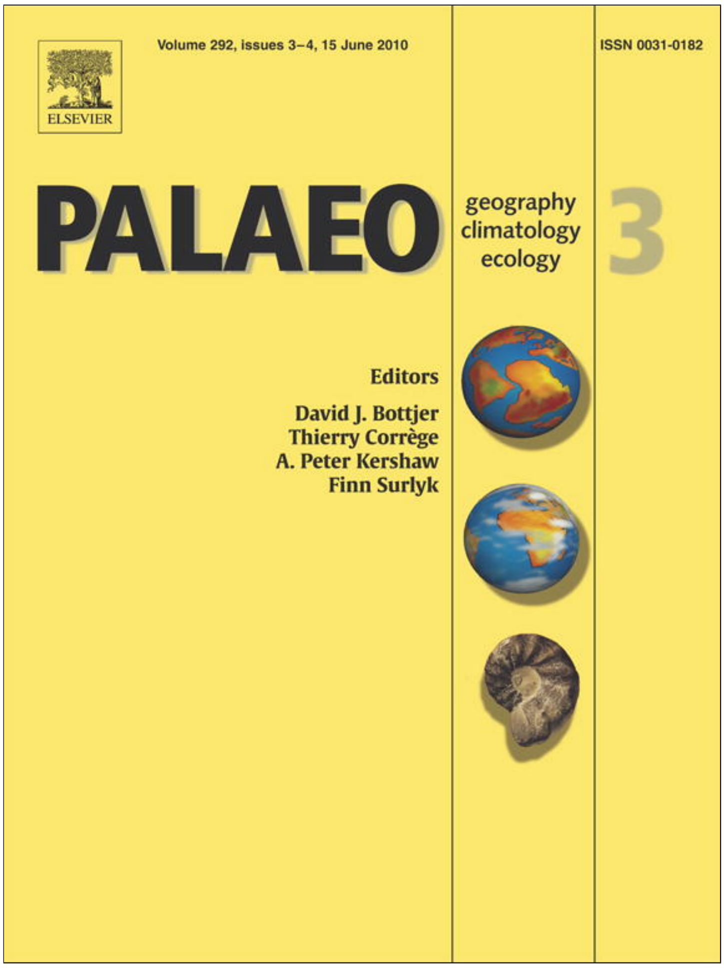


Volume 292, issues 3–4, 15 June 2010

ISSN 0031-0182

ELSEVIER

PALAEO geography climatology ecology 3

Editors
David J. Bottjer
Thierry Corrège
A. Peter Kershaw
Finn Surlyk

Palaeogeography, Palaeoclimatology, Palaeoecology 292 (2010) 391–408

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

An autochthonous glossopterid flora with latest Permian palynomorphs and its depositional setting in the *Dicynodon* Assemblage Zone of the southern Karoo Basin, South Africa

Rose Prevec [a], Robert A. Gastaldo [b,*], Johann Neveling [c], Samuel B. Reid [b], Cindy V. Looy [d]

[a] *Department of Geology, Rhodes University, Grahamstown, 6140, South Africa*
[b] *Department of Geology, Colby College, Waterville, ME 04901, USA*
[c] *Council for Geosciences, Silverton, Pretoria, South Africa*
[d] *Department of Integrative Biology and Museum of Paleontology, University of California, Berkeley, CA 94720, USA*

ARTICLE INFO

Article history:
Received 6 May 2009
Received in revised form 6 March 2010
Accepted 23 March 2010
Available online 31 March 2010

Keywords:
Palaeobotany
Palaeoecology
Glossopteris
Permian–Triassic boundary
Changhsingian

ABSTRACT

The discovery of a plant-fossil assemblage, situated ~70 m below the vertebrate-defined Permian–Triassic boundary, allows for the characterization of part of the Late Permian landscape in the southern Karoo Basin. The megafloral and microfloral assemblages are preserved in association with an O-horizon above a weakly developed palaeosol, exposed in both New and Old Wapadsberg Pass, Eastern Cape Province, South Africa. Stable-isotope geochemical evidence indicates that pedogenesis occurred under conditions of a high regional water table, and the palaeosol was entombed by overbank or avulsion deposits in an aggradational landscape that includes tuffite. The low-diversity macroflora contains gymnospermous (*Glossopteris*) and sphenopsid (*Phyllotheca*, *Trizygia*) elements that include vegetative (axial, leaf) and reproductive (strobilar) remains. *Glossopteris* leaves are microphyllous and may reflect the taxon's physiological response to purported climate perturbation or wetland edaphic conditions, and exhibit a range of plant–animal interactions. Palynological residues contain sphenophyllalean cuticles, and the microfloral assemblage is consistent with a low-diversity glossoperid-dominated woodland with a sphenopsid understory. Extrabasinal elements include representatives of peltasperms (*Alisporites*), corystosperms (*Falcisporites*), and conifers (*Lueckisporites*). Pollen conforming to *Lunatisporites pellucidus* is present in the assemblage and is considered an indicator taxon for the latest Permian to Early Triassic. When compared to palynological assemblage zones in Australia, the Wapadsberg Pass flora is assigned a Late Changhsingian age and, therefore, represents the youngest autochthonous, *Glossopteris*-dominated flora to be reported from Gondwana. These results extend a palynostratigraphic framework across the Southern Hemisphere that complements other zonations presently applied to the Karoo Basin succession.

1. Introduction

Our understanding of the latest Palaeozoic terrestrial biota across Gondwana is based on palaeobotanical collections primarily composed of gymnospermous glossopterids. Following continental deglaciation at high palaeolatitudes, this plant group came to dominate both peat and non-peat accumulating Permian wetlands under a cool-to-cold temperate regime (Rees et al., 1999; Greb et al., 2006). Macroremains of these plants persist into the youngest Permian strata and, based on dispersed pollen, the group possibly ranged into the earliest Triassic (Lindström and McLoughlin, 2007), where the level of regional diversity is believed to have decreased in overall systematic composition. This decrease is attributed to low sample numbers with reported low diversity (Rees, 2002), an interpreted broad climate change from a wetter to drier climate (Ward et al., 2000; Retallack et al., 2003), and a concomitant change in taphonomic processes that impacted plant-part preservation potential (Gastaldo et al., 2005). The record of Permian ecosystems in South Africa is preserved mostly in the sediments of the Karoo Basin, a large foreland basin that formed in southern Gondwana during the Late Palaeozoic to mid-Mesozoic (Johnson et al., 1997).

Past studies of South African Permian floras have focused almost entirely on (1) the richly fossiliferous, coal-associated beds of the Lower Permian Vryheid Formation in the northern part of the Karoo Basin, preserved in fluvio-deltaic settings (e.g., Plumstead, 1969; Kovács-Endrödy, 1991; Anderson and Anderson, 1985; Cairncross, 2001; Adendorff et al., 2002, 2003; Prevec et al., 2008); and (2) assemblages of the Upper Permian Normandien (previously Estcourt) Formation and equivalents of KwaZulu-Natal in the north-eastern parts of the basin, preserved in oxbow-lake settings within

---

* Corresponding author.
E-mail address: ragastal@colby.edu (R.A. Gastaldo).

0031-0182/$ – see front matter © 2010 Elsevier B.V. All rights reserved.
doi:10.1016/j.palaeo.2010.03.052

floodplains (Lacey, 1974, 1978; Lacey et al, 1975; Anderson and Anderson, 1985; van Dijk, 1981, 2000; Gastaldo et al., 2005; Bordy and Prevec, 2008; Prevec et al., 2009). Many of these records represent the remains of aerial parts (branches, leaves, reproductive structures [fructifications, seeds, pollen and spores]) of riparian plants preserved either in parautochthonous or allochthonous assemblages (Gastaldo et al., 2005).

The remaining expanse of the Karoo Basin, although widely recognized for its exceptional vertebrate fossil record (e.g., Rubidge et al., 1995; Smith, 1995; Botha and Smith, 2006), is notorious for its absence of well-preserved plant material. Sparse occurrences of commonly fragmentary glossopterid and sphenopsid remains are reported from the Dwyka and Ecca groups, representing mainly allochthonous assemblages in the Middle Permian Waterford Formation (Anderson and McLachlan, 1976; Anderson and Anderson, 1985). Rare *in situ* sphenopsids are reported from crevasse splay and floodplain deposits of the lowermost Beaufort Group (Anderson and Anderson, 1985; unpublished observations).

The low-diversity and fragmentary nature of most plant remains from the region and the absence of fertile glossopterid material has hindered meaningful floral reconstructions, diversity assessments, and correlations with other parts of the basin. No floral elements typical of the Late Permian in KwaZulu-Natal (north-eastern Karoo Basin) have been reported previously from the southern parts of the Karoo Basin, apart from the sphenopsids *Phyllotheca australis* and *Schizoneura africana*, and the broadly defined species *Glossopteris symmetrifolia* (Anderson and Anderson, 1985).

The apparent dearth of plant fossils in the southern reaches of the Karoo Basin is particularly unfortunate, as this region provides a reportedly continuous succession of terrestrial deposits spanning the Permian Triassic Boundary (PTB; Smith, 1995; Ward et al., 2000; but see Pace et al., 2009; Gastaldo et al., 2009). Although studies have been hampered by an absence of chronometric data, a detailed vertebrate biostratigraphic framework has been established (Rubidge et al., 1995; Rubidge, 2005). Recently, research activity has focused on the vertebrate palaeontology of the PTB (e.g., Ward et al., 2005; Retallack et al., 2003; Smith and Botha, 2005; Botha and Smith, 2006) within an environmental context (e.g., Ward et al., 2000; Smith and Ward, 2001), but floral studies have lagged (e.g., Steiner et al., 2003; Gastaldo et al., 2005). The recognition of vegetational changes associated with the PT extinction event have been confounded doubly by an apparently global scarcity of macroplant remains during this period of biotic turnover (Retallack et al., 2003; Gastaldo et al., 2005). In the Karoo Basin, this poor record can be attributed, in part, to a widespread prevalence of taphonomic factors unfavourable for plant-fossil preservation (Gastaldo et al., 2005; Gastaldo and Demko, in press). But, the apparent absence of South African plant-fossil collections of this critical age is also the product of a lack of palaeobotanical research effort in the southern and western parts of the basin, partly stemming from the generally-held perception that productive fossil-plant localities do not exist in these regions.

Recent investigations into the well-documented Wapadsberg Pass exposures in the Eastern Cape Province, which previously have featured prominently in geological and vertebrate palaeontological studies of the PTB in South Africa (e.g., Ward et al., 2000, 2005), have led to the discovery of a remarkable plant-fossil assemblage that challenges current perceptions of the palaeobotanical potential of the southern Karoo Basin (Reid et al., 2006). The well-preserved autochthonous flora was found exposed at two lithostratigraphically equivalent localities, here referred to as the Old and New Wapadsberg Pass localities, respectively. The discovery is particularly significant because this represents the youngest autochthonous glossopterid flora to be described from South Africa. Here, the Wapadsberg Pass assemblage is described and placed within a geologic and taphonomic context, and palynological analyses are used to provide temporal constraints.

2. The Late Permian of the Karoo Basin

The Karoo Supergroup records deposition in a broad range of sedimentological environments over a 110 million year interval (Late Carboniferous–Early Jurassic). Of its constituent units, the Beaufort Group is the most extensive in terms of both areal distribution and stratigraphic thickness. Presently, it is subdivided into the lower Adelaide and upper Tarkastad subgroups (Johnson, 1976; Johnson et al., 2006). The Adelaide Subgroup is a 3000–4000 m thick sequence of Middle Permian (Roadian) to lowermost Triassic deposits (Rubidge, 2005) that is subdivided into two or three formations. Earliest stratigraphic nomenclature for these was based on exposures in the south-eastern part of the basin (Johnson, 1966; Johnson et al., 2006) where the Koonap, Middleton, and Balfour formations are recognized in ascending stratigraphic order. The latter is broadly correlative with the more distally positioned Normandien Formation of the northern Free State and KwaZulu-Natal provinces. Five lithostratigraphic members are recognized currently within the Balfour Formation (S.A.C.S., 1980). Exposures of the two uppermost members of the Balfour Formation, the argillaceous Elandsberg (greenish-grey siltstones) and Palingkloof (reddish grey siltstones) members, are considered to span the PTB. Consequently, it is this interval on which many prior PTB studies have focused.

The PTB is not defined lithostratigraphically but, rather, has been recognized solely on the stratigraphic level of the highest Permian taxon, *Dicynodon* sp. (Ward et al., 2005) and its coincidence with a unique "event bed" (Ward et al., 2000). But, as Ward et al. (2005), p. 714 note, "this is a practice that runs contrary to accepted stratigraphic procedure." Recent high-resolution stratigraphic studies of the purported "event bed" (Ward et al., 2000; Retallack et al., 2003) marking the PT boundary indicate that neither the "event bed" nor the stratigraphic position of the last *Dicynodon* sp. can be correlated across a distance of 1 km in the Bethulie region, let alone across the basin or into Antarctica (Gastaldo et al., 2009). And, with the recognition that *Lystrosaurus* no longer is considered to be an indicator of the Early Triassic (Smith, 1995; Rubidge, 2005) due to its First Appearance Datum in the latest Permian, recognition of the PTB must rely upon other criteria including stable isotopic trends (Ward et al., 2005) or palaeomagnetic signatures (DeKock and Kirschvink, 2004), presently without chronometric control.

The loss of a plant-fossil record, also reported to be indicative of the terminal Phanerozoic extinction event (Ward et al., 2000; Smith and Ward, 2001), has been used as a proxy for recognizing the PTB. The apparent paucity of plant-fossil assemblages in the southern part of the Karoo Basin may be, in part, the result of taphonomic conditions that prevailed during the development of the Late Permian landscape (Gastaldo et al., 2005). In general, argillaceous overbank deposits are relatively coarse and contain a large silt fraction. Thick plugs of fine-grained siliciclastics (siltstone or claystone), which represent low-energy environments such as oxbow lakes and are more conducive to plant preservation, appear to be rare (Kubler, 1977; Stear, 1980; Hiller and Stavrakis, 1984; Smith, 1980, 1990). In many cases, these environments are accompanied by pedogenic alteration resulting in the destruction of any previously entombed plant debris (e.g., Gastaldo and Demko, in press). As a result, there were few settings suitable for the accumulation and/or preservation of Late Permian plant-fossil assemblages in the southern Karoo (Anderson and Anderson, 1985; Gastaldo et al., 2005) making the present discovery more compelling.

3. Locality and methodologies

The fossiliferous deposit reported herein crops out at three sites within a small study area situated between the towns of Graaff-Reinet, Cradock, and Middelburg (Fig. 1) in the Eastern Cape Province, South Africa. The New Wapadsberg Pass locality is a road cutting along

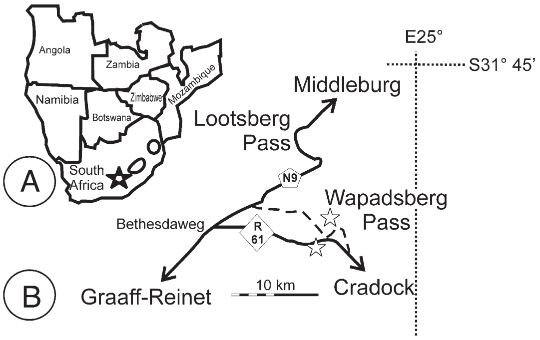


Fig. 1. General maps showing (A) the Wapadsberg Pass location in South Africa, and (B) the sites (stars) at which the fossil flora has been recovered along the R61 in Wapadsberg Pass and in dongas below Old Wapadsberg Pass. Eastern Cape Province.

highway R61 near the top of the Wapadsberg Pass (S31 55.927′, E24 52.872′ WGS84 Meridian; Fig. 2). Two other fossiliferous exposures occur at Old Wapadsberg Pass located <1 km to the northwest of the R61 site. The first is located near the base of a donga (erosion gully) exposure associated with the original, now abandoned, Wapadsberg Pass road (S31 55.199′, E24 53.666′; Fig. 1). Here, the fossiliferous bed is located ~70 m below the PTB as identified by Ward et al. (2000, 2005) and subsequent workers (Fig. 3). The second occurs approximately 200 m to the west in another small donga (S31 55.108′, E24 53.692′). Field-based correlation of the strata at both New and Old Wapadsberg Pass was accomplished by following a laterally continuous sandstone between the two sites and by comparison of lithofacies associations. This confirmed that the fossiliferous interval in the R61 exposure lies at the same stratigraphic level as the fossils seen at the Old Wapadsberg Pass localities. The area was affected by Jurassic Karoo dolerite intrusions that thermally altered the sandstone and siltstone at the top of New Wapadsberg Pass; hence, DeKock and Kirschvink (2004) were unable to obtain any palaeomagnetic signature from the section.

Lithologic logs were compiled using a Jacob's staff, with sight level, and standard field methods. Lithofacies identifications based on grain size, primary and secondary structures, mineralogical composition, and Munsell colour were defined on a sub-metric scale for two stratigraphic sections. Representative hand samples of lithofacies and carbonate nodules preserved therein were collected throughout the studied sections for thin-section, micro-structure, and stable-isotope analyses.

Analyses of δ^{13}C and δ^{18}O isotopes from calcite cement in carbonate nodules were conducted in the Department of Geological Sciences, Southern Methodist University (SMU), Dallas, Texas (for analytical details, see Tabor et al., 2007; Gastaldo and Rolerson, 2008). Carbon dioxide samples are reported relative to standard delta notation:

$$\delta^{13}C\left(\mathrm{or}\,^{18}O\right) = \left(R_{\mathrm{sample}} / R_{\mathrm{standard}} - 1\right)^{*}1000 \qquad (1)$$

where R is the ratio of heavy to light stable isotope present in the sample or standard. Delta values are reported relative to the PeeDee Belemnite standard (PDB; Craig, 1957) for carbon-isotope values, and standard mean ocean water (SMOW; Gonfiantini, 1978) for oxygen isotope values.

More than 700 fossiliferous hand specimens were collected at New Wapadsberg Pass and over 300 from Old Wapadsberg Pass. All plant fossils are impressions, apparently devoid of cuticle and carbonaceous residue, although fragmentary cuticle has been recovered in palynological preparations (see below). All specimens were assigned field numbers with the prefixes ‘WO’ and ‘WN’ for Old Wapadsberg Pass

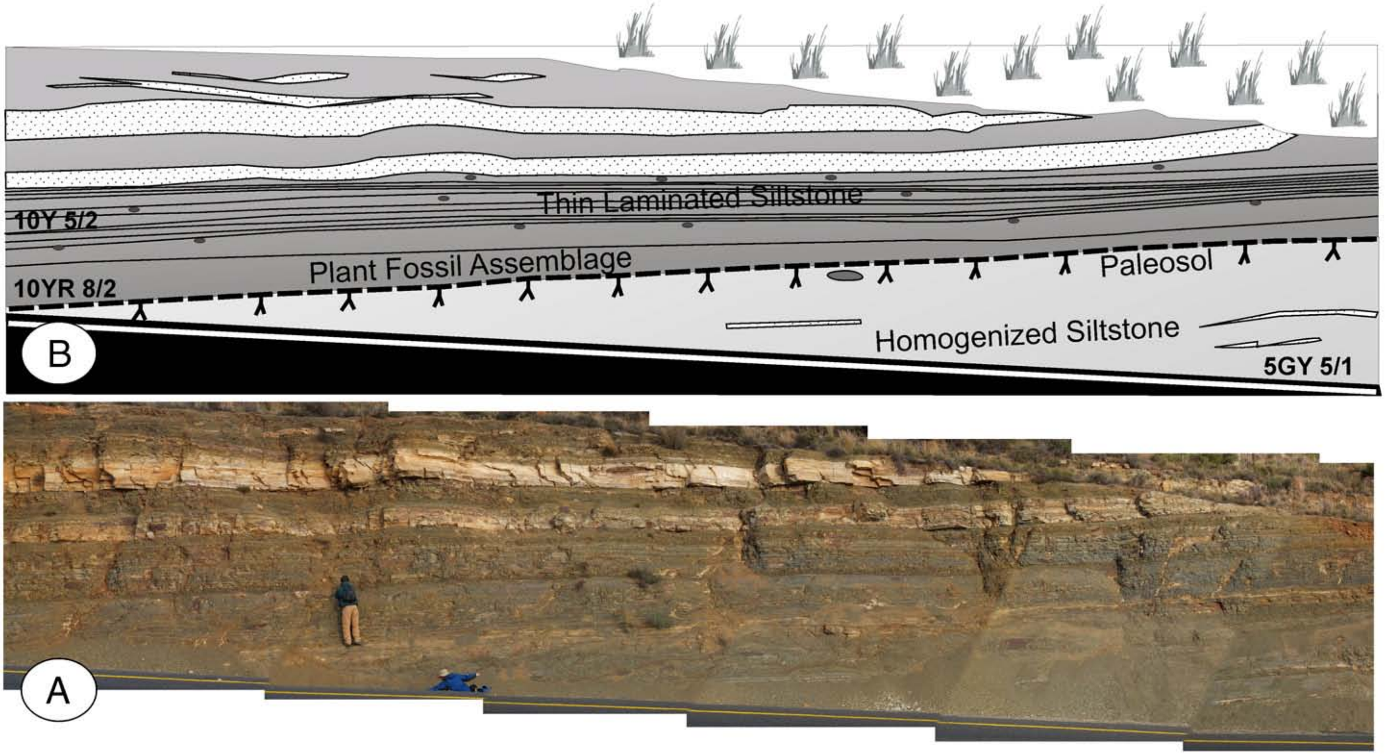


Fig. 2. Strata exposed along the R61 in which the fossil flora is preserved. (A) Photomosaic of outcrop showing a siltstone-dominated succession overlain by sheet sandstone bodies. (B) Line tracing of photomosaic in which siltstone lithofacies, a rooted palaeosol, and fossil-plant-bearing sediments are identified.

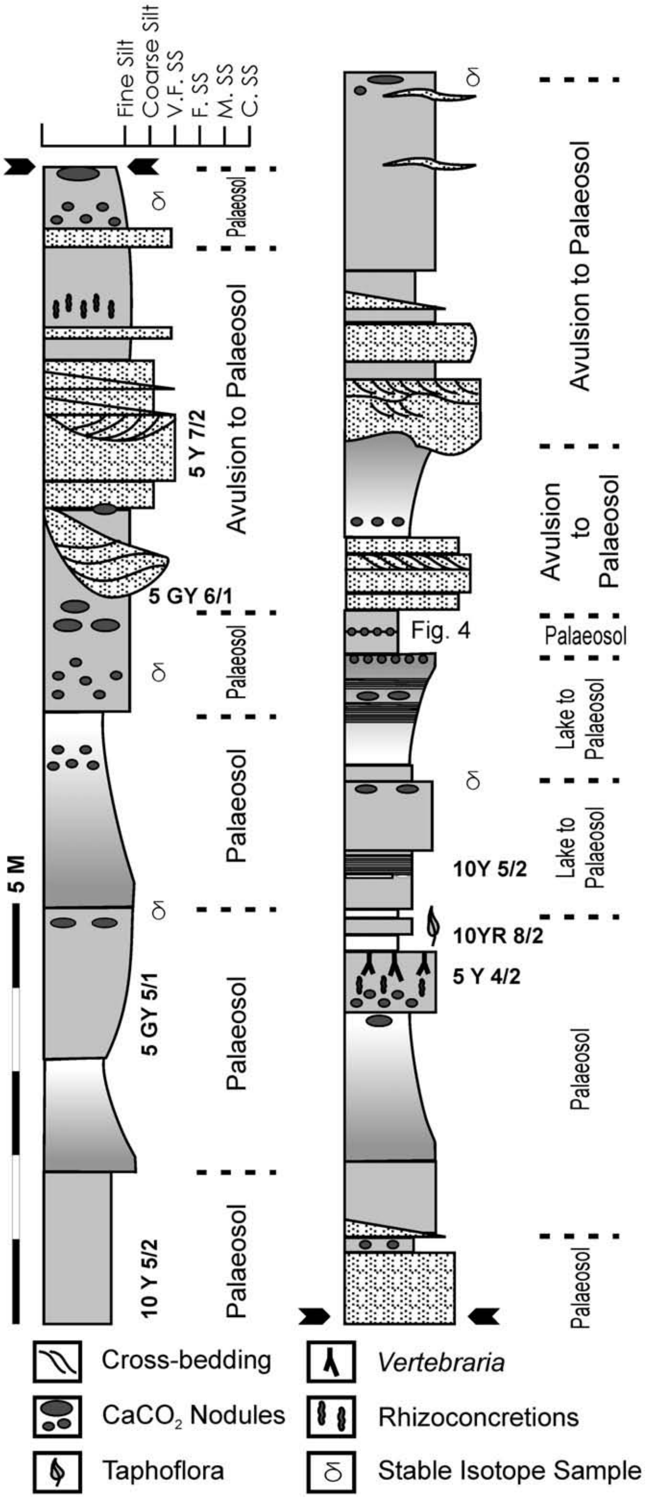


Fig. 3. Measured stratigraphic section along the R61 along side of which are interpreted depositional environments of each aggradational sequence. The plant-fossil assemblage preserved directly above a *Vertebraria*-rooted siltstone (palaeosol) is entombed in a yellow–white devitrified claystone. Additional floral elements also are preserved within a mixed siltstone and claystone lithology up to 40 cm above the contact with the palaeosol.

and New Wapadsberg Pass, respectively, and have been curated at the Albany Museum in Grahamstown, Eastern Cape Province. In a survey of the flora from both localities, all fossil fragments >1 cm in diameter, present on a random sample of bulk collected hand specimens, were identified and documented. This amounted to 3297 and 2184 entries from the New and Old Wapadsberg Pass localities, respectively (survey conducted by C.C. Labandeira and R. Prevec).

Palynomorphs were extracted from two samples from the New Wapadsberg Pass locality following standard palynological techniques, using HCl (30%), HF (40%), and $ZnCl_2$. One of the samples contained a relatively mature and corroded palynological assemblage. The sample was screened for identifiable palynomorphs. A quantitative analysis was not performed, as most palynomorphs were too damaged or thermally mature for identification beyond generic level. Photographs were taken with either a Leica DFC 320 digital camera mounted to a Leica DM LB2 microscope or a Nikon DXM1200F digital camera mounted to a Nikon Eclipse 80i microscope. Extended depth of field images were generated for specimens of variable height. A series of images was taken at focal planes at set intervals, after which MediaCy Image Pro software was used to extract the separate images for creation of a composite. The stacking of images sometimes generated visual artefacts. Sample residues and slides are housed in the Palaeobotanical Collections of the University of California Museum of Palaeontology, Berkeley, CA.

4. Lithostratigraphy and facies distribution

The uppermost Permian stratigraphic section at Old Wapadsberg Pass is reported to comprise interbedded olive-grey mudstone and sandstone (e.g., Ward et al., 2000, 2005) assigned to the Elandsberg Member. The plant-fossil-bearing bed lies near the base of a donga exposure that roughly parallels the R61 highway (Fig. 1B). The following description is based on the New Wapadsberg Pass R61 highway outcrop where the strata are best exposed, allowing for the fossiliferous interval to be placed into sedimentological context.

4.1. Lithofacies

4.1.1. Fine lithic wacke

Moderately sorted fine-grained wacke occurs in both lenticular and planar beds distributed within a predominantly siltstone succession. It is greenish (5GY 6/1) to yellowish-grey (5Y 7/2), weathering greyish orange (5YR 8/4), and containing subangular to subrounded quartz, feldspar, and lithic clasts that are moderately to well sorted. The wacke is silica-cemented, and beds are bounded by sharp contacts that may be erosional into underlying siltstone (Fig. 2). Primary structures include flow structures, trough cross beds, and small-scale ($A = 1$ cm; $\lambda = 12$ cm) asymmetrical and climbing ripples; uncommon soft-sediment deformational features include flame structures. Planar–tabular beds are most common, where lenticular sandstone beds in channel-form geometries may be interbedded with siltstone in an imbricate pattern.

4.1.2. Very fine wacke/coarse siltstone

The proportion of coarse silt and very fine sand grains in this lithofacies is difficult to distinguish because of the poor sorting and massive character of the beds. The lithofacies is olive-grey (5Y 6/1) to greenish-grey (5GY 6/1), silica-cemented, and may weather a yellowish-grey (5Y 8/4). It occurs in tabular or lenticular beds, the latter of which are at a low angle (3°–11°) to the underlying contact. Small, angular mud rip-up clasts of coarse sand size, along with mica flakes and disseminated organic matter, may be present. In general, primary structures are absent.

4.1.3. Homogenous siltstone

Massive siltstone units are dark greenish-grey (5GY 5/1) to greenish-grey (10Y 5/2) or olive grey (5Y 5/2), and vary from coarse to fine-grained, respectively. Siltstone is heavily weathered, resulting in a rubbly and blocky appearance, and some units contain carbonate concretions within ~0.5 m of the upper contact (Fig. 3). Siltstone units, ranging in thickness from <1 m to >2 m thick, fine upwards and generally exhibit sharp upper and lower contacts, although gradational contacts also are present. Vertically oriented rhizoconcretions are preserved in one siltstone unit, whereas large, *in situ* rooting structures assignable to *Vertebraria*, and smaller roots are restricted to the siltstone directly beneath the preserved megaflora. These roots and rootlets extend downwards for 60 cm.

Carbonate nodules are greyish-red (10 R 4/2) in colour, and vary in size from 3 cm to >100 cm in diameter. Concretions generally occur along individual stratigraphic horizons across the outcrop, and are cemented to varying degrees. In some instances, vertical roots served as the nucleating biomass around which the concretion formed (Fig. 4), whereas other concretions show no evidence of roots. Two horizons, above the level of the fossil flora, preserve root-nucleated spherical nodules that are spaced evenly across the outcrop (Figs. 3, 4).

Results of stable-isotope analyses on calcite cements from carbonate concretions (Table 1) indicate that δ^{13}C values range from −9.17 to −14.4 PBD, whereas δ^{18}O values range from 8.33 to 14.00 SMOW. A bivariate plot of δ^{13}C vs. δ^{18}O values shows that all nodules cluster within the same broad field, indicating that precipitated calcite cements have the same origin (Fig. 5).

4.1.4. Thinly laminated siltstone

One coarse siltstone unit is distinguished in the R61 section by its greyish olive (10 Y 5/2) colour and thin, horizontal lamination (Figs. 2, 3). Parallel laminations, averaging 2 mm in thickness, continue across the extent of the outcrop and are interrupted by a horizon across which carbonate concretions occur. Individual beds show internal fining-upward trends from coarser to fine silt-sized clasts. There is no evidence for either bioturbation or soft-sediment deformation.

4.1.5. Claystone

Three thin, very pale orange (10 YR 8/2) silty claystone beds occur above a well developed, rooted siltstone; in addition, claystone clasts up to 6 cm in diameter are dispersed throughout the rooted siltstone. Each claystone bed is no more than a few centimetres thick, without discernible primary structures. The lowest bed pinches out eastward, while the second bed can be traced across the outcrop (Fig. 2A). The macrofloral assemblage is preserved within these lowermost lithologies, and the intervening siltstone bed. In thin section, this lithology contains no obvious relict primary structures, and the fine-grained clasts consist of fibrous minerals with low bi-refringence. Several haematized bands and some post-depositionally filled fractures exist. Mineralogically, the claystone is devitrified and consists of clay minerals. A third bed occurs at the contact between the thinly laminated siltstone facies and the underlying siltstone bed. The bed is continuous to the east of the outcrop, but becomes partitioned into ball-like structures westward.

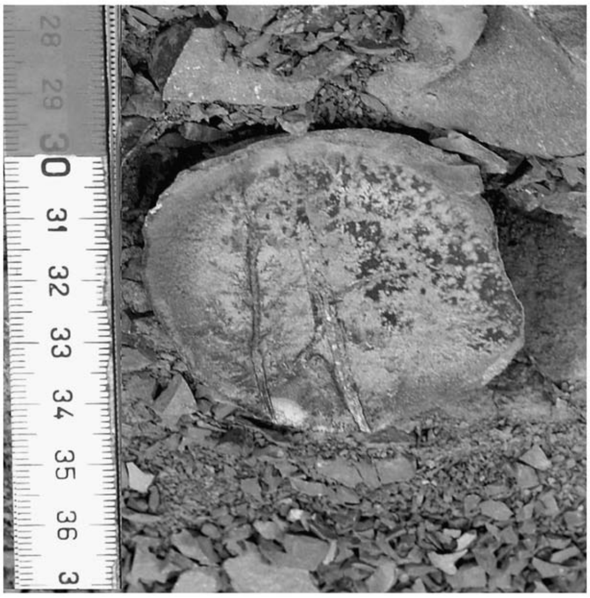


Fig. 4. Spherical carbonate-cemented concretion, in which vertical rooting structures are preserved, are derived from 3 m above the megafloral assemblage. See Fig. 3 for stratigraphic position of the specimen.

Table 1
Stable-isotope values for calcite cements within carbonate concretions from strata along Highway R61 that are directly below and above the New Wapadsberg Pass plant-fossil assemblage.

Sample	Stratigraphic position (m)	δ^{13}C (PDB)	δ^{18}O (PDB)	δ^{18}O (SMOW)	wt.% Calcite
21606-9a	4.6	−12.5	−21.7	8.54	35.5
21606-9b	4.6	−13.3	−21.9	8.33	39.2
21606-10	8.6	−14.4	−16.4	14.11	38.6
21606-11	14.2	−14	−22	8.33	43
Plant-fossil assemblage					
21606-12a	22.4	−12.5	−21.7	8.54	35.5
21606-12b	22.4	−10.7	−17.2	13.18	36.5
21606-13	30.6	−9.17	−20.5	9.78	13.7

The claystone also is present in exposures at Old Wapadsberg Pass, but varies in the number of beds and their geometries. Along a south–north transect, the claystone first is expressed as isolated millimetre-thick beds intercalated with and above the fossiliferous assemblage (S31 55.199′, E24 53.666′). Several tens of metres north (S31 55.108′, E24 53.692′), two distinct claystone beds occur in association with the plant-fossil assemblage in a similar relationship to that seen in the R61 exposure. Further west, the claystone is found at three stratigraphic levels (S31 54.983, E24 53.705). The lowest consists of a cm-thick bed that is continuous across the donga exposure, whereas the next two stratigraphically higher beds contain rounded claystone clasts (≥12 cm in longest dimension) within a siltstone matrix.

4.2. Interpreted sedimentary environments

The stratigraphic section exposed along the R61 highway and correlatives in the donga sections at Old Wapadsberg Pass record sedimentation within an overall aggradational landscape (e.g., Bull, 1991; Quirk, 1996). Massive siltstone intervals, in which rhizoconcretions, carbonate nodules, and/or *in situ* rooting structures occur, are

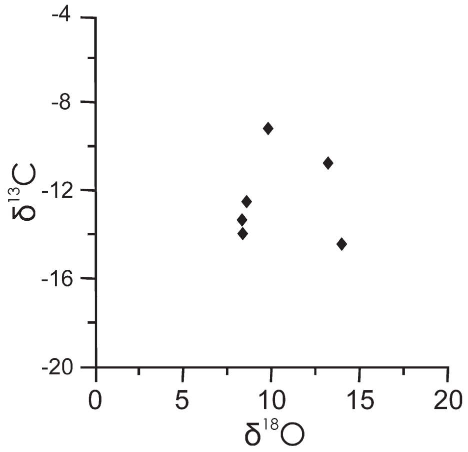


Fig. 5. Plot of stable carbon (δ^{13}C) and oxygen (δ^{18}O) isotopes from micrite within carbonate-cemented concretions recovered from this part of the section. See Fig. 3 for stratigraphic position of samples.

interpreted as poorly developed palaeosols (inceptisols — Mack et al., 1993; Kraus and Hasiotis, 2006; Fig. 3). Similar, poorly developed drab palaeosols with concretionary horizons have been reported elsewhere across the Karoo Basin and have been interpreted as entisols (Smith, 1995), inceptisols overprinted as gleysols (Gastaldo and Rolerson, 2008), nondescript drab soils (Smith and Botha, 2005; Botha and Smith, 2006), or calcisols (Bada soil type — Retallack et al., 2003). The nature of the palaeosol and whether or not the carbonate concretions formed in an open (calcisol) or closed (inceptisol, gleysol) atmospheric system only can be resolved using stable carbon-and-oxygen isotopes (Tabor et al., 2007). Although all Late Permian nodule-bearing soils previously are interpreted as having formed under increasingly arid climates (MacLeod et al., 2000; Ward et al., 2005), geochemical data now indicate that many formed under wetland conditions (Tabor et al., 2007; Gastaldo and Rolerson, 2008). Isotopic data for the nodule horizons in the present study (Fig. 5) indicate that carbonate precipitation occurred under closed atmospheric conditions within a wetland soil setting (for discussion see: Tabor et al., 2007). Hence, the R61 palaeosols represent interfluves or avulsion-channel fills (see below) that were in a non-steady state and subjected to high watertables at times when the landscape was in equilibrium (Bull, 1991; Gastaldo and Demko, in press). Additionally, several of these probably represent compound soils where overbank and/or crevasse sand and silt underwent weak pedogenic alteration in muddy interchannel areas of an avulsion belt (Knight et al., 2009).

Such vertically stacked, weakly developed palaeosols are separated by minimally weathered alluvium (Kraus and Aslan, 1999) as evidenced by little or no change in colour. The palaeosol over which the macrofloral assemblage is preserved shows a slight change in colouration over a 60 cm thick rooted interval. Near the base, the siltstone is dark greenish-grey (5GY 6/1) and lightens to an olive grey (5 Y 6/1) upwards to beneath a 10 cm interval in which roots, degraded axes, and decayed, but identifiable, *Glossopteris* leaves are preserved. Such downward changes in grey colouration have been interpreted in other terrestrial basins as indicating seasonal or periodic soil saturation, during which time cations are leached and concentrated at depth. Such downwards colour change reflects proximity to groundwater table (Kraus and Aslan, 1999). However, the presence of unaltered claystone clasts indicates that the soil had not undergone multiple generations of colonization wherein all sediment types would have been homogenized. Hence, this interval is interpreted as an inceptisol.

Overbank sedimentation and crevasse or avulsion events that resulted in interfluvial deposition are marked by planar tabular and thin lenticular, very fine-grained sandstone and coarse siltstone that exhibit ribbon geometries (Kraus and Davies-Vollum, 2004). These either are interbedded within the generally fine-grained palaeosols or act as the base of fining-upward sequences (Figs. 2, 3). Several sandstones pinch out within the palaeosols, and possess flat-lying basal contacts or show little erosional incision into the underlying mudrock. These lithologies contain disseminated organic material together with hydrodynamically equivalent mica flakes and other minerals. They are overlain by coarse-to-fine siltstone, and many of these mudrocks have undergone pedogenic alteration (Fig. 2).

Stacked palaeosols in this part of the Wapadsberg Pass succession (Fig. 2) are interrupted by a few episodes of landscape degradation that are marked by erosional contacts of channel-form sandstone and mixed sandstone-and-siltstone bodies. There was minimal effect on the landscape as evidenced by the shallow depth (1 m) to which the erosional contact impacted the underlying mudrock. Late Permian fluvial regimes of the Karoo Basin are described as large, meandering river systems (Smith, 1995; Ward et al., 2000; Gastaldo et al., 2005) with trunk channel depths approaching 25 m or more (Prevec et al., 2009). Channel-form geometries in this part of the section do not approach these magnitudes, attaining thicknesses of only a few metres (Fig. 3). As such, the erosional-based sandstones with overlying siltstones are interpreted as avulsion-channel fill sequences that subsequently were colonized by plants and altered to soils. This is evidenced by the presence of carbonate nodular horizons (Kraus and Hasiotis, 2006) in the upper parts of the mudrock intervals.

The thinly laminated siltstone facies that overlies the entombed fossiliferous litter (O-horizon) reflects a different depositional environment to the rest of the succession. The presence of millimetre-scale bedding and a fining-upwards signature in many individual beds showing no evidence of bioturbation or soft-sediment deformation indicate that this mudrock interval represents suspension-load sedimentation in a quiet water setting. Flat-lying bedding, the absence of fossils, and the overall geometry of the unit negate the possibility that these represent fluvial point-bar deposits. Rather these features are similar to those reported for other upper Permian laminated siltstones (e.g., Selover and Gastaldo, 2005) and are interpreted as lake-bottom deposits. The absence of bioturbation either parallel to or across bedding indicates that bottom conditions did not support life, either due to anoxia at depth or as a function of high sediment load precluding colonization. Evidence exists for overall drying of this water body followed by pedogenic alteration. At two stratigraphic horizons (Fig. 2) this interval contains regularly spaced, carbonate concretions in which vertical roots are preserved (Fig. 4), indicating plant colonization and a reversion to a subaerial environment.

5. Palaeontology

5.1. Plant taphonomy

Both aerial and subterranean macroplant parts are preserved within the fossiliferous interval, with concentrated aerial debris found at the contact between a rooted palaeosol and overlying claystone and siltstone. The plant assemblage in the palaeosol consists of vertically oriented roots up to 2 cm wide together with interspersed fine (mm-scale) rootlets that crosscut the siltstone matrix. Root penetration exceeds 0.6 m in depth, and degraded flat-lying, prostrate axes of uncertain affinity (aerial or subterranean) are common. A 10-cm thick zone at the top of the palaeosol includes well-preserved *Vertebraria* axes and degraded, but identifiable, glossopterid leaves and aerial axial remains (Fig. 6B). Degraded aerial axes and glossopterid leaves also are preserved in the 8-cm thick claystone that overlies this horizon. A concentrated heteromeric (Krassilov, 1975) assemblage of stems, glossopterid leaves, sphenopsid axes with attached leaf whorls, reproductive structures, and insect remains, occurs in the overlying 3–12 cm of pale olive-grey siltstone. Mats of *Trizygia*, consisting of axes with attached leaves together with isolated leaf whorls, occur in the donga sections within this interval. *Trizygia* whorls are, however, very rare in the R61 section. Identifiable plant parts become dispersed within the matrix a few centimetres higher in the section; further upsection only dispersed organic clasts are found in the massive siltstone. Glossopterid leaves in the lower part of the siltstone interval were found, in places, to be concentrated in troughs of mesoscale bedforms (Fig. 6A) indicating water-borne sediment and phytoclast transport. There is a change in the sedimentological character 0.5 m above the plant-bearing interval where mm-scale laminations occur and reflect accumulation under standing water (lake) conditions.

Glossopterid leaves, axial, and sphenophyll remains generally lie parallel to bedding and are prostrate. In some instances, they are preserved inclined to bedding and several leaves were found to be recumbent in a c-shaped cross-sectional configuration. The quality of preservation increases upsection from the contact between the claystone and underlying palaeosol into the more massive siltstone. Claystone matrix occurs between each leaf in the lowest interval, indicating that this sediment covered and infilled inter-leaf voids over a short time interval. The best preserved aerial debris is found in the overlying siltstone where there is more matrix between plant parts.

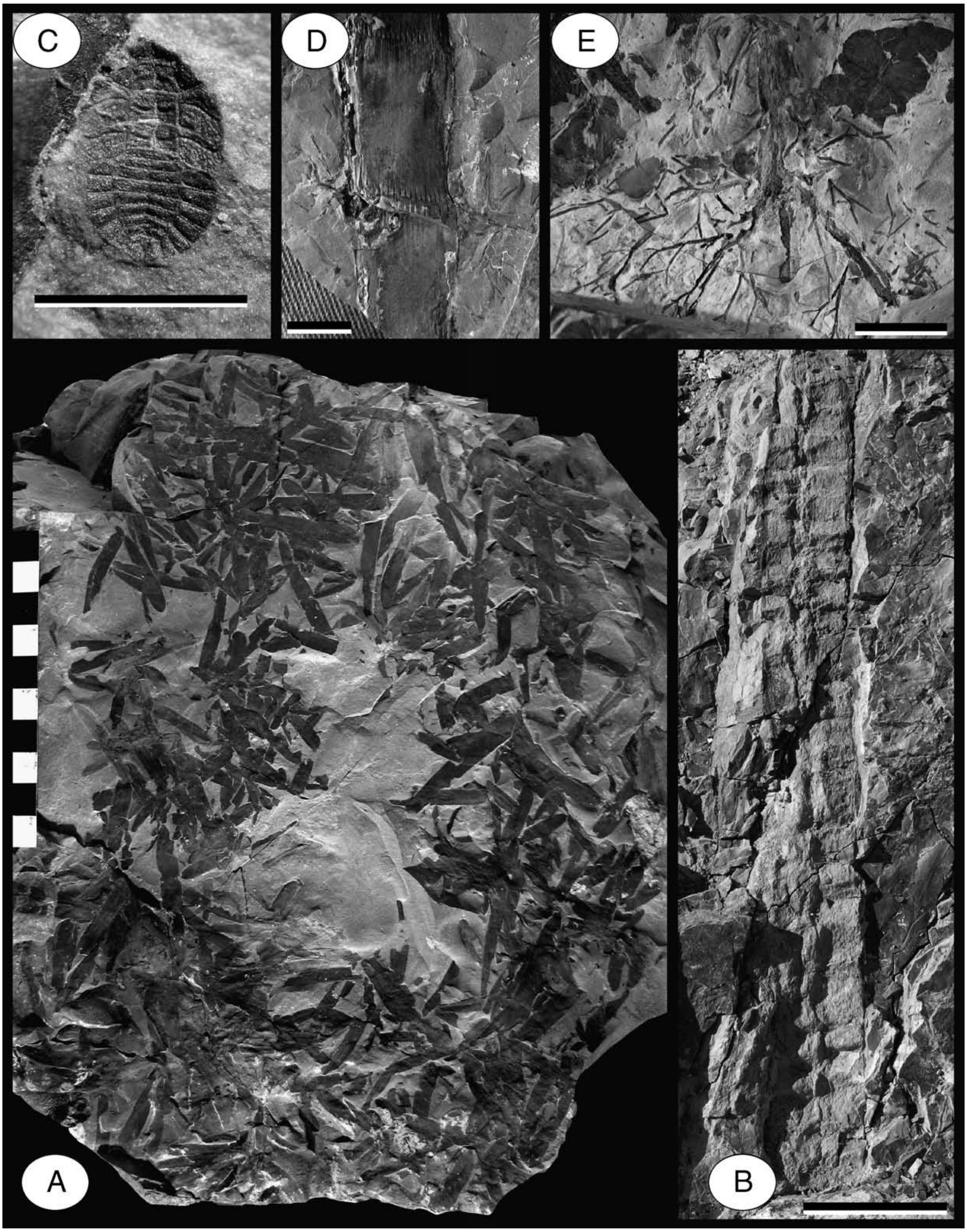


Fig. 6. Taphonomic and palaeontologic attributes of the fossiliferous interval. (A) Bedding surface of specimen recovered at New Wapadsberg Pass with unaligned leaves of *Glossopteris* W1, concentrated in mesoform troughs (scale bar = 10 cm). (B) A large *Vertebraria indica* axis in the New Wapadsberg Pass palaeosol (field photograph; scale bar = 5 cm). (C) Hemipteran nymph from New Wapadsberg Pass (WN 360a; scale bar = 2 mm). (D) An axis of *Paracalamites australis* with rootlets originating from nodes (WO 136; scale bar = 10 mm). (E) A small axis from which a mass of fine rootlets has developed (WO 170a; scale bar = 10 mm).

The stratigraphic interval in which decayed and degraded plant parts occurs, at the interface between the rooted palaeosol and the overlying claystone, is interpreted to represent the original O-horizon of a weakly developed soil. As such, the macroflora is autochthonous, and represents one of the few Late Permian *in situ* forest litters identified in Gondwana (see: Taylor et al., 1992). In contrast, the palynological assemblage likely includes not only autochthonous pollen and spores that originated from the local flora, but also distinctive allochthonous elements that reflect the composition of the regional (extrabasinal) flora. The claystone, isolated within and overlying the palaeosol is an allogenetic unit consisting of fluvially-derived silt and volcanoclasts (tuffite) that were transported into the area, burying both the prevailing groundcover and plant organs derived from the surrounding vegetation (Fig. 6A). The rate of sedimentation exceeded that of organic decay, preserving these plant parts in fine detail. Additionally, a rise in regional watertable accompanied the burial of the plant detritus protecting it from decay and loss from the potential palaeobotanical record (DiMichele and Gastaldo, 2008; Gastaldo and Demko, in press).

5.2. Palaeobotany

The Wapadsberg Pass flora is represented by a low-diversity assemblage including glossopterid leaves, fertile organs and roots, and two sphenopsid taxa (Fig. 7).

5.2.1. Glossopteridales sensu Pant 1982

Only two *Glossopteris* morphotypes are recognised, although there are more subtle variations within these groups that may necessitate further refinement of this classification. Morphometric analysis indicates that the majority of leaf morphotypes fall within the microphyll leaf-size category as defined by Webb (1955), although some exceptional specimens of morphotype W2 reach the very uppermost limits of this size category as defined by leaf area.

Glossopteris morphotype W1 (Fig. 8G, H, L) generally is the smaller and more common of the two morphotypes representing 65% of Glossopteris leaves recorded at New Wapadsberg, and 82% at Old Wapadsberg (Fig. 7; Prevec and Labandeira, unpub. data). It is 50–85 mm long, 4–8 mm wide with a length:width ratio approaching 9. It has a narrowly oblong to oblanceolate shape, gently tapering at the apex to an acute rounded tip; the base is long and cuneate. The midrib is narrow but well defined, comprising several distinct, medio-longitudinal, parallel veins, and is persistent to the apex. Veins depart from the midrib at a steep angle (10°–18° to the midrib) then arch gently to the margin (25° to 35° to the midrib), and produce one to two anastomoses from midrib to margin. Marginal vein density is approximately 22 veins per 10 mm, and mesh width is consistently 0.3–0.4 mm from midrib to margin. Meshes are narrowly polygonal to trullate near the midrib, becoming narrowly falcate across the lamina.

Glossopteris morphotype W2 (Fig. 8I, J) has an observed width of 8–23 mm, and a length ranging from approximately 60 to over 120 mm, although the fragmentary nature of the specimens examined precluded confident length estimates. Length to width ratio is approximately 5. This elongate elliptical to narrowly oblong morphotype has an acute apex, tapering to a pointed tip, and a long, gradually tapering, cuneate base. The midrib is narrow but persistent to the apex with individual veins clearly defined. Veins depart from the midrib at a steep angle (15° to 25°) and then arch gently to the margin at 40° to 60° to the midrib, following a more moderate angle near the margin (65°–75°). Marginal vein density ranges from 28 to 34 per 10 mm, and veins anastomose two to three times from midrib to margin. In the medial portion of the leaf, mesh widths range from a maximum of 0.4–0.5 mm wide proximal to the midrib, becoming narrower towards the margin, where they are generally 0.2–0.3 mm wide. The meshes lie parallel to the long axis of the leaf and are elongate polygonal immediately adjacent to the midrib, becoming elongate elliptical to linear across the lamina.

Glossopteris W2 tends to be larger than W1, with venation that arches less steeply across the lamina, and with meshes that are broader adjacent to the midrib and in the mid-laminar region than near the margin. W2 is elongate elliptical rather than oblong–oblanceolate as in W1.

Both *Glossopteris* W1 and W2 fall within the morphological ranges accommodated by Anderson and Anderson (1985) within their concept of *Lidgettonia*, which includes those leaves consistently associated with *Lidgettonia* spp. fructifications. This leaf type is small, long and narrow with fine, gently arching venation and a moderately well-defined and persistent midrib. It is the most

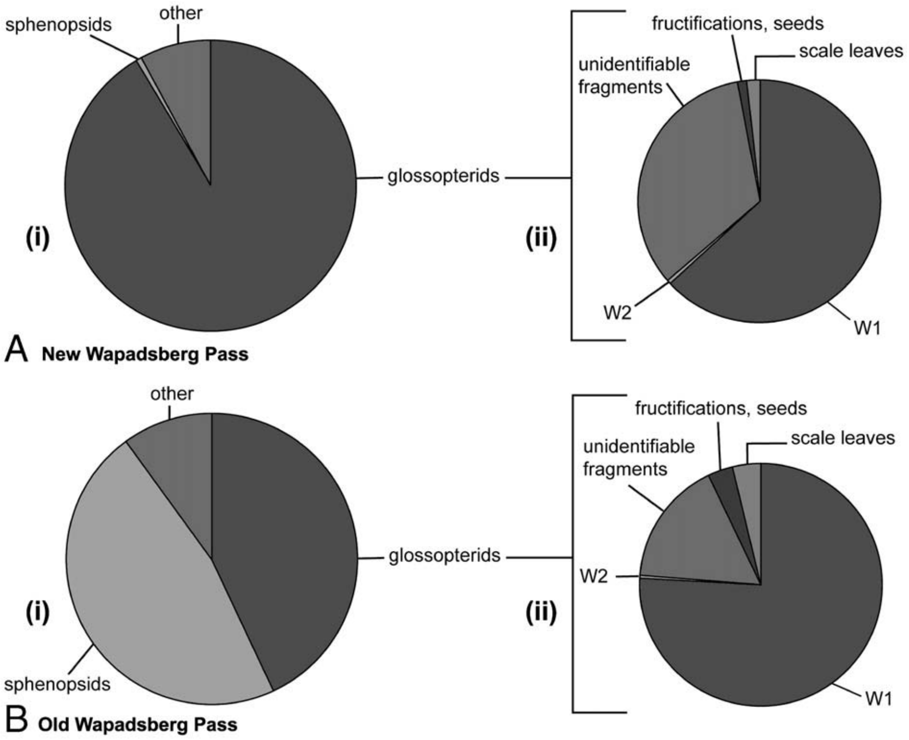


Fig. 7. Composition of floras from A: New Wapadsberg Pass, and B: Old Wapadsberg Pass. Figs A (i) and B (i) illustrate proportions of floral elements present in a survey of over 3000 and 2000 bulk-collected specimens, respectively, and A (ii) and B (ii) provide a breakdown of the glossopterid elements at each site. Sphenopsids = *Trizygia speciosa*, *Phyllotheca africana*, *Paracalamites*; Other = unidentifiable axes and fragments, roots, ferns, and ?lycopsids.

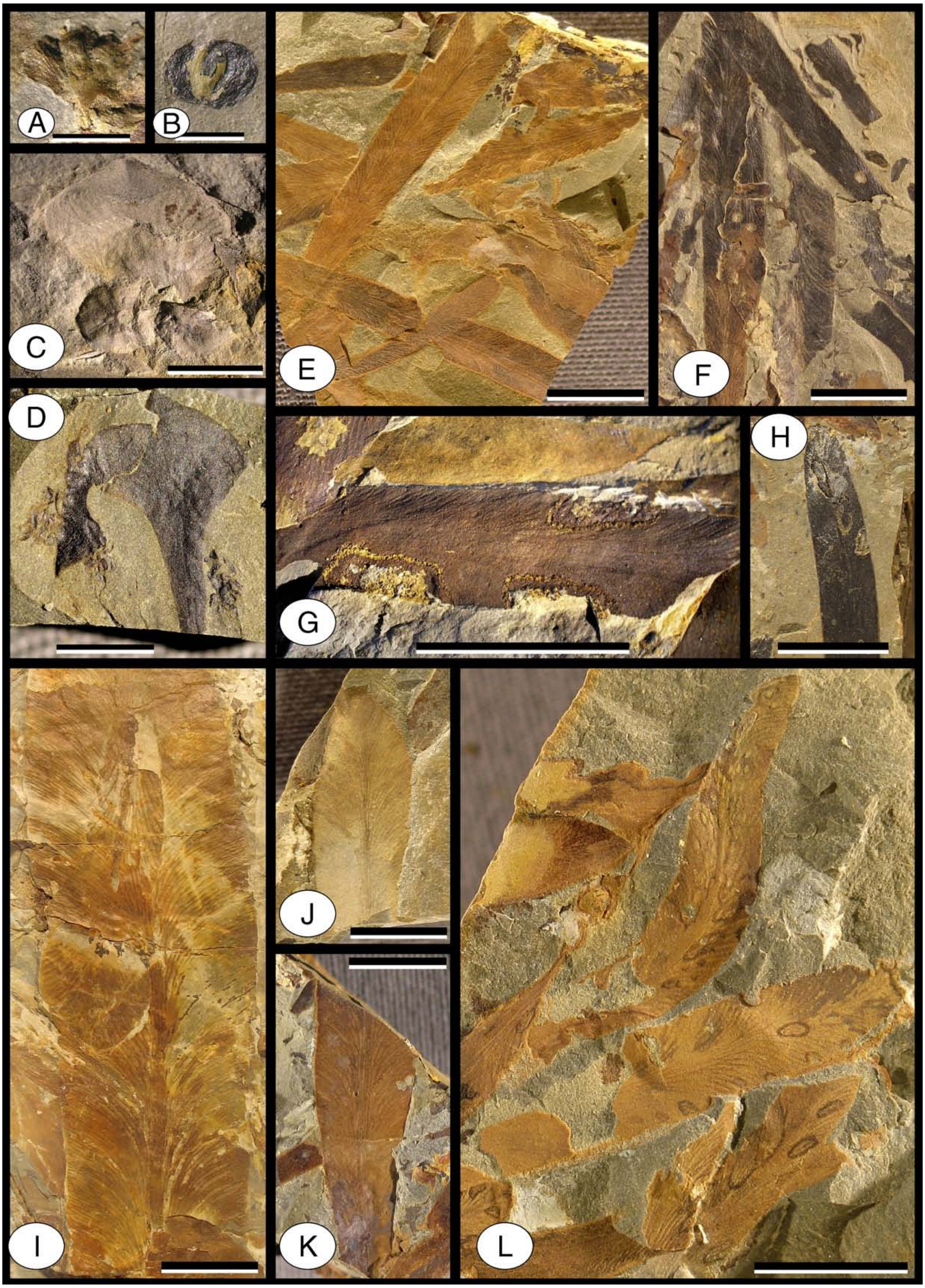


Fig. 8. Glossopterid organs recovered from the New and Old Wapadsberg Pass localities. (A) Isolated capitula of *Lidgettonia africana* (WN 106a; scale bar = 2 mm). (B) Samaropsoid seed (WN 37; scale bar = 5 mm). (C) A scale leaf of *Lidgettonia africana* with two closely associated capitulae (WN 319a; scale bar = 5 mm). (D) Two scale leaves of *Eretmonia natalensis* with closely associated clusters of *Arberiella* pollen sacs (WN 70b; scale bar = 5 mm). (E) *Glossopteris* W1 (WN 107b; scale bar = 1 cm). (F) *Glossopteris* W1 (scale bar = 1 cm). (G) *Glossopteris* W1 with three rectangular margin feeding traces; note the well-defined reaction rims (WN 127c; scale bar = 1 cm). (H) An apical portion of *Glossopteris* W1 on which three oviposition scars occur, each scar exhibits a prominent reaction rim (WN 46c; scale bar = 1 cm). (I) *Glossopteris* W2 illustrating is the largest specimen of this morphotype found, to date. (J) *Glossopteris* W2 (WN 101; scale bar = 1 cm). (K) *Glossopteris* W2 (WN 112c; scale bar = 1 cm). (L) Typical examples of *Glossopteris* W1 leaves with evidence of insect damage (WN 108a; scale bar = 1 cm).

broadly occurring and, in many cases, the dominant leaf form in Late Permian assemblages in the Normandien (previously Estcourt) Formation in KwaZulu-Natal (Anderson and Anderson, 1985; Prevec et al., 2009).

Although morphotype W1 does not deviate radically from other lidgettonioid forms collected in South Africa, it lies at one end of an apparent size continuum. An average example of W1 would lie within the minimum size range for lidgettonioid leaves from Late Permian assemblages, such as that from Inhluzani (see Anderson and Anderson, 1985). *Glossopteris* W2, which is considerably less common than *Glossopteris* W1 (comprising <1% of floral elements recorded at both New Wapadsberg Pass and Old Wapadsberg Pass; Prevec and Labandeira, unpub. data; Fig. 7), is comparable to some of the leaves incorporated within *L. lidgettonioides* as defined by Anderson and Anderson (1985), and lies more within the size ranges typical of this leaf form in other Late Permian assemblages.

The lidgettonioid affiliations of the *Glossopteris* leaves are supported by the presence of *Lidgettonia africana* capitula (Fig. 8A, C). These fertile glossopterid organs, found isolated or in close association with scale leaves, are approximately 3 mm in diameter, with a central receptacle 1.8 mm wide, and a gently scalloped peripheral wing, approximately 1 mm wide, with at least 5 wing segments. Seed scars are 0.4 mm in diameter. These capitula fall comfortably within the circumscription the taxon (Adendorff, 2005).

Frequently associated with *Lidgettonia* are specimens of the glossopterid pollenate organ *Eretmonia natalensis* du Toit emend. Lacey et al., 1975, and both isolated and clustered *Arberiella* sp. pollen sacs (Fig. 8D) occur. *Eretmonia* is a typical component of Late Permian floras in South Africa (Lacey et al., 1975; Anderson and Anderson, 1985; Bordy and Prevec, 2008; Prevec et al., 2009).

Platyspermic, samaropsoid seeds with conspicuous lateral wings were recovered (Fig. 8B). These are typical of the seed type found attached to *Lidgettonia* capitula at other South African localities (Anderson and Anderson, 1985; Prevec et al., 2009). The seeds are 2×3 mm in size, with lateral wings that are 0.6 to 0.8 mm wide and contracted at both micropylar and chalazal ends. The sclerotesta is ovate, 1.4 mm wide and 1.8 mm long, with truncate or slightly recessed micropylar and chalazal ends.

Vertebraria indica Royle 1834 axes, the unmistakable rooting structures characteristic of the *Glossopteris* plant, are abundant at the New Wapadsberg Pass locality. The jointed, chambered, aerenchymatous roots reached 40 mm in diameter, and cross-cut bedding planes (Fig. 6B).

5.2.2. Equisetales

Phyllotheca australis Brongniart 1828 emend. Townrow 1955 is a common element in Late Permian floras of South Africa, and is broadly distributed across Gondwana (Pant and Kidwai, 1968; McLoughlin, 1992; Rayner, 1992; Anderson and Anderson, 1985). Many isolated leaf whorls of *P. australis*, and examples of consecutive leaf whorls attached to axes, were recovered primarily from the Old Wapadsberg Pass locality (Fig. 9A, E), although the foliage of this taxon represented less than 1% of the floral elements surveyed from both the Old and New Wapadsberg Pass localities (Prevec and Labandeira, unpub. data). The narrow, strap-shaped leaves with tapering, pointed apices and a single midvein, are fused proximally into a funnel-shaped sheath. The morphotaxon *Paracalamites australis* Rigby 1966 is common at both localities and represents the leafless stems or rhizomes of *Phyllotheca australis*. Numerous *Paracalamites australis* axes occur associated with fine masses of rootlets; in some cases rootlets are attached to the axes at nodes (Fig. 6D).

5.2.3. Sphenophyllales

The Old Wapadsberg Pass flora is characterised by an unprecedented abundance of well-preserved foliar shoots of *Trizygia speciosa* Royle 1840 emend. Pant and Mehra 1963 (Fig. 9C, D, E), comprising over 40% of floral elements at the site (Prevec and Labandeira, unpub. data). This sphenophyllalean taxon is found mainly in the Late Permian of India (Maheshwari, 1968; Pant and Mehra, 1963), Australia (McLoughlin, 1992), and the Middle and Late Permian of southern Africa (Lacey et al., 1975; Anderson and Anderson, 1985; Rayner and Coventry, 1985). It is a typical, but rare, element of the Normandien (previously Estcourt) Formation floras of KwaZulu-Natal.

Slender, longitudinally striated axes are expanded at nodes bearing bilaterally symmetrical leaf whorls. Leaf whorls comprise three pairs of unequal, oblanceolate leaves with entire margins. The leaf whorls of trizygioid sphenophylls appear to lie parallel or subparallel to the axis, suggesting that these may have been prostrate, creeping, groundcover plants (Galtier and Daviero, 1999).

This apparently delicate sphenopsid is not abundant at other South African sites and, in most cases, specimens are represented by individual leaf whorls or, at most, two or three foliar whorls attached to a stem. However, at the Old Wapadsberg Pass locality, *T. speciosa* is the dominant floral element, and shoots with over five whorls attached to a single axis are common (Fig. 9D, E). Additionally, over 20 sphenopsid cones were found in close association (Fig. 9B) and may represent the first recorded fertile structures of *T. speciosa*, although organic attachment has not yet been demonstrated. The cones and associated foliage will be detailed elsewhere.

5.3. Palynology

5.3.1. Palynological assemblage

The New Wapadsberg Pass palynological assemblage, characterized by taeniate and alete bisaccates and acavate spores, is of average diversity when compared to coeval assemblages (Fig. 10). Most multitaeniate pollen grains are damaged and/or have detached sacci, and are difficult to differentiate even at the generic level. The majority of multitaeniate grains are small (40 µm wide); several are assignable to *Protohaploxypinus limpidus* (Fig. 10P) and *Striatopodocarpites cancellatus* (Fig. 10Q). Larger forms include *Protohaploxypinus goraiensis* (Fig. 10K). Common elements are taeniate bisaccates including *Lueckisporites virkkiae* (Fig. 10I), *Guttulapollenites hannonicus* (Fig. 10M), *Lunatisporites noviaulensis* (Fig. 10O) and *L.* cf. *pellucidus* (Fig. 10J), and taeniate asaccate *Weylandites lucifer* (Fig. 10M). *Alisporites tenuicorpus* (Fig. 10 A–B) is the most common non-taeniate bisaccate. Less abundant are cf. *Chordasporites* (Fig. 10H), *Klausipollenites schaubergeri* (Fig. 10C), cf. *Hamiapollenites* (Fig. 10D), *Falcisporites stabilis* (Fig. 10F) and *F. australis* (Fig. 10E). Abnormal forms of *A. tenuicorpus* are found frequently, those of *K. schaubergeri* are more rare (Fig. 10B–C). The aberrances include trisaccate (Fig. 10C) and tetrasaccate (Fig. 10B) pollen grains, or clusters of normal looking pollen with exoexine connections, or combinations of these (Fig. 10B). Two spore types are common: oval forms with conspicuous ridges (*Columinisporites* sp. cf. *C. peppersii*; Fig. 10R), and smooth, rounded forms (tentatively assigned to *Calamospora*). In addition to palynomorphs, small cuticle fragments, the most recognizable of which have sinuous epidermal cell walls (Fig. 10S), are assignable to *Trizygia* (see below).

5.3.2. Botanical affinities

The pollen record is consistent with macrofloral observations of a low-diversity glossopterid-dominated woodland with an understory of sphenophytes, but also indicates the presence of a variety of other gymnosperms, peltasperms, corystosperms and conifers that are not represented in the autochthonous macrofossil record of New Wapadsberg Pass. Monosaccate pollen, cavate spores characteristic of lycopsids, and acavate spore types representing ferns are not present.

In Gondwana, several morphospecies of the dispersed pollen genera *Protohaploxypinus* and *Striatopodocarpites* are associated with glossopterids (Balme, 1995; Lindström et al., 1997). These

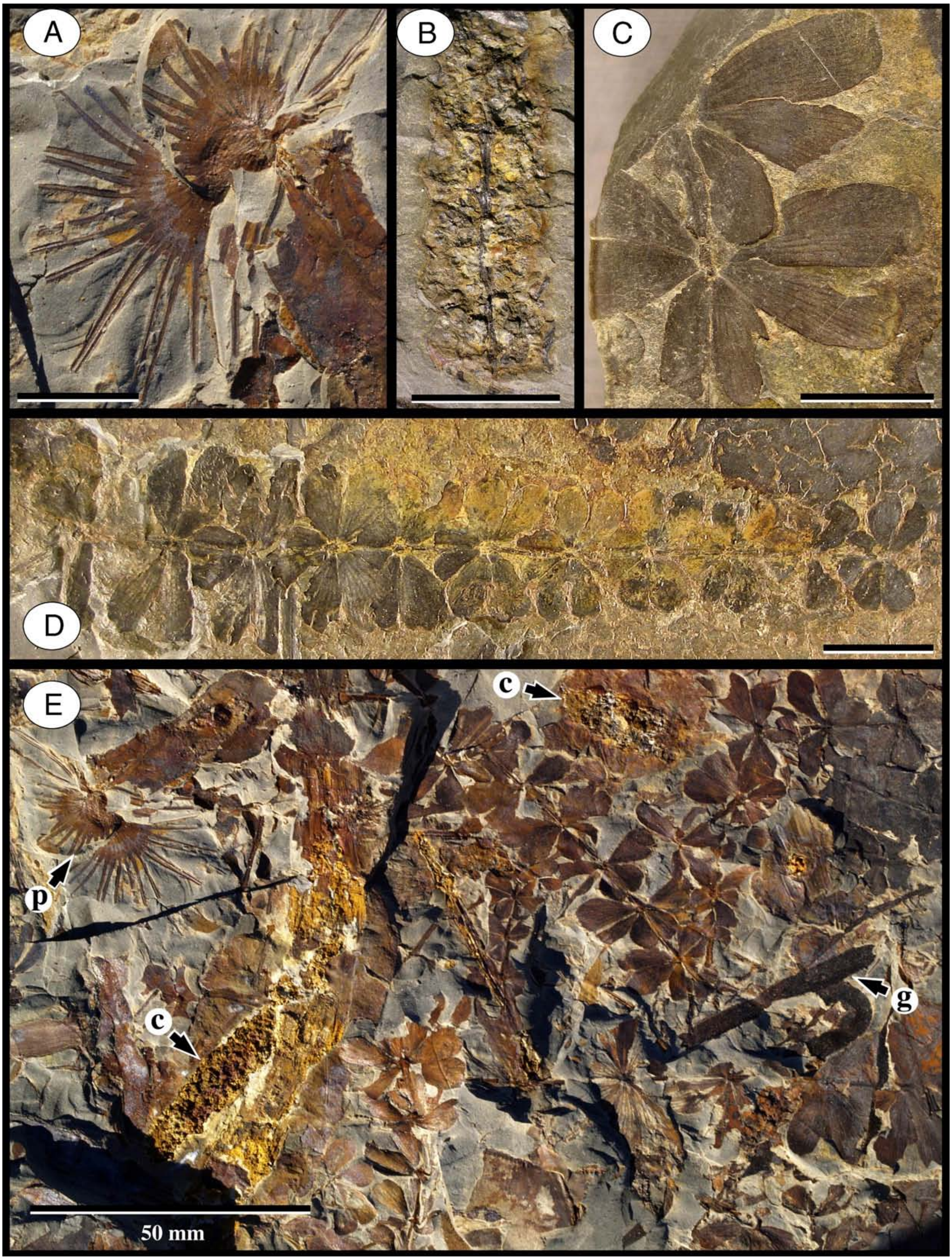
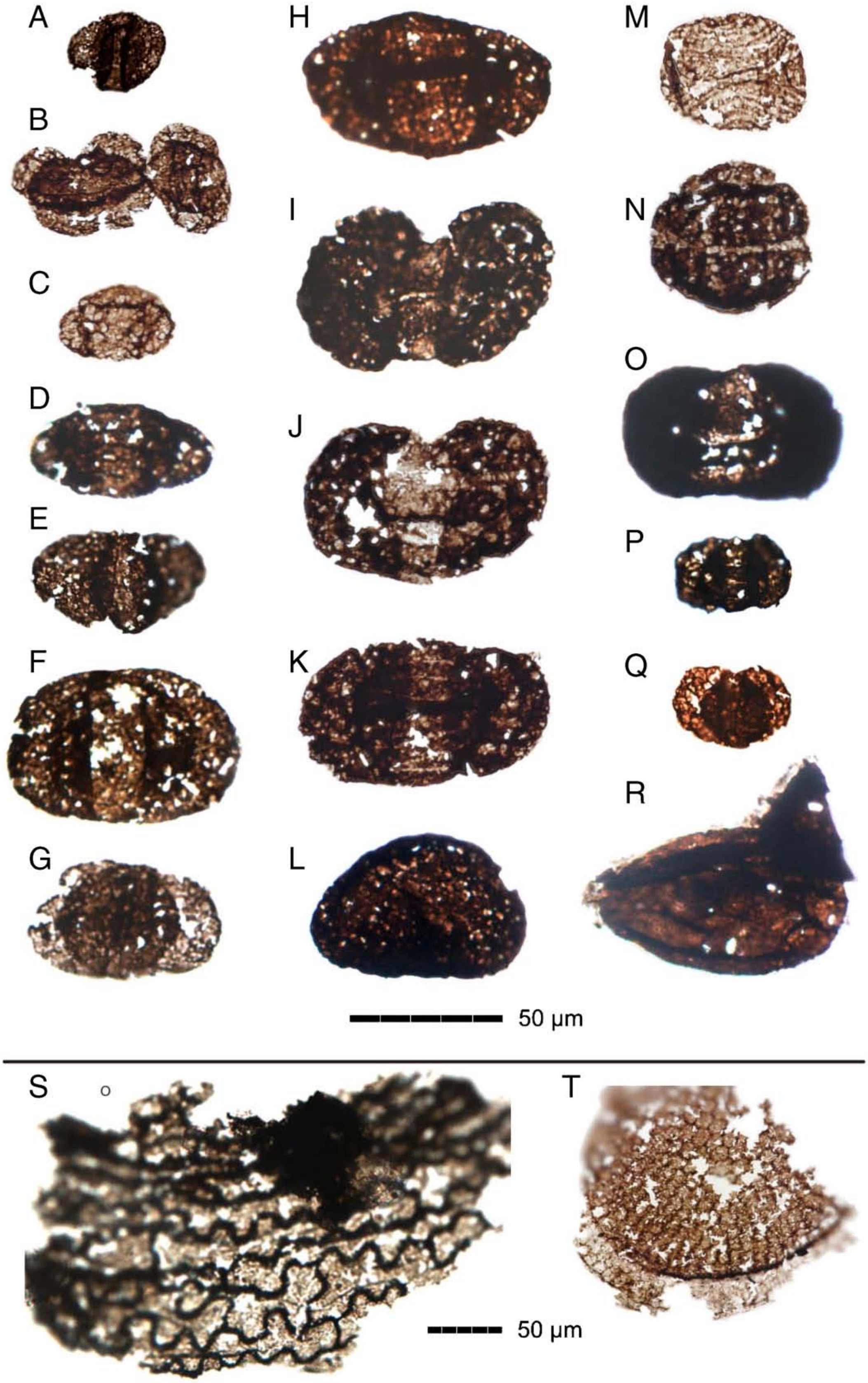


Fig. 9. Sphenopsid taxa recovered from donga sites at Old Wapadsberg Pass. (A) Two foliar whorls of *Phyllotheca australis* illustrating the long, narrow leaves with pointed apices, fused proximally into a funnel-shaped sheath (WO 102; scale bar = 1 cm). (B) One of many sphenopsid cones in association with *Trizygia speciosa* (WO 16a; scale bar = 1 cm). (C) Foliar whorls of *T. speciosa* exhibiting three pairs of unequal leaves with a simple, dichotomous venation pattern (WO 12a; scale bar = 1 cm). (D) An exceptionally long foliar shoot of *T. speciosa*, with 11 attached leaf whorls (WO 12a; scale bar = 1 cm). (E) Multiple foliar shoots of *T. speciosa* associated with sphenopsid cones, *Paracalamites australis* axes, *Phyllotheca australis* and *Glossopteris* morphotype W1 (WO 102; c — sphenopsid cones; p — *Phyllotheca australis*; g — *Glossopteris* W1).

multitaeniate bisaccate pollen grains have been found *in situ* in sporangia of *Arberiella* (Zavada, 1991; Pant and Nautiyal, 1960; Lindström et al., 1997), pollen sacs morphologically identical to those found in attachment to a range of purported glossopterid pollen organs including *Eretmonia* (Surange and Chandra, 1975). Together, *P. limpidus* and *S. cancellatus* may represent one or more of the glossopterid leaf morphotypes. These taxa are the haploxylonoid and diploxylonoid multitaeniate forms known from *A. africana*-type sporangia (Lindström et al., 1997). The multitaeniate asaccate taxon *Weylandites* is known from the synangium *Rugatheca*, a pollen organ with a possible glossopterid affinity (Pant and Basu, 1977; Balme, 1995).



Taeniate bisaccate *Lueckisporites* and *Lunatisporites* pollen were likely to have been produced by peltasperms and conifers, taxa not represented in the macroflora. *Lueckisporites* is known from the Euramerican conifer family Majonicaceae (Clement-Westerhof, 1987). It is uncertain which plants produced the bulk of Gondwanan *Lunatisporites* forms, but small amounts of pollen assignable to this dispersed form-genus are reported from glossopterid pollen sacs (Zavada 1991; Lindström et al., 1997). The affinities of plants that produced *Hamiapollenites* and *Chordasporites* are unknown. Dispersed alete bisaccate pollen, such as *Falcisporites* and *Alisporites*, represent peltasperms or corystosperms (Zavada and Crepet, 1985; Balme, 1995; Lindström et al., 1997). *Falcisporites* occurs *in situ*, in the microsporangiate organ *Pteruchus* (e.g. Zavada and Crepet, 1985; Balme, 1995; Taylor et al., 2006). This fertile organ, known from Triassic floras of India, South Africa, Antarctica, and Australia, is attributed to the corystosperm *Dicroidium* (Balme, 1995; Taylor et al., 2006). Long considered to have been restricted to the Triassic (Retallack, 1995), this widespread Gondwanan taxon recently was reported from the Upper Permian strata of Jordan (Kerp et al., 2006), and the female fructification *(Umkomasia)* from Late Permian deposits in India (Chandra et al., 2008). The dispersed pollen taxon *Falcisporites australis* is associated with the peltasperm *Lepidopteris callipteroides*, known from the Lower Triassic deposits of Antarctica and Australia (Retallack, 2002; Lindström et al., 1997). *Alisporites* is reported from *Autunia conferta,* a Euramerican Permian peltasperm, and voltzian conifer cones (Balme, 1995). The parent plant of *Alisporites tenuicorpus* is unknown. To date, peltasperms, corystosperms, and conifers are not documented, with certainty, from Late Permian Karoo Basin macrofloras (Gastaldo et al., 2005 report a possible peltasperm from Carlton Heights). Therefore, the pollen types from Wapadsberg Pass are either allochthonous elements, representing extrabasinal gymnosperms, or indicative of plant groups known from the basin but to which they have hitherto not been associated.

Two dispersed spore types, *Columinisporites* and *Calamospora*, both are associated with Equisetopsida (Balme, 1995). *Calamospora* originated from sporangia of Equisetales and Sphenophyllales, and could represent both *Phyllotheca australis* and *Trizygia speciosa*. *Columinisporites* is one of the three other spore genera known to have been produced by members of the Sphenophyllales (Balme, 1995). In addition to these spores, the assemblage contains small fragments of relatively well-preserved cuticles. The most characteristic cuticles have epidermal cells with sinuous cell walls, and are identical to those described from Indian specimens of *Trizygia speciosa* Royle (*Sphenophyllum speciosum*; Pant and Mehra, 1963; Maheshwari, 1968).

5.3.3. Age interpretations

An age assessment for the New Wapadsberg Pass assemblage is based on a comparison with the Australian palynostratigraphic zones which serve as the standard biostratigraphic classification for the southern hemisphere (Fig. 11). These biozones are defined according to the first or consistent appearance of spores and pollen taxa in Western (e.g., Helby et al., 1987; Mory and Backhouse, 1997) and Eastern Australian basins (e.g., Foster, 1982; Price, 1997). These zones are calibrated against independently dated marine invertebrate zones (Foster and Archbold, 2001; Metcalfe et al., 2008), carbon-isotope stratigraphy, and radio-isotopic dates (Metcalfe et al., 2008), although the latter are yet to be published. The comparison of the present assemblage with Australian palynozones is based on overall species associations and the relative proportions of major spore-and-pollen groups.

A floral turnover and excursion in δ^{13}C kerogen, corresponding to the end-Permian biotic crisis, is reported within the basal part of *P. microcorpus* and APP6 Zones of Western and Eastern Australia (Metcalfe et al., 2008). Recent studies by Thomas et al. (2004) and Metcalfe et al. (2008) place the PTB within the lower part of the succeeding *Lunatisporites pellucidus* and APT1 Zones (Fig. 11). In general, assemblages dominated by taeniate bisaccates (e.g., *Protohaploxypinus* and *Striatopodocarpites*) are characteristic of the Late Permian in Gondwana. The *Protohaploxypinus microcorpus* Zone in Western Australia has been dated independently as Late (but not latest) Changsingian in age (Metcalfe et al., 2008). The APP6 zone, the interval between the oldest occurrences of the cavate spore *Triplexisporites playfordii* and pollen *Lunatisporites pellucidus,* is its Eastern Australian equivalent (Price, 1997). The APP6 zone is subdivided into subzones APP601 and APP602. A dramatic change from taeniate bisaccate-dominated assemblages to those characterized by alete bisaccates and cavate spores takes place within the basal part of the *P. microcorpus* Zone and the transition of the APP601 and APP602 subzones. High-resolution palynological records from Antarctica indicate that this palynological turnover indicates a stepwise extinction of characteristic Late Permian taxa (Collinson et al., 2006; Lindström and McLoughlin, 2007; Vajda and McLoughlin, 2007).

The basal parts of the *P. microcorpus* Zone and the APP601 subzone in Australia retain a high diversity and abundance of taeniate bisaccate pollen grains (e.g., *Protohaploxypinus limpidus*) and non-taeniate bisaccates (such as *Scheuringipollenites ovatus* = *Alisporites ovatus*). The assemblages from these stratigraphic intervals differ from the subjacent *Dulhuntyspora parvithola* and APP5 zones in that they contain the first occurrences of several acavate and cavate spores, and distinctive pollen (e.g., *Guttulapollenites* and *Weylandites*), that are consistently present. Generally, these assemblages are associated temporally with the last occurrences of typical Late Permian macrofloras. For example, Foster (1982) recorded assemblages of the APP601 subzone (or *Playfordiaspora crenulata* zone) co-occurring with the last known *Glossopteris*-dominated macrofloras in the Bowen Basin. The youngest Permian palynological assemblage with a similar composition from the basal Buckley Formation, Graphite Peak, Antarctica, was recorded less than 2 m below the last occurrence of *Vertebraria* fossils (Collinson et al., 2006). Hence, the presence of *P. crenulata* in the Antarctic record allows for correlation with the Australian assemblages. Lindström and McLoughlin (2007) described a comparable association from the last *Glossopteris*-bearing beds of the PTB section in the McKinnon Member, Prince Charles Mountains (PCM), Antarctica. Although indicator taxa for the AAP601 zone or its equivalent *(Playfordiaspora crenulata* Zone) were not encountered, the assemblages are dominated by taeniate bisaccates (*Protohaploxypinus* and *Striatopodocarpites*) and an alete bisaccate (*Scheuringipollenites*), as recorded by Collinson et al. (2006) at Graphite Peak.

The Western Australian *P. microcorpus* Zone and correlative Eastern Australian APP602 subzone are both defined as the interval between the first occurrences of *P. microcorpus* and *Lunatisporites pellucidus*, respectively (Foster, 1982; Mory and Backhouse, 1997;

Fig. 10. Selected pollen and spores from the New Wapadsberg Pass plant locality, Palingkloof Member, South Africa. Scale bar is 10 μm. Specimen names are followed by UCMP numbers, slide code and England Finder graticule coordinates. (A) *Alisporites tenuicorpus (*UCMP 398600, SA-NWP2.F, W25-2); (B) tetrasaccate *Alisporites tenuicorpus* (UCMP 398601, SA-NWP2.V U40-4); (C) trisaccate *Klausipollenites schaubergeri* (UCMP 398602, SA-NWP2.J, F43-2); (D) cf. *Hamiapollenites* (UCMP 398603, SA-NWP2.F, U28-2); (E) *Falcisporites australis* (UCMP 398604, SA-NWP2.A, T38-4); (F) *Falcisporites stabilis* (UCMP 398605, SA-NWP2.H, H33-1); (G) bisaccate indet. (UCMP 398606, SA-NWP2.H, H33-3); (H) cf. *Chordasporites* (UCMP 398607, SA-NWP2.A, U28-3); (I) *Lueckisporites virkkiae* (UCMP 398608, SA-NWP2.B, Z45-3); (J) *Lunatisporites* cf. *pellucidus* (UCMP 398609, SA-NWP2.N, O26-3); (K) *Protohaploxypinus goraiensis* (UCMP 398610, SA-NWP2.W, N41-4); (L) cf. bisaccate saccus (UCMP398611, SA-NWP2.F, J30-3); (M) *Weylandites lucifer* (UCMP 398612, SA-NWP2.K, B45-4); (N) *Guttulapollenites hannonicus* (UCMP 398613, SA-NWP2.L, B47-3); (O) *Lunatisporites* cf. *noviaulensis* (UCMP 398614, SA-NWP2.A, C25-4); (P) *Protohaploxypinus limpidus* (UCMP 398615, SA-NWP2KOH.A); (Q) *Striatopodocarpites cancellatus* (UCMP 398616, SA-NWP2.F, M27-1); (R) *Columinisporites* sp. cf. *C. peppersii* (UCMP 398617, SA-NWP2.A, E37-1); (S) cuticle of *Trizygia speciosa* with sinuous epidermal cell walls (UCMP 398618, SA-NWP2.D, N43-4); (T) unidentified palynomorph (UCMP 398619, SA-NWP2.K, P39-3).

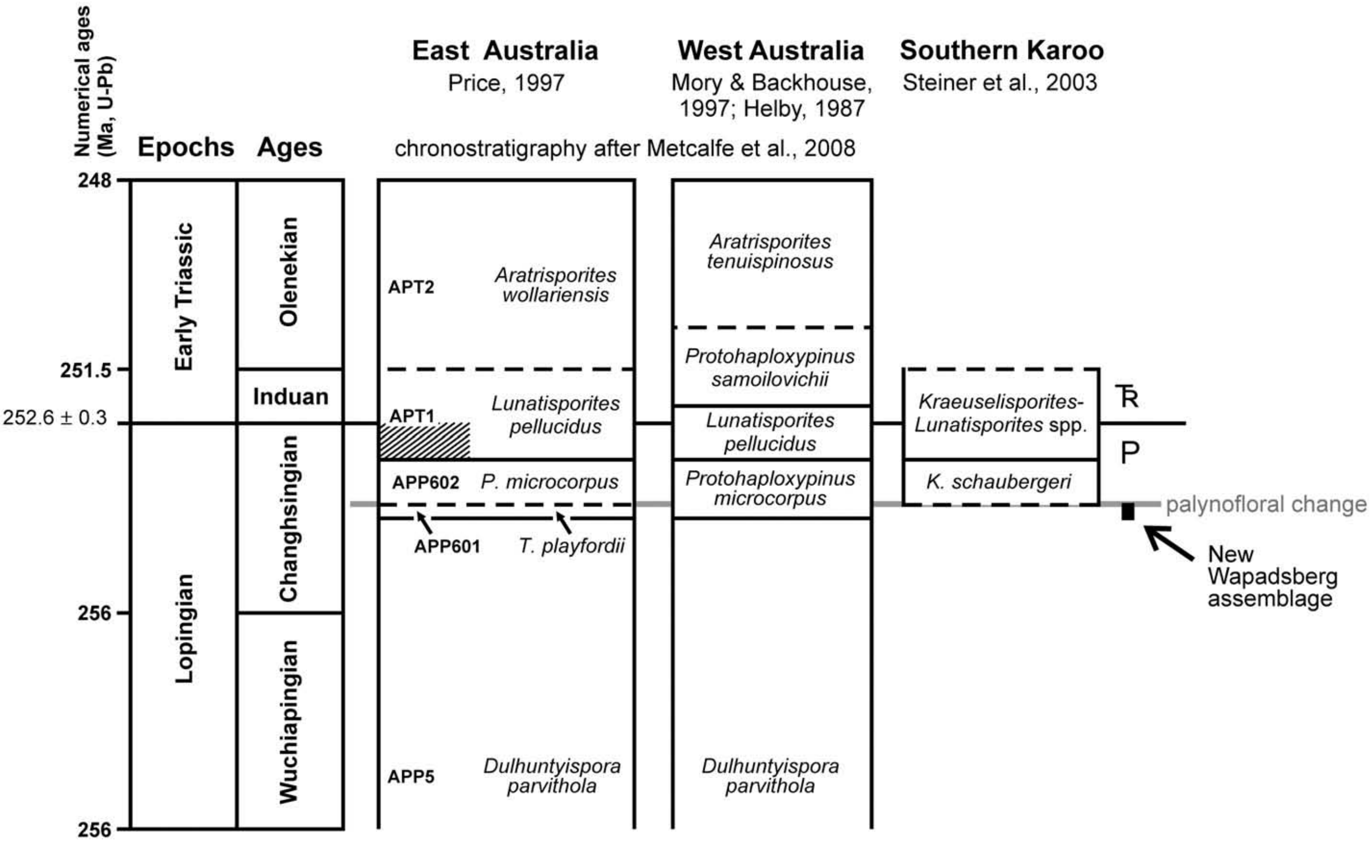


Fig. 11. The correlation of palynological assemblages of the Carlton Heights (Steiner et al., 2003) and the New Wapadsberg (this paper) localities to the Western (Price, 1997) and Eastern Australian (Mory and Backhouse, 1997; Helby et al., 1987) palynological zonation schemes. The top of the Western Australian *Dulhuntyspora parvithola*, and base of the *Protohaploxypinus microcorpus*, *Lunatisporites pellucidus*, and *Protohaploxypinus samoilovichii* Zones are independently dated (Foster and Archbold, 2001; Metcalfe et al., 2008). The dates of the Capitanian–Wuchiapingian and Wuchiapingian–Changsingian boundaries, and interpolated base of the Induan are from Mundil et al. (2004). The Olenekian (early Spathian) and Early–Middle Triassic age is from Ovtcharova et al. (2006). Palynostratigraphy partly after Lindström and McLoughlin (2007), chronostratigraphy after Metcalfe et al. (2008).

Price, 1997). Here, there is a decrease in abundance and diversity of taeniate bisaccates just above the boundary of the *P. microcorpus* Zone and at the base of the APP602 subzone. The number of multitaeniate bisaccate taxa (e.g., *Striatopodocarpites*) decreases, while taxa including *P. microcorpus*, *Lunatisporites noviaulensis*, and *Lueckisporites*, in addition to alete bisaccates (e.g., *Falcisporites*), assume dominance together with cavate (e.g., *Lundbladispora* and *Densoisporites*) and acavate spores. Collinson et al. (2006) described *P. microcorpus* Zone assemblages about 0.5 m below the last occurrence of *Vertebraria* fossils in the Buckley Formation, central Transantarctic Mountains, Antarctica. The palynofloral turnover in the Prince Charles Mountains is associated with the synchronous first occurrence of three Australian indicator taxa: *Triplexisporites playfordii*, *P. microcorpus*, and *L. pellucidus* (Lindström and McLoughlin, 2007). And, the palynoassemblage of the Richie Member, which succeeds the McKinnon Member, is characterized by an increasingly high abundance of (a) cavate spore and alete bisaccate taxa (i.e., *Falcisporites* spp.).

The first South African assemblage to be correlated with the *P. microcorpus* Zone was described from Carlton Heights in the southern Karoo Basin (Steiner et al., 2003). Their samples originated from an interval of interbedded siltstone and thin sandstone exposed along the railroad cut thought to be equivalent to the “event bed” (Ward et al., 2000). Recently, Gastaldo et al. (2005) and Gastaldo and Rolerson (2008) demonstrated that this interval lies beneath the highest stratigraphic position at which large nodular concretions occur above which the PTB is reported to lie (e.g., Ward et al., 2005). Hence, although Steiner et al. (2003) place their samples in the overlying Lower Triassic Katberg Sandstone, these samples originate from the Upper Permian Elandsberg Formation. Important taxa recognized in the *Protohaploxypinus*- and *Falcisporites*-dominated zone include the indicator taxon *P. microcorpus* and several cavate spore taxa (*Triplexisporites playfordii*, *Playfordiaspora crenulata*, *Guthoerlisporites cancellosus* [≈ *Playfordiaspora cancellosa*/*P. crenulata*; Raine et al., 2008], and *Densoisporites* spp.).

The Wapadsberg Pass assemblage is placed in a stratigraphic position corresponding to the subzone APP601 of Price (1997) and in the basal part of the *Protohaploxypinus microcorpus* Zone (Mory and Backhouse, 1997) based on (1) the dominance of characteristic Late Permian pollen taxa (i.e., *Protohaploxypinus* and *Striatopodocarpites*), (2) subordinate numbers of pollen taxa that become dominant in latest Permian and Triassic palynofloras (*Lunatisporites* and *Falcisporites*), and (3) the absence of large numbers of (a)cavate spores. The *Klausipollenites schaubergeri* Zone described from Carlton Heights (Steiner et al., 2003) represents a younger assemblage that can be assigned to the *P. microcorpus* and APP602 (sub)zones. Several poorly preserved pollen grains attributed to cf. *Lunatisporites pellucidus* are found in the New Wapadsberg Pass assemblage (Fig. 10J). Subordinate amounts of this latest Permian to Early Triassic indicator taxon and the APT1 Zone have been recorded in other *Protohaploxypinus*- and *Striatopodocarpites*-dominated Late Permian Karoo sequences (e.g., in Tanzania and Madagascar; Hankel, 1992), and also in the Late Permian of Australia (Foster, 1982).

Overall, this correlation supports a Late Changhsingian (late Lopingian) age assignment that is in accordance with the megafloral record. The relatively high amounts of abnormal pollen (*Alisporites* and *Klausipollenites schaubergeri*; Fig. 10B-C) support, indirectly, an age close to the end of the Permian. Unusual amounts of aberrant pollen have been reported previously from end-Permian localities in Russia (Nedubrovo) and north-west China (Dalongkou, Junggar Basin; Foster and Afonin, 2005). Surprisingly, the same pollen taxa (*Klausipollenites* and *Alisporites*) are affected in the South African assemblage, and the morphological deviations also are similar in nature (trisaccates, tetrasaccates, etc.). Abnormal forms are not restricted to pollen in this time interval; for example, lycopsid spores retained in tetrads have been recognized in several Permian–Triassic sequences (Visscher et al., 2004; Looy et al., 2005). These morphological aberrations in taxonomically unrelated groups, gymnosperms and lycopsids, have been attributed to environmental stress associated with atmospheric perturbations close to the end of the Permian (Visscher et al., 2004; Foster and Afonin, 2005).

5.4. Invertebrates

Several burrows attributable to the broadly defined ichnotaxon *Planolites* (B. de Klerk pers. comm. 2007) occur within the fossiliferous horizons at Old Wapadsberg Pass. Two specimens of unidentified invertebrates, conforming to previously reported conchostracans from the Normandien Formation (Van Dijk, 2000), also were recovered at New Wapadsberg Pass.

Rare Permian insect fossils have been reported previously from the Ecca Group in the southern Karoo Basin. These include specimens from the Whitehill (McLachlan and Anderson, 1977; Oelofsen, 1981; Geertsema and van den Heever, 1996) and the Laingsburg formations (Geertsema and Van Dijk, 1999). However, the insect fossils identified here are the first reported from the Late Permian *Dicynodon* Assemblage Zone of the Beaufort Group in this part of the basin which is in contrast to the wealth of insect remains collected from the same biozone in the Normandien Formation of KwaZulu-Natal (Riek, 1973, 1974, 1976; Van Dijk, 1998; Van Dijk and Geertsema, 1999).

The Wapadsberg Pass locality has yielded several insect-body fossils (Fig. 6C), including a hemipteran nymph (Fig. 6C; C. Labandeira, pers. comm. 2007). This immature form is similar to a stenorrhynchian nymph found recently at the Late Permian Clouston Farm locality in KwaZulu-Natal (Prevec et al., 2009), and is comparable to several specimens recorded from the Normandien Formation (Riek, 1974, 1976; van Dijk, 1981).

The flora records extensive evidence of utilisation by insects as both a food source and reproductive platform, manifested as a profusion of oviposition scars (Fig. 8H, L) and feeding traces (Fig. 8G). A detailed study of the insect fauna and plant–insect interactions is underway (Labandeira and Prevec, unpub. data), and will fill an important gap in our knowledge of trophic relationships during this critical time period.

6. Discussion

Although Late Permian floras have been documented from numerous localities in the northeastern parts of the Karoo Basin (Lacey et al., 1975; Anderson and Anderson, 1985), poor chronostratigraphic and lithostratigraphic constraints have precluded precise placement of these floras within a biostratigraphic framework. In other parts of the basin, where more precise stratigraphic placement is possible through a constructed vertebrate biozonation in conjunction with limited chronometric data, only sparse and poorly preserved plant-fossil material has been documented. The apparent dearth of a palaeobotanical record in the very latest Permian has been attributed to regional extirpation and extinction of vegetational cover in response to the Permian/Triassic extinction event (Ward et al., 2000), although recent work has demonstrated an absence of consistent lithostratigraphic criteria that can be used to identify that event anywhere in the Karoo Basin (Gastaldo et al., 2009). Rather, a change in the physico-chemical conditions requisite for plant preservation (DiMichele and Gastaldo, 2008; Gastaldo and Demko, in press) in this part of the section is a more likely explanation for the absence of a record (Gastaldo et al., 2005) as opposed to a catastrophic floral extinction event. Hence, the present report of a well-preserved Changhsingian plant-fossil assemblage, constrained palynologically, as well as the identification of a more poorly preserved macroflora some 65 m upsection (Gastaldo et al., 2005), indicate the potential for the existence of other assemblages near the vertebrate-defined PTB that previously have been overlooked.

The occurrence of an *in situ* forest-floor (O-horizon) litter above a mineral substrate (non-peat) soil is highly unusual for the Karoo Basin. To date, our understanding of Late Permian South African floras is based almost entirely on parautochthonous assemblages within oxbow-lake deposits (e.g., Lacey et al., 1975; Anderson and Anderson, 1985; Gastaldo et al., 2005; Prevec et al., 2009), or allochthonous assemblages within point-bar and other barform deposits within fluvial channels (e.g., van Dijk, 1998; Anderson and Anderson, 1985; Gastaldo et al., 2005). Although palaeosols are recognized throughout the fully continental stratigraphic record beginning in the Middle Permian Beaufort Group (e.g., Smith, 1995; Retallack et al., 2003; Smith and Botha, 2005; Gastaldo and Rolerson, 2008), few autochthonous assemblages have been identified (Bordy and Prevec, 2008) probably due, in part, to a lack of awareness and documentation of the taphonomic factors associated with fossil floras examined in the past.

The latest Permian at Wapadsberg Pass provides a snapshot of a low-diversity flora comprising exclusively gymnospermous (glossopterid) and sphenopsid taxa. The inferred growth habits of the glossopterids include arborescent trees (e.g., Gould and Delevoryas, 1977; Retallack and Dilcher, 1981; Pigg and Taylor, 1993), shrubs (e.g., White, 1986; Retallack and Dilcher, 1988), and even woody climbers (Pant, 1999) that lost their leaves on a periodic basis (Rees et al., 2002). The absence of preserved erect stems or axes in the limited available exposures precludes an assignment of either *Glossopteris* morphotype to a specific growth habit. However, the presence of woody axes >10 cm in diameter and the large size of the *Vertebraria* roots associated with leaves at both New and Old Wapadsberg localities may indicate that some of the *Glossopteris* plants were larger than small shrubs. At present, *Phyllotheca* is considered similar in its growth strategy to other equisetaleans. Upright axes, with whorled leaves restricted to nodes, originated from a subterranean rhizome imparting an herbaceous growth habit to the r-strategist groundcover (Rayner, 1992). Although the growth habit of *Trizygia* has not been confirmed, it is probably similar to the scrambling growth habit inferred by Galtier and Daviero (1999) for *Sphenophyllum oblongifolium* and other Late Palaeozoic sphenophyllaleans (Gastaldo et al., 2004). The uncommon occurrence of *Trizygia* throughout Gondwana (Srivastava and Rigby, 1983; Anderson and Anderson, 1985) may be due to the occupation of a groundcover niche, with representation of the taxon in parautochthonous lake assemblages (Gastaldo et al., 2005) the result of liana-like growth. Hence, based on the present collections, the Late Permian landscape in this part of the Karoo Basin consisted of a canopy and possible understory dominated by gymnosperms that was underlain by sphenopsid groundcover.

There may be several separate or related explanations to account for the low systematic Changhsingian diversity, often attributed to a drying trend in the Late Permian (Ward et al., 2000; Retallack et al., 2003). First, the assemblage characteristics may be a function of the sample size recovered from limited exposure. In total, the collection represents approximately an area of 1.5 m^2 due to outcrop logistics. Low systematic diversities are common when “single hole” collections have been compared across space (Ellis et al., 2003) and time (Wing and DiMichele, 1995). Secondly, the diversity in this part of the Eastern Cape Province may be a function of regional variation related to localized edaphic (i.e., wetland soils, soil fabric, nutrient availability) or short-term climatic conditions prevailing at the time of growth and entombment (DiMichele and Gastaldo, 2008). Lastly, the documented composition may be a function of longer-term trends that influenced the systematic makeup of the Late Permian landscape leading up to the extinction of these taxa within the Karoo Basin.

The microphyllous nature of *Glossopteris* leaves in this part of the succession has been used to infer a physiological response of these gymnosperms to changing climates in the latest Permian. For example, Anderson and Anderson (1985) and McLoughlin et al. (1997) proposed that a reduction in leaf size among glossopterids near the end of the Permian, observed in at least some parts of Gondwana, may have been a response to an overall climatic warming and drying. This also was adopted by Retallack et al. (2003) who asserted a causal relationship with the end-Permian extinction. However, attributing the reduction in leaf-size to long-term climatic effects, alone, may be inappropriate in the case of South Africa and elsewhere because these communities grew in localized wetland soils located within floodplains (Tabor et al., 2007; Prevec et al., 2009). The results of stable isotopic analyses presented herein also confirm wetland conditions for much of the Wapadsberg section. A reduction in leaf size may have been in response to the presence of a high water table during the growing season (Kozlowski, 1984), particularly if there was a high concentration of available iron in an impoverished soil and/or if the plants were Fe-sensitive taxa (Fe toxicity; Snowden and Wheeler, 1995).

Although the Late Permian floras of KwaZulu-Natal are known from numerous localities (Anderson and Anderson, 1985), the stratigraphical and temporal relationships between these sites are obscure, mainly because of poor lateral continuity stemming from an abundance of Jurassic dolerite intrusives and associated faulting (Anderson and Anderson, 1985; Gastaldo et al., 2005). Currently, there are insufficient data to adequately distinguish between floral variations attributable to differences in regional and localised habitat, as opposed to temporal changes related to broader phenomena such as climate perturbation and evolutionary change. The rarity of plant-fossil assemblages close to the vertebrate-defined PTB (Ward et al., 2005) compounds the difficulties in recognising reliable floral trends in the prelude to the reported end Palaeozoic terrestrial mass extinction event. Hence, it is not possible at this time to comment on whether plants in South Africa mirror the apparently step-wise pattern of vertebrate extinctions (Ward et al., 2005) as is reflected in palynological studies from Australia and Antarctica (Collinson et al., 2006; Lindström and McLoughlin, 2007; Vajda and McLoughlin, 2007). Because the Wapadsberg flora may reflect the diversity within a localised habitat, extreme caution should be exercised in elevating these observations to the status of a regional or hemispherical climatic and diversity trend. Only more comprehensive and wide-range sampling of latest Permian floras, combined with appropriately detailed taphonomic and lithostratigraphic data, can allow for more confident assessments of the floral changes below the presently recognized terrestrial PTB.

7. Conclusions

An autochthonous leaf litter and root-bearing palaeosol, in which both macro- and microfossil assemblages are preserved ~70 m below the vertebrate-defined Permian–Triassic boundary at Wapadsberg Pass in the Eastern Cape Province, allows for a Changhsingian age assignment correlative with palynozones in Eastern (Price, 1997) and Western (Helby et al., 1987; Mory and Backhouse, 1997) Australia. It is the youngest autochthonous plant-fossil assemblage documented in Gondwana, to date. The low-diversity macroflora consists of both groundcover (*Trizygia*) and subaerial (*Glossopteris*, *Phyllotheca*) vegetation. The plants are preserved in an O-horizon of a weakly developed palaeosol entombed by overbank or avulsion deposits, in which devitrified volcanic ash occurs. This palaeosol is one in an aggradational sequence of palaeosols, many of which retain geochemical evidence for pedogenesis under high watertable conditions (see: Tabor et al., 2007; Gastaldo and Rolerson, 2008).

The fossil assemblage exhibits several unique ecological aspects of the latest Permian landscape. There is evidence for a profusion of insect-mediated damage to diminutive *Glossopteris* leaves, and these modifications are associated with the first insect-body fossils found in the *Dicynodon* zone of the southern Karoo Basin. The microphyllous (sensu Webb, 1955) nature of the *Glossopteris* leaves may have been a physiological response to climate perturbation or waterlogged edaphic conditions where high Fe^{+} was available in the pore waters. The new assemblage extends the known geographical distributions of several South African macrofloral taxa including *Lidgettonia africana*, *Eretmonia natalensis*, *Trizygia speciosa*, and lidgettonioid *Glossopteris* leaves. The palynological spectrum includes taxa (e.g., *Lunatisporites* cf. *pellucidus*) previously recognized as indicative of the Early Triassic, but recently recognized as extending down into the Late Permian (Metcalfe et al., 2008). As in other reported palynological assemblages preserved in close proximity to the PTB (e.g., Looy et al., 2005), there is a high proportion of abnormal pollen grains in this assemblage. Whether or not such diminution in leaf size and associated pollen-grain abnormalities is a function of conditions leading up to the end of Phanerozoic extinction is not known at this time.

Acknowledgements

The authors would like to thank the following individuals: Phillip and Stella Loock of Quaggasfontein for kindly providing us access to their property at Old Wapadsberg Pass (Farm no. 79); Dr. Neil Tabor, Southern Methodist University, Dallas, TX, for stable-isotope analyses and meaningful discussion about the significance of the results; Dr. Conrad C. Labandeira for his collaboration on quantifying and assessing the floral composition and insect damage types; Dr. Stephen A. Prevec, Rhodes University, for field assistance; Dr. Billy de Klerk and the Albany Museum, Grahamstown, for the use of curatorial and storage facilities; Hester and J.P. Steynberg, Ganora Guest Farm, Nieu Bethesda, for their hospitality and assistance. This research was supported, in part, by: the Council for Geosciences, Pretoria; Rhodes University, Grahamstown; the Department of Geology Endowment funds at Colby College; NSF EAR 0417317 to RAG; and NSF EAR 0230024 to Hallie J. Sims, Marion K. Bamford, and Conrad C. Labandeira; ETE funding from the Department of Palaeobiology, USNM-Smithsonian Institution, Washington, DC; and the National Research Foundation (African Origins Grant, UID: 65241) (R. Prevec). This is ETE publication 182.

References

Adendorff, R. 2005. A revision of the ovuliferous fructifications of glossopterids from the Permian of South Africa. Ph.D. thesis (unpub.), University of the Witwatersrand, Johannesburg, 241 pp.

Adendorff, R., McLoughlin, S., Bamford, M.K., 2002. A new genus of ovuliferous glossopterid fructifications from South Africa. Palaeont. afric. 38, 1–7.

Adendorff, R., Bamford, M.K., McLoughlin, S., 2003. Liknopetalon: a review of a rare gondwanan, Permian pteridophyte. Rev. Palaeobot. Palynol. 126, 83–101.

Anderson, J.M., Anderson, H.M., 1985. Palaeoflora of southern Africa. Prodomus of South African megafloras. Devonian to Lower Cretaceous. Rotterdam, Balkema, 423 p.

Anderson, A.M., McLachlan, I.R., 1976. The plant record in the Dwyka and Ecca Series (Permian) of the South-Western Half of the Great Karroo Basin, South Africa. Palaeontol. Africana 19, 31–42.

Balme, B.E., 1995. Fossil *in situ* spores and pollen grains: an annotated catalogue. Rev. Palaeobot. Palynol. 87, 81–323.

Bordy, E.M., Prevec, R., 2008. Sedimentology, palaeontology and palaeoenvironments of the Middle (?) to Upper Permian Emakwezini Formation (Karoo Supergroup, South Africa). S. Afr. J. Geol. 111, 429–456.

Botha, J., Smith, R.M.H., 2006. Rapid vertebrate recuperation in the Karoo Basin of South Africa following the End-Permian extinction. J. Afr. Earth Sci. 45, 502–514.

Bull, W.B., 1991. Geomorphic Responses to Climatic Change. Oxford University Press, Oxford, UK. 326 pp.

Cairncross, B., 2001. An overview of the Permian (Karoo) coal deposits of southern Africa. J. Afr. Earth Sci. 33, 529–562.

Chandra, S., Sing, K.J., Jha, N., 2008. First report of the fertile plant genus *Umkomasia* from Late Permian beds in India and its biostratigraphic significance. Palaeontology 51, 817–826.

Clement-Westerhof, J.A., 1987. Aspects of Permian palaeobotany and palynology, VII. The Majonicaceae, a new family of Late Permian conifers. Rev. Palaeobot. Palynol. 52, 375–402.

Collinson, J.W., Hammer, W.R., Askin, R.A., Elliot, D.H., 2006. Permian–Triassic boundary in the central Transantarctic Mountains, Antarctica. Geol. Soc. Am. Bull. 118, 747–763.

Craig, H., 1957. Isotopic standards for carbon and oxygen and correction factors for mass-spectrometric analysis of carbon dioxide. Geochim. Cosmochim. Acta 12, 133–149.

DeKock, M.O., Kirschvink, J.L., 2004. Paleomagnetic constraints on the Permian–Triassic boundary in terrestrial strata of the Karoo Supergroup, South Africa: implications for causes of the end-Permian extinction event. Gondwana Res. 7, 175–183.

DiMichele, W.A., Gastaldo, R.A., 2008. Deep time plant paleoecology. Annals Missouri Botanical Gardens 95, 144–198.

Ellis, B., Johnson, K.R., Dunn, R.E., 2003. Evidence for an *in situ* early Paleocene rainforest from Castle Rock, Colorado. Rocky Mt. Geol. 38, 73–100.

Foster, C.B., 1982. Spore-pollen assemblages of the Bowen Basin, Queensland (Australia): their relationship to the Permian/Triassic boundary. Rev. Palaeobot. Palynol. 36, 165–183.

Foster, C.B., Afonin, S.A., 2005. Abnormal pollen grains: an outcome of deteriorating atmospheric conditions around the Permian–Triassic boundary. J. Geol. Soc. 162, 653–659.

Foster, C.B., Archbold, N.W., 2001. Chronologic anchor points for the Permian and Early Triassic of the Eastern Australian Basins. In: Weiss, R.H. (Ed.), Contributions to Geology and Palaeontology of Gondwana in Honour of Helmut Wopfner. Geological Institute, University of Cologne, Germany, pp. 175–197.

Galtier, J., Daviero, V., 1999. Structure and development of *Sphenophyllum oblongifolium* from the Upper Carboniferous of France. Int. J. Plant Sci. 160, 1021–1033.

Gastaldo, R.A., and Demko, T.M., in press, The relationship between continental landscape evolution and the plant-fossil record: long term hydrologic controls on preservation: *in* Bottjer, D.J., and Allison, P.A., eds., Temporal Trends in Taphonomic Processes, Topics in Geobiology, Springer Verlag, Germany.

Gastaldo, R.A., Rolerson, M.W., 2008. *Katbergia* gen. nov., a new trace fossil from the Late Permian and Early Triassic of the Karoo Basin: implications for paleoenvironmental conditions at the P/Tr extinction event. Palaeontology 51, 215–229.

Gastaldo, R.A., Stevanovic-Walls, I., Ware, W.N., Greb, S.F., 2004. Community heterogeneity of Early Pennsylvanian peat mires. Geology 32, 693–696.

Gastaldo, R.A., Adendorff, R., Bamford, M., Labandeira, C.C., Neveling, J., Sims, H., 2005. Taphonomic trends of macrofloral assemblages across the Permian–Triassic Boundary, Karoo Basin, South Africa. Palaios 20, 479–497.

Gastaldo, R.A., Neveling, J., Clark, C.K., Newbury, S.S., 2009. The terrestrial Permian–Triassic boundary event bed is a non-event. Geology 37, 199–202.

Geertsema, H., van den Heever, J.A., 1996. A new beetle, *Afrocupes firmae* gen. et sp. nov. (Permocupedidae), from the Late Palaeozoic Whitehill Formation of South Africa. S. Afr. J. Sci. 92, 497–499.

Geertsema, H., van Dijk, D.E., 1999. The earliest known Palaeozoic ensiferan insect from Africa, *Afroedischia oosthuizeni* gen. et sp. nov. (Orthoptera: Oedischiidae). S. Afr. J. Sci. 95, 229–230.

Gonfiantini, R., 1978. Standards for stable isotope measurements in natural compounds. Nature 271, 534–536.

Gould, R.E., Delevoryas, T., 1977. The biology of Glossopteris: evidence from petrified seed-bearing and pollen-bearing organs. Alcheringa 1, 387–399.

Greb, S.F., DiMichele, W.D., Gastaldo, R.A., 2006. Evolution of wetland types and the importance of wetlands in Earth history. In: DiMichele, W.A., Greb, S. (Eds.), Wetlands Through Time: Geological Society of America, Special Publication, 399, pp. 1–40.

Hankel, O., 1992. Late Permian to Early Triassic microfloral assemblages from the Maji ya Chumvi Formation, Kenya. Rev. Palaeobot. Palynol. 72, 129–147.

Helby, R., Morgan, R., Partridge, A.D., 1987. A palynological zonation of the Australian Mesozoic. Mem. Assoc. Australas. Paleontol. 4, 1–94.

Hiller, N., Stavrakis, N., 1984. Permo-Triassic fluvial systems in the Southeastern Karoo basin, South Africa: Palaeo. Palaeo. Palaeo. 45, 1–21.

Johnson, M.R., 1966. The stratigraphy of the Cape and Karroo Systems in the Eastern Cape Province: Unpublished M.Sc. Thesis, Rhodes University, Grahamstown, South Africa, 76 pp.

Johnson, M.R., 1976. Stratigraphy and sedimentology of the Cape and Karoo Sequences in the Eastern Cape Province: Unpublished Ph.D. Thesis, Rhodes University, Grahamstown, South Africa, 336 pp.

Johnson, M.R., Van Vuuren, C.J., Visser, J.N.J., Cole, D.I., Wickens, D., de V., Christie, A.D.M., Roberts, D.L., 1997. The Foreland Karoo Basin, South Africa. In: Selley, R.C. (Ed.), Elsevier, African Basins, Amsterdam, pp. 269–317. Sedimentary Basins of the World, 3.

The Geology of South Africa. Geological. In: Johnson, M.R., Anhaeusser, C.R., Thomas, R.J. (Eds.), Society of South Africa, Johannesburg, and Council for Geoscience, Pretoria.

Kerp, H., Hamad, A.A., Vörding, B., Bandel, K., 2006. Typical Gondwanan floral elements in the Upper Permian of the paleotropics. Geology 34, 265–268.

Knight, C., Gastaldo, R.A., Neveling, J., 2009. Late Permian paleoenvironmental factors expounded through analysis of a forest-floor paleosol profile, Karoo Basin, South Africa. Geol. Soc. Am. 41 (7), 101 Abstracts with Program.

Kovács-Endrödy, É., 1991. On the Late Permian age of Ecca Glossopteris floras in the Transvaal Province with a key to and description of twenty five Glossopteris species. Geol. Surv. S. Afr. Mem. 77, 111.

Kozlowski, T.T., 1984. Plant responses to flooding of soil. Bioscience 34, 162–167.

Krassilov, V.A., 1975. Paleoecology of Terrestrial Plants. Wiley Publishing, New York. 283 pp.

Kraus, M.J., Aslan, A., 1999. Palaeosol sequences in floodplain environments: a hierarchical approach. Int. Assoc. Sedimentol. Spec. Publ. 27, 303–321.

Kraus, M.J., Davies-Vollum, K.S., 2004. Mudrock-dominated fills formed in avulsion splay channels: examples from the Willwood Formation, Wyoming. Sedimentology 51, 1127–1144.

Kraus, M.J., Hasiotis, S.T., 2006. Significance of different modes of rhizolith preservation to interpreting paleoenvironmental and paleohydrologic settings: examples from Paleogene paleosols, Bighorn Basin, Wyoming, USA. J. Sed. Res. 76, 333–346.

Kubler, M., 1977. The sedimentology and uranium mineralization of the Beaufort Group in the Beaufort West – Fraserburg – Merweville area, Cape Province: Unpublished M.Sc. Thesis, University of the Witwatersrand, Johannesburg, South Africa, 124 pp.

Lacey, W.S., 1974. New Permian Glossopteris flora from Natal. S. Afr. J. Sci. 70, 154–156.

Lacey, W.S., 1978. A review of the Upper Permian Glossopteris flora in western Natal. Palaeobotanist 25, 185–189.

Lacey, W.S., van Dijk, D.E., Gordon-Gray, K.D., 1975. Fossil plants from the Upper Permian in the Mooi River district of Natal, South Africa. Ann. Natal Mus. 22, 349–420.

Lindström, S., McLoughlin, S., 2007. Synchronous palynofloristic extinction and recovery after the end-Permian event in the Prince Charles Mountains. Antarctica: implications for palynofloristic turnover across Gondwana. Rev. Palaeobot. Palynol. 145, 89–122.

Lindström, S., McLoughlin, S., Drinnan, A.N., 1997. Intraspecific variation of taeniate bisaccate pollen within Permian glossopterid sporangia, from the Prince Charles Mountains, Antarctica. Int. J. Plant Sci. 158, 673–684.

Looy, C.V., Collinson, M.E., Van Konijnenburg-Van Cittert, J.H.A., Visscher, H., 2005. The ultrastructure and botanical affinity of end-Permian spore tetrads. Int. J. Plant Sci. 166, 875–887.

Mack, G.H., James, W.C., Monger, H.C., 1993. Classification of paleosols. Geol. Soc. Am. Bull. 105, 129–136.

MacLeod, K.G., Smith, R.M.H., Koch, P.L., Ward, P.D., 2000. Timing of mammal-like reptile extinctions across the Permian–Triassic boundary in South Africa. Geology 28, 227–230.

Maheshwari, H.K., 1968. Studies in the *Glossopteris* flora of India — 38. Remarks on *Trizygia speciosa* Royle with reference to the genus *Sphenophyllum*. Palaeobotanist 283–287 16 pp.

McLachlan, I.R., Anderson, A.M., 1977. Fossil insect wings from the Early Permian White Band Formation, South Africa. Palaeontol. Africana 20, 83–86.

McLoughlin, S., 1992. Late Permian plant megafossils from the Bowen Basin, Queensland, Australia: Part 1. Palaeontographica Abt B 228, 105–149.

McLoughlin, S., Lindström, S., Drinnan, A.N., 1997. Gondwanan floristic and sedimentological trends during the Permian–Triassic transition: new evidence from the Amery Group, northern Prince Charles Mountains, East Antarctica. Antarct. Sci. 9, 281–298.

Metcalfe, I., Nicoll, R.S., Willink, R.J., 2008. Conodonts from the Permian–Triassic transition in Australia and the position of the Permian–Triassic boundary. Aust. J. Earth Sci. 55, 365–377.

Mory, A.J., Backhouse, J., 1997. Permian stratigraphy and palynology of the Carnarvon Basin, Western Australia. Geol. Surv. W. Aust. Rep. 51, 1–101.

Mundil, R., Ludwig, K.R., Metcalfe, I., Renne, P.R., 2004. Age and timing of the Permian Mass Extinctions: U/Pb dating of closed-system zircons. Science 305, 1760–1763.

Oelofsen, B.W. 1981. An anatomical and systematic study of the Family Mesosauridae (Reptilia: Proganosauria) with special reference to its associated fauna and paleoecological environment in the White-Hill Sea. Ph.D. Thesis, University of Stellenbosch, 164 pp, (unpub.).

Ovtcharova, M., Bucher, H., Schaltegger, U., Galfetti, A., Brayard, J., Guex, J., 2006. New early to middle Triassic U–Pb ages from South China: calibration with ammonoid biochronozones and implications for the timing of the Triassic biotic recovery. Earth Planet. Sci. Lett. 243, 463–475.

Pace, D.W., Gastaldo, R.A., Neveling, J., 2009. Aggradational and Degradational Landscapes in the Early Triassic of the Karoo Basin and Evidence for Dramatic Climate Shifts Following the P/Tr Event. J. Sed. Res. 79, 276–291.

Pant, D.D., 1999. Dominant gymnosperms of the *Glossopteris* flora. Palaeobotanist 48, 111–123.

Pant, D.D., Basu, N., 1977. On some seeds, synangia and scales from the Triassic of Nipur, India. Palaeontographica Abt B. 163, 162–178.

Pant, D.D., Kidwai, P.F., 1968. On the structure of stems and leaves of *Phyllotheca indica* Bunbury, and its affinities. Palaeontographica Abt. B. 121, 102–121.

Pant, D.D., Mehra, B., 1963. On the epidermal structure of *Sphenophyllum speciosum* (Royle) Zeiller. Palaeontographica B. 112, 51–57.

Pant, D.D., Nautiyal, D.D., 1960. Some seeds and sporangia of Glossopteris flora from Raniganj Coalfield, India. Palaeontographica B. 107, 41–64.

Pigg, K.B., Taylor, T.N., 1993. Anatomically preserved Glossopteris stems with attached leaves from the central Transantarctic Mountains, Antarctica. Am. J. Bot. 80, 500–516.

Plumstead, E.P., 1969. Three thousand million years of plant life in Africa. Alex L Du Toit Memorial Lectures 11. Geol. Soc. SA 72 pp..

Prevec, R., McLoughlin, S., Bamford, M.K., 2008. Novel double wing morphology revealed in a South African ovuliferous glossopterid fructification: *Bifariala intermittens* (Plumstead 1958) *comb. nov*. Rev. Palaeobot. Palynol. 150, 22–36.

Prevec, R., Labandeira, C.C., Neveling, J., Gastaldo, R.A., Bamford, M.K., Looy, C.V., 2009. Portrait of a Gondwanan Ecosystem: a new Late Permian locality from Kwazulu-Natal, South Africa. Rev. Palaeobot. Palynol. 156, 454–493.

Price, P.L., 1997. Permian to Jurassic palynostratigraphic nomenclature of the Bowen and Surat Basins. In: Green, P.M. (Ed.), The Surat and Bowen Basins, South-East Queensland. Queensland Department of Mines and Energy, pp. 137–178.

Quirk, D.G., 1996. Base profile': a unifying concept in alluvial sequence stratigraphy. In: Howell, J.A., Aitken, J.F. (Eds.), High Resolution Sequence Stratigraphy: Innovations and Applications: Geol. Soc. Am. Spec. Pub.\, 104, pp. 37–49.

Raine, J.I., Mildenhall, D.C., and Kennedy, E.M., 2008. New Zealand fossil spores and pollen: an illustrated catalogue. 3rd edition. GNS Science miscellaneous series no. 4. http://www.gns.cri.nz/what/earthhist/fossils/spore_pollen/catalog/index.htm.

Rayner, R.J., 1992. *Phyllotheca*: the pastures of the Late Permian: palaeogeography. Palaeoclimatol. Palaeoecol. 92, 31–40.

Rayner, R.J., Coventry, M.K., 1985. A Glossopteris flora from the Permian of South Africa. S. Afr. J. Sci. 81, 21–32.

Rees, P.M., 2002. Land–plant diversity and the end-Permian mass extinction. Geology 30, 827–830.

Rees, P.M., Gibbs, M.T., Ziegler, A.M., Behling, P.J., 1999. Permian climates: evaluating model predictions using global paleobotanical data. Geology 27, 891–894.

Rees, P.M., Ziegler, A.M., Gibbs, M.T., Kutzbach, J.E., Behling, P.J., Rowley, D.B., 2002. Permian phytogeographic patterns and climate data/model comparisons. J. Geol. 110, 1–31.

Reid, S.B., Gastaldo, R.A., Neveling, J., Adendorff, R., 2006. Late Permian Fluvial Facies and Architectures Preserving an Autochthonous Leaf Litter, Wapadsberg Pass, Eastern Cape Province, South Africa. Geol. Soc. Amer. Abstr. Progr. 38 (7), 144.

Retallack, G.J., 1995. Permian-Triassic life crisis on land. Science 267, 77–80.

Retallack, G.J., 2002. *Lepidopteris callipteroides*, an early Triassic seedfern of the Sydney Basin, southeastern Australia. Alcheringa 1, 475–500.

Retallack, G.J., Dilcher, D.L., 1981. Arguments for a glossopterid ancestry of angiosperms. Paleobiology 7, 54–67.

Retallack, G.J., Dilcher, D.L., 1988. Reconstructions of selected seed ferns. Ann. Mo. Gard. 75, 1010–1057.

Retallack, G.J., Smith, R.M.H., Ward, P.D., 2003. Vertebrate extinction across Permian–Triassic boundary in Karoo Basin, South Africa. Geol. Soc. Am. Bull. 115, 1133–1152.

Riek, E.F., 1973. Fossil insects from the Upper Permian of Natal, South Africa. Ann. Natal Mus. 21, 513–532.

Riek, E.F., 1974. An unusual immature insect from the Upper Permian of Natal. Ann. Natal Mus. 22, 271–274.

Riek, E.F., 1976. New Upper Permian insects from Natal, South Africa. Ann. Natal Mus. 22, 755–789.

Rubidge, B.S., 2005. 27th Du Toit Memorial Lecture: re-uniting lost continents — fossil reptiles from the ancient Karoo and their wanderlust. 2005. S. Afr. J. Geol. 108, 135–172.

Rubidge, B.S., Johnson, M.R., Kitching, J.W., Smith, R.M.H., Keyser, A.W., Groenewald, G. H., 1995. An introduction to the biozonation of the Beaufort Group. In: Rubidge, B.S. (Ed.), Reptilian Biostratigraphy of the Permian–Triassic Beaufort Group (Karoo Supergroup): SACS Biostratigraphic Series, 1, pp. 1–2.

Selover, R.W., Gastaldo, R.A., 2005. A reinterpretation of the Wagendrift Quarry, Estcourt, Kwazulu Natal Province, and its implications for Karoo Basin palaeogeography. J. S.A. Geol. 108, 17–26.

Smith, R.M.H., 1980. The lithology, sedimentology and taphonomy of flood-plain deposits of the lower Beaufort (Adelaide Subgroup) strata near Beaufort West. Trans. Geol. Soc. S. Afr. 83, 399–413.

Smith, R.M.H., 1990. Alluvial paleosols and pedofacies sequences in the Permian Lower Beaufort of the southwestern Karoo Basin South Africa. J. Sed. Petrol. 60, 258–276.

Smith, R.M.H., 1995. Changing fluvial environments across the Permian–Triassic boundary in the Karoo Basin, S. Africa and possible causes of tetrapod extinctions. Palaeogeogr. Palaeoclimatol. Palaeoecol. 117, 81–104.

Smith, R.H.M., Botha, J., 2005. The recovery of terrestrial vertebrate diversity in the South African Karoo Basin after the end-Permian extinction. Compte. Rendu. Palevol. 4, 555–568.

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

Snowden, R.E.D., Wheeler, B.D., 1995. Chemical changes in selected species with increasing FE supply, with specific reference to root precipitates and Fe tolerance. New Phytol. 131, 503–520.

South African Committee for Stratigraphy, 1980. Stratigraphy of South Africa. Part 1: lithostratigraphy of the Republic of South Africa, South West Africa/ Namibia, and the republics of Bophuthatswana, Transkei and Venda. In: Kent, L.E. (Ed.), Geol. Surv. SA, Handbook, 8, pp. 535–548.

Srivastava, A.K., Rigby, J.F., 1983. *Sphenophyllum*, *Trizygia* and *Gondwanophyton* from the Barakar Formation of Raniganj Coalfield, with a revision of Lower Gondwana Sphenophyllales. Geophytology 13, 55–62.

Stear, W.M. 1980. The Sedimentary Environment of the Beaufort Group Uranium Province in the vicinity of Beaufort West, South Africa. Unpublished Ph.D. Thesis, University of Port Elizabeth, South Africa, 188 pp.

Steiner, M.B., Eshet, Y., Rampino, M.R., Schwindt, D.M., 2003. Fungal abundance spike and the Permian–Triassic boundary in the Karoo Supergroup (South Africa). Palaeogeogr. Palaeoclimatol. Palaeoecol. 194, 405–414.

Surange, K.R., Chandra, S., 1975. Morphology of the gymnospermous fructifications of the glossopteris flora and their relationships. Palaeontographica B. 149, 153–180.

Tabor, N.J., Montanez, I.P., Steiner, M.B., Schwindt, D., 2007. δ^{13}C values of carbonate nodules across the Permian–Triassic boundary in the Karoo Supergroup (South Africa) reflect a stinking sulfurous swamp, not atmospheric CO_2. Palaegeogr. Palaeoclimatol. Palaeoecol. 252, 370–381.

Taylor, E.L., Taylor, T.N., Cúneo, N.R., 1992. The present is not the key to the past: a polar forest from the Permian of Antarctica. Science 257, 1675–1677.

Taylor, E.L., Taylor, T.N., Kerp, H., Hermsen, E.J., 2006. Mesozoic seedferns: old paradigms, new discoveries. J. Torrey Botanical Soc. 133, 62–82.

Thomas, B.M., Willink, R.J., Grice, K., Twitchett, R.J., Purcell, R.R., Archbold, N.W., George, A.D., Tye, S., Alexander, R., Foster, C.B., Barber, C.J., 2004. Unique marine Permian–Triassic boundary section from Western Australia. Aust. J. Earth Sci. 51, 423–430.

Vajda, V., McLoughlin, S., 2007. Extinction and recovery patterns of the vegetation across the Cretaceous–Palaeogene boundary — a tool for unravelling the causes of the end-Permian mass extinction. Rev. Palaeobot. Palynol. 144, 99–112.

Van Dijk, D.E., 1981. A study of the type locality of *Lidgettonia africana* Thomas 1958. Palaeontologia Africana 24, 43–61.

Van Dijk, D.E., 1998. Insect faunas of South Africa from the Upper Permian and the Permian/Triassic Boundary. Palaeontologia Africana 34, 34–48.

Van Dijk, D.E 2000. Contributions to knowledge of some southern African fossil sites and their fossils [M.Sc. dissertation]: University of Stellenbosch, Cape Town, 167 pp.

Van Dijk, D.E., Geertsema, H., 1999. Permian insects from the Beaufort Group of Natal, South Africa. Ann. Natal Mus. 40, 137–171.

Visscher, H., Looy, C.V., Collinson, M.E., Brinkhuis, H., van Konijnenburg-van Cittert, J.H.A., Kürschner, W.M., Sephton, M., 2004. Environmental mutagenesis during the end-Permian ecological crisis. Proc. Nat. Acad. Sci. USA 101, 12952–12956.

Ward, P.D., Montgomery, D.R., Smith, R.M.H., 2000. Altered river morphology in South Africa related to the Permian–Triassic extinction. Science 289, 1740–1743.

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

Webb, L.J., 1955. A physiognomic classification of Australian rain forests. J. Ecol. 47, 551–570.

White, M.E., 1986. The greening of Gondwana. Reed. NSW, Frenchs Forest. 246 pp.

Wing, S.L., DiMichele, W.A., 1995. Conflict between local and global changes in plant diversity through geological time. Palaios 10, 551–564.

Zavada, M.S., 1991. The ultrastructure of pollen found in dispersed sporangia of *Arberiella* (Glossopteridaceae). Bot. Gaz. 152, 248–255.

Zavada, M.S., Crepet, W.L., 1985. Pollen wall ultrastructure of the type material of *Pteruchus africanus. P. dubius* and *P. papillatus*. Pollen Spores 27, 271–276.