS vertebrates reported by Smith and Botha-Brink (2014) have been placed (Fig. 4; see Online Supplemental Data for .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 Viglietti et al. 2016), are reported from the area between Old Lootsberg Pass and Tweefontein¹. 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. maccaigi*) is reported as having been collected 57 m below the boundary at Tweefontein¹. 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 porcellanite 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 Lootsberg Pass section maintain a logical ordering, at least 50 m of stratigraphic section separate RS 80 (-50 m) and RS 25 (-69 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* (= *Dicynodon*) AZ from the Blaauwater Farm (Fig. 13). Two of these, RS 17 and RS19, were considered by Viglietti 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 incongruity by comparing where that boundary is placed in the Old Lootsberg 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 Tweefontein¹ section that has been physically correlated less than 2 km away.

At Old Lootsberg 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 Tweefontein¹ 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 Tweefontein¹ 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 Lootsberg Pass and Tweefontein¹ 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 Lootsberg 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 of the Katberg Formation (Fig. 13). This is consistent with where Ward et al. (2000, 2005) mark the base of their Old Lootsberg section (Fig. 3). Hence, the proposed position of the boundary between the *Daptocephalus* (Viglietti 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 physically correlated stratigraphic framework, separated by up to 70 m of section.

Gastaldo et al. (2015) argued for an upward extension of the, then, *Dicynodon* (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 Lootsberg Pass. Our suggested placement of the biozone boundary is based on the stratigraphic position of the dicynodontoid 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). Viglietti et al. (2016, their supplemental data) use specimens RS19 at Old Lootsberg Pass and RS 17 (yellow highlighted) at Tweefontein¹ to circumscribe the uppermost *Daptocephalus* zone. Reported vertebrate positions relative to the *Daptocephalus* (*Dicynodon*)/*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 Tweefontein¹ and the highest possible boundary at Old Lootsberg 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 Lootsberg Pass and our Tweefontein¹ 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 (Roonarine 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 Blaauwater Farm (Old Lootsberg Pass and Tweefontein¹; 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 understood 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 Blaauwater 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 megafloora 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, *Katbergia*, 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 parautochthonous or allochthonous palynomorphs with corystosperm, 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 megafloreal taphonomic wetland window. The presence of *Katbergia*-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, mottling, 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, supplemental data), four different horizons in our physically correlated sections are identified as the “unique” datum. Over the ~ 2 km distance on the Blaauwater farms, these occur anywhere from ~ 25 m to ~ 70 m apart stratigraphically. The inferred biozone boundary in our Tweefontein¹ section is lower than that at Old Lootsberg 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.

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SUPPLEMENTAL MATERIAL

Data are available from the PALAIOS Data Archive: <http://www.sepm.org/pages.aspx?pageid=332>.

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