

Taphonomic Trends of Macrofloral Assemblages Across the Permian–Triassic Boundary, Karoo Basin, South Africa

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The terrestrial crisis that reportedly parallels the P/Tr marine mass extinction is based mainly on Northern Hemisphere microfloral assemblages and Southern Hemisphere Gondwanan macrofloral collections. It is well established that taphonomic filters control the ultimate collectable fossil assemblage in any depositional regime. Recognition and comparison of isotaphonomic assemblages are critical before conclusions can be drawn about evolutionary trends over time. Such an approach has been taken in the investigation of pre-boundary, trans-boundary, and post-boundary plant-fossil assemblages in the Karoo Basin, South Africa.

Fourteen stratigraphic sections were evaluated in the Balfour and Normandien formations (Lower Beaufort Group), Katberg Formation, and overlying Burgersdorp Formation (Upper Beaufort Group). These include previously published (e.g., Bulwer, Bethulie, Carlton Heights, Wapadsberg, Commando Drift) as well as newly discovered (e.g., Clouston Farm) localities, and span the Late Permian to Middle Triassic. Fossiliferous intervals were characterized with respect to their sedimentology and plant taphonomy, and bulk collections were made at several stratigraphic levels for future evaluation of floristic and plant-insect associational trends.

The depositional regimes and plant taphonomic character of assemblages change through time. Much of the Lower Beaufort Group is characterized by parautochthonous assemblages within oxbow-lake channel fills. Below the P/Tr boundary, these are replaced by allochthonous assemblages, poorly preserved in lateral-accretion deposits and barforms of relatively shallow fluvial nature. Allochthonous assemblages within the same fluvial context continue across the boundary into the earliest Triassic (Palingkloof Member and Katberg Formation, and typify the Middle Triassic where scour-and-fill structures preserve plant debris. Based

on the literature, parautochthonous assemblages reappear in the Upper Triassic Molteno Formation. Hence, the change in taphonomic regime to poorly preserved allochthonous assemblages (dispersed, fragmentary adpressions) at the critical interval on either side of the P/Tr extinction event, but not coincident with, requires extreme caution when interpreting global patterns from these data. Additionally, the presence of plant fossils in the Early Triassic provides evidence for a vegetated landscape during a time when sedimentation patterns are interpreted to be the result of a land-plant die-off.

INTRODUCTION

Biodiversity loss as a consequence of the Mother of All Mass Extinctions (Erwin, 1993), marking the Permian–Triassic boundary at the end of the Paleozoic Era (251 ± 0.4 Ma; Gradstein et al., 2005), is estimated to range between 75–90% of known organisms in the marine fossil record. Similar estimates have been made for both land plants and vertebrates (e.g., Retallack, 1995; Visscher et al., 1996; Looy et al., 1999; Rubidge and Sidor, 2001; Rees et al., 2002), and recent proposals suggest that the decimation in the oceans was accompanied by a synchronous collapse in the terrestrial realm (Twitchett et al., 2001). There is some agreement that woody plants experienced a decline regionally (Retallack, 1995; Visscher et al., 1996; Looy et al., 1999; Kerp, 2000; Rees, 2002), which would have had direct effects on erosional rates, changes in atmospheric CO₂ levels, carbon cycling, and ecosystem structure (MacLeod et al., 2000; Ward et al., 2000). However, these syntheses are based on macrofloral data originating from localities that are isolated spatially (mainly South Africa and Australia), and not well constrained in time, and that may or may not actually contain the terrestrial P/Tr boundary interval (De Kock and Kirschvink, 2004; Steiner et al., 2003; Ward et al., 2005). Therefore, it

is possible that the extinction event may have varied regionally in magnitude and timing, and the effects on land may pre-date, be coincident with, or post-date the effects documented in the oceans. Hence, it is essential that high-quality, comparable data sets be acquired and evaluated to understand continental biodiversity loss at this critical time in Earth history.

The Karoo Basin of South Africa has been the focus of intense activity because it is one of the few basins in which the terrestrial record across this critical interval is preserved and exposed. To date, most of the attention has been paid to the changes in tetrapod assemblages throughout the section (e.g., Rubidge, 1995; Smith, 1995; MacLeod et al., 2000; Smith and Ward, 2001; Ward et al., 2005), with the documented replacement of the *Dicynodon* Assemblage Zone (latest Permian) with an Early Triassic *Lystrosaurus* Assemblage Zone (Groenewald and Kitching, 1995; Kitching, 1995a, b). Recent data presented on palynomorphs (Steiner et al., 2003) and plant macrofossils and paleosols (Retallack et al., 2003) both supplement and confound the interpreted trends. It is well established (Behrensmeyer et al., 2000; Gastaldo, 2001) that before diversity measures can be compared across space and time, it is essential that isotaphonomic assemblages be identified and assessed. This contribution addresses the plant taphonomic character of assemblages in the non-marine Beaufort Group, which spans the Late Permian (Wujiaopingian; Gradstein et al., 2005) to Middle Triassic (Anisian), to place the preserved megafloora into such a context. To date, no additional published data exist on the plant taphonomic character of this, or any part of the Karoo, although interpretations of plant assemblages and the ecosystems they represent have been made for the Late Triassic Molteno based on paleontological and sedimentological evidence (Cairncross et al., 1995; Anderson et al., 1998).

KAROO BASIN STRATIGRAPHY

The Karoo Basin formed in southwestern Gondwana (South America, Africa, Antarctica, India, and Australia) in response to collision and subduction of the paleo-Pacific plate under the Gondwanan plate during the Pennsylvanian (Veevers et al., 1994). A mountain chain, the Cape Fold Belt (which formed part of the Pan-Gondwanan Mountain Belt), consisting of folded and thrust-faulted rock, formed ~1500 km north of the collisional margin (Smith, 1995). A foredeep basin developed adjacent to the Cape Fold Belt towards the interior of the continent in response to continental closure (Catuneanu et al., 1998). This basin, the Karoo Basin, began to accumulate sediments shed from the mountain belt in the Pennsylvanian (~300 Ma), with its last sediments deposited in the Early Jurassic (190 Ma), when rifting of the Gondwanan supercontinent began (Johnson et al., 1997). In total, a rock sequence with a maximum thickness of 12 km accumulated within the basin (the Karoo Supergroup), providing for one of the few continuous sequences of continental deposits that encompasses the Permian–Triassic boundary event. These rocks are exposed over some 600,000 km², which represents more than half the land surface of South Africa.

Several lithostratigraphic groups are recognized in the

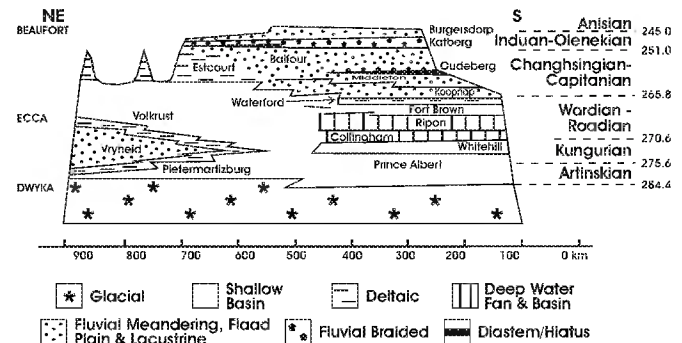


FIGURE 1—Time–space diagram of the Karoo Basin showing the overall stratigraphy and generalized depositional environments into the Early Triassic (Anisian), where a hiatus with overlying Late Triassic rocks occurs. Diagram modified and updated from Cole (1992) and Veevers et al. (1994), and based on Catuneanu et al. (1998) and unpublished Council for Geoscience data. Age assignments and age/stage names from Gradstein et al. (2005).

Karoo Supergroup, with the most basal, the Dwyka Group, consisting of Pennsylvanian and Early Permian glacial tillites, glacial outwash, and lake deposits formed from the retreat of continental glaciers that had spread across Gondwana (Visser, 1991; Fig. 1). This thick sequence is overlain by the Eccca Group, a time-transgressive unit that becomes younger across the basin from south to northeast in both its lower and upper contacts. These rocks accumulated in deep-water, pelagic, and reducing environments (Visser, 1992), including distal submarine fans in which volcanic-ash deposits have been identified (e.g., Johnson et al., 2001). Towards the northeast, a terrestrial sequence is notable with the presence of coals and transitional fluvial-deltaic environments (Johnson et al., 1997; Cairncross, 2001; Catuneanu et al., 2002).

The Eccca Group is superceded by the Permian–Triassic Beaufort Group, which prograded over the former from the south to north. By the latest Permian, accumulation throughout the basin took place under nonmarine conditions, which continued until the Early Jurassic. Several upwards-fining sequences have been documented in the uppermost formations (Balfour and Normandien formations) of the lower Beaufort Group (Visser and Dukas, 1979; Groenewald, 1989; Catuneanu and Elango, 2001). The coarse-grained portions of these cycles are interpreted as sandy braided or sand-bedload meandering channel systems, overlain by finer-grained meandering channel systems. Lake deposits of varying characteristics occur within these fine-grained systems. The succession of upwards-fining sequences has been linked to pulsed mountain-building episodes in the Cape Fold Belt (Catuneanu et al., 1998; Catuneanu and Elango, 2001). In general, deposition of this part of the sequence was dominated by meandering fluvial systems (Visser and Dukas, 1979; Hiller and Stavrakis, 1984; Smith, 1995).

The Late Permian–Early Triassic Balfour Formation is overlain by a thick arenaceous unit, the Katberg Formation, interpreted to represent deposition by shallow, braided river systems with pulsed discharge and sediment accumulation (Hiller and Stavrakis, 1984; Groenewald, 1996; Haycock et al., 1997; Neveling, 2004). The thin mudstones within the Katberg Formation probably represent abandoned channel fills and braidplain environments.

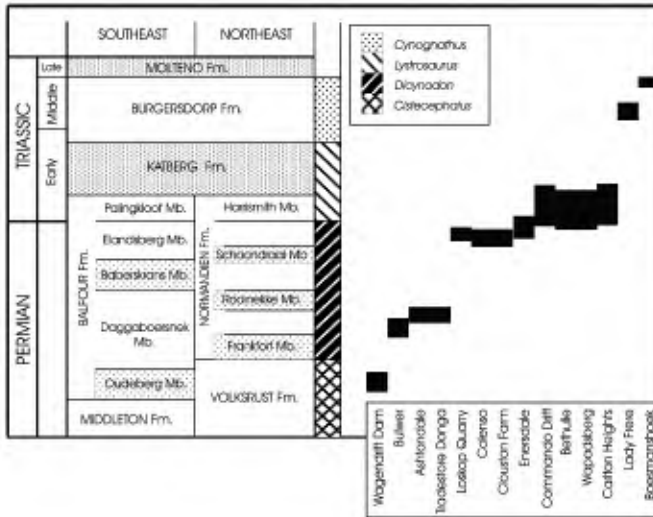


FIGURE 2—Stratigraphic placement of localities used in this study within the Late Permian to Middle Triassic stratigraphy of the Karoo Basin east of 24°E Longitude.

The overlying rocks (Burgersdorp Formation) consist of fine- to medium-grained sandstones overlain by maroon-colored siltstone and mudstone, and have been interpreted to represent mixed-load meandering-river and floodplain deposits (Catuneanu et al., 1998; Hancox, 1998). Finer average grain size and smaller channel deposits, exposed in the northernmost outcrops of the Burgersdorp Formation, are interpreted to represent suspension-load deposition in a system of semi-permanent ponds, playa lakes, and floodplain channels fed by simple channels (Neveling, 2004). Ultimately, these rocks are overlain unconformably by the Stormberg Group. The Upper Triassic Molteno Formation occurs at the base and is separated from the Burgersdorp Formation by a major stratigraphic gap/unconformity (Hancox, 1998).

Considerable lateral variation has been documented in the Beaufort Group, and different stratigraphic nomenclature is applied to different regions. The sedimentary rocks that encompass the Late Permian to Early Triassic are assigned to the Balfour Formation in the southern part of the basin east of 24°E longitude (Hiller and Stavakis, 1984; Rubidge et al., 1995) and to the Normandien Formation in the north (e.g., northern Free State Province: Groenewald, 1989; Rubidge et al., 1995; Fig. 2). Where this interval crops out along the eastern flank of the basin in KwaZulu-Natal Province, the rocks have been equated to the Estcourt Formation. The Katberg Formation (Scythian; Catuneanu et al., 1998), with a maximum preserved thickness of 1200 m (Groenewald, 1996), has been placed stratigraphically just at (Ward et al., 2000) or above (Smith, 1995; Retallack et al., 2003; Ward et al., 2005) the P/Tr boundary event based on vertebrate biostratigraphy (Rubidge, 1995).

Various members are recognized in the Balfour Formation, with the uppermost Palingkloof Member distinguished by red and maroon mudstone, compared to the grayish mudstones of the underlying Elandsberg Member (Keyser and Smith, 1977–78; South African Committee for Stratigraphy, 1980; Smith, 1995). Most workers place the P/Tr boundary at or just above the base of the Palingkloof

Member (Smith, 1995; Retallack et al., 2003; Ward et al., 2005). A similar red argillaceous unit, the Harrismith Member, caps the Normandien Formation in the north.

The placement of the P/Tr boundary is based on vertebrate biostratigraphy, with the Permian fauna of the *Dicynodon* Assemblage Zone occurring in the Elandsberg Member and the overlying Early Triassic *Lystrosaurus* Assemblage Zone fossils restricted to the Palingkloof Member in the south and the Harrismith Member in the north. However, recent data indicate that these two biozones overlap the P/Tr boundary (Smith, 1995; Smith and Ward, 2001; Retallack et al., 2003) with Late Permian elements extending into the P/Tr event beds above the circumscribed boundary at the End Permian Paleosol (EPP; R. Smith, pers. comm., 2004; Ward et al., 2005). Hence, within a 40–60-m-thick interval, where the sandstone:mudrock ratio increases, there is evidence for fairly continuous sedimentation within the Katberg complex in the north-central parts of the basin (Smith, 1995).

The Burgersdorp Formation (Spathian–Anisian) overlies the Katberg Formation and is characterized by the *Cynognathus* Assemblage Zone (Kitching, 1995b). It is subdivided into three horizons—A, B, and C—based on vertebrate paleontology (Hancox et al., 1995) and sedimentology (Hancox, 2000). The interval mainly is composed of reddish mudstone alternating with subordinate light gray sandstone, arranged in upward-fining cycles of a few tens of meters thick (Johnson and Hiller, 1990; Groenewald, 1996).

COLLECTION SITES AND METHODS

The present study encompasses 14 Beaufort Group localities spanning the Late Permian to Middle Triassic in KwaZulu-Natal, the Free State, and the Eastern Cape Provinces (Fig. 3; Appendix; Appendix is reposted online at <<http://www.sepm.org/archive/index.html>>). Karoo basin localities are localized, with a compounding problem that identification of the Permian–Triassic boundary is problematic in some, if not most, localities. The P/Tr boundary is defined based on the first appearance of the conodont *Hindeodus parvus* in marine strata (Yin et al., 2001). As Ward et al. (2005, p. 714) note in the Karoo, they place the P/Tr boundary at the level of the highest Permian vertebrate taxon, “a practice that runs contrary to accepted stratigraphic procedure,” until a suitable terrestrial index taxon can be identified.

The only Late Permian plant-fossil localities reported in South Africa occur in KwaZulu-Natal Province (e.g., Lacey et al., 1975; Anderson and Anderson, 1985) where exposures are restricted to quarries, dongas, and river beds due to dense vegetation across the landscape. Hence, exposures are not laterally extensive and Jurassic dolerite intrusions complicate lithostratigraphic correlations. Early Triassic rocks are more extensive in their distribution, but plant-fossil assemblages are extremely rare and poorly preserved. These conditions require reconnaissance and exploration for potential fossiliferous lithologies in localities where the Palingkloof Member and Katberg Formation are exposed and mapped, but undocumented.

All stratigraphic sections, including those previously reported in the literature, were measured or re-measured and described using conventional parameters (e.g., body

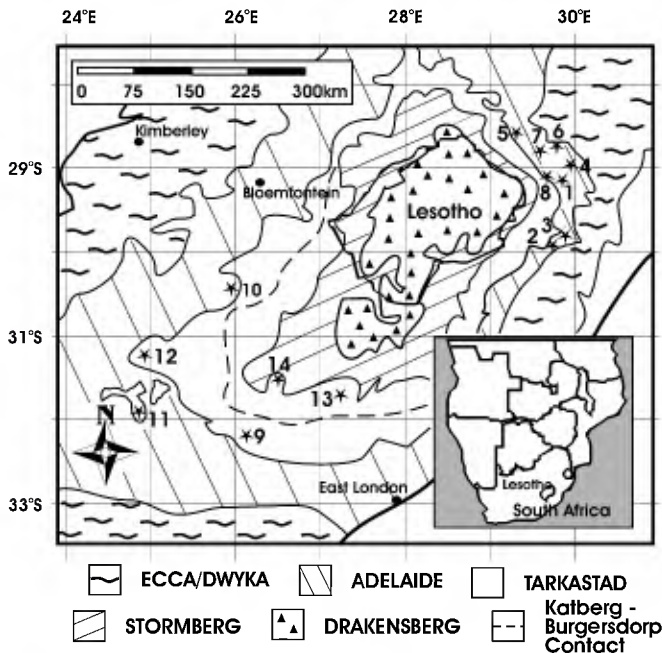


FIGURE 3—Map of South African localities included in the present study within geologic context. 1—Wagendrift Dam Quarry; 2—Bulwer Quarry; 3—Ashtonvale Farm; 4—Tradestore Donga; 5—Loskop Quarry; 6—Colenso R7 Roadcut; 7—Clouston Farm; 8—Ennersdale; 9—Commando Drift; 10—Bethulie, Bethel Farm; 11—Wapadsberg Pass; 12—Carlton Heights; 13—Lady Frere; 14—Boesmanshoek Pass. See Appendix, reposted online at <<http://www.sepm.org/archive/index.html>> for GPS coordinates of each locality, stratigraphic placement, and sedimentological and paleontological details.

geometry, grain size, Munsell color, primary sedimentary structures, paleontological attributes, biogenic structures, etc.). A new section in Bethulie was measured at the same locality used by previous workers (e.g., Smith and Ward, 2001; Retallack et al., 2003; Ward et al., 2005; see Appendix, reposted online at <<http://www.sepm.org/archive/index.html>> for locality and sedimentary data). Microstratigraphic analyses were conducted on the intervals that cross the P/Tr boundary, and included macroscopic and microscopic (thin-section) characterization (Gray et al., 2004).

Each locality was placed into stratigraphic order relative to the P/Tr boundary using regional geological relationships and data available at the Council for Geosciences (Fig. 2). The stratigraphic resolution of many locations is coarse due to tectonic displacement by Early Jurassic dolerite intrusions, the geographic distances between exposed sections (which may be on the order of several hundred kilometers; Fig. 3), and the absence of radiometrically datable volcanic tuffs in the Balfour and Normandien Formations. Two reconnaissance surveys (2002 and 2003), based on previously published and unpublished literature, including field notes, identified paleontologically rich intervals that resulted in the collection of new macrofloral and microfloral assemblages. Hence, to date, palynological assemblages that have been processed and evaluated help to constrain the ages of the Wagendrift, Colenso, Clouston Farm, and Ennersdale localities using the biozonation of Aitken (1998; Looy, pers. comm., 2004). In addition, the spatial relationships at most sites allow for stratigraphic

placement relative to the Eccca-Beaufort contact (i.e., Tradestore Donga) or within meters below or above the P/Tr boundary (as variously defined for particular localities by Ward et al., 2000; Smith and Ward, 2001; MacLeod et al., 2000; and Retallack et al., 2003) based on field logging (e.g., Bulwer and Ashtonvale Farm, Ennersdale, Commando Drift, Bethulie, Wapadsberg, Carlton Heights).

Plant-fossil assemblages were examined in vertical and lateral (spatial) context at each collection horizon. Taphonomic criteria evaluated followed Krassilov (1975) as modified by Allen and Gastaldo (in press) and included: thickness of the plant-bearing unit, order and arrangement of plant debris (including, whenever feasible, leaf orientation as a vector measured towards the apex; axial orientation also was measured, although this feature when used alone is an unreliable proxy for paleocurrent analysis, see Gastaldo, 2004, for a discussion), diversity of plant-part assemblage, size of remains (heteromeric versus isomeric), concentration of debris, and mode of preservation. Orientations of plant debris were plotted and analyzed statistically (Bateman, 1999) using Oriana v. 2.02 (Kovach Computing). The Rayleigh Test of Uniformity was applied to vector data from individual bedding surfaces and beds, whereas the F-test was used to test the mean vectors of superposed beds. All collections are housed at the Bernard Price Institute of Palaeontology, Witwatersrand University, Johannesburg.

LATE PERMIAN LOCALITIES

Wagendrift Dam Quarry

Wagendrift Dam Quarry, near the town of Escourt, KwaZulu-Natal Province, is mapped as the base of the Escourt Formation in the Lower Beaufort Group. The spatial and stratigraphic variation of this formation, which is defined as consisting of ~400 m of carbonaceous shale and sandstone with thin, intermittent coal seams (Botha and Linström, 1978; Johnson et al., 1997), is understood poorly. This formation, which is situated between the shelf deposits of the Eccca Group below and the braided channels of the Katberg Formation above (Fig. 1), has been interpreted as a series of river-mouth bars and deltas that alternate with swampy floodplains (Botha and Linström, 1978). Within this setting, van Dijk et al. (1978) interpreted the Wagendrift Quarry as an interdistributary bayfill. The quarry section consists of millimeter-scale, interlaminated, very fine-grained sandstone and siltstone, or siltstone and mudstone couplets overlying a thick unstructured siltstone that is laterally adjacent to olistoliths. The fine-grained couplets onlap and overlap the olistoliths. Couplets coarsen up-section to where individual sandstone beds are cm- to dm-scale in thickness, consisting of ripple-laminated and ball-and-pillow structures. Thick, ripple-bedded sandstones cap the section, representing a major change in the depositional setting (Selover and Gastaldo, 2005; Appendix, <<http://www.sepm.org/archive/index.html>>).

Plant megafossils are rare and restricted only to two stratigraphic intervals, although they were more common in the past when the quarry was active (van Dijk et al., 1978). Isolated and dispersed, very small (<3 cm long) leaves of *Glossopteris*, and very small (1–2 cm) *Phyllothea*

whorls, are well preserved as adpressions and impressions parallel to bedding in the basalmost siltstone laminae. In addition, there are rare unidentifiable axial remains sporadically encountered in the lowermost part of the couplet interval. None of these phytoclasts shows any abiotic ordering. In contrast, small, isolated, and contorted *Glossopteris* leaves are preserved within the ball-and-pillow sandstones higher in the section. Here, similar-sized leaves are oriented parallel to the flow direction of the sand, but may be perpendicular, flexed, or folded relative to bedding features.

Selover and Gastaldo (2003, 2005) interpreted the facies in the quarry section and other area outcrops as characteristic of a submarine turbidite system. Palynomorphs recovered from Wagendrift Dam Quarry consist of a low-diversity assemblage that is moderately to well preserved (Looy, pers. comm., 2004). The most common elements are Middle Permian saccate pollen grains assigned to *Protohaploxylinus*, *Lunatisporites*, *Weylandites*, and *Acanthotriletes* (Krassilov et al., 1999). But, what is significant is the presence of cf. *Lueckisporites*, a biostratigraphic indicator of the Late Permian. Looy (pers. comm., 2005) correlates the palynological assemblage with the *Guttulapollenites hannonicus*–*Protohaploxylinus rugatus* zones of Aitken (1998), which lies in the Volkrust Formation (Wujiapingian). The stratigraphy is reminiscent of Middle Permian rocks noted throughout the basin, but the palynology indicates a younger age (Selover and Gastaldo, 2005).

Bulwer, Ashtonvale, and Tradestore Donga

Van Dijk et al. (1991; van Dijk and Geertsema, 1999) reported that both plant and insect fossils were preserved within a bedded siltstone in the Bulwer Quarry, KwaZulu-Natal Province (Fig. 4B; Appendix, <<http://www.sepm.org/archive/index.html>>). This site exposes a fluvial system composed of 2- to 3-meter-thick bed sets, each of which is separated by a 4th-order bounding surface (Miall, 1997). Most bed sets are composed of very thin to thinly bedded (3 mm) dark gray siltstone, whereas one siltstone interval in the middle of the exposure is composed of low-angle crossbeds on the decimeter scale. At the top of this interval are well developed, meter-scale ball-and-pillow structures marking the contact with the overlying thinly bedded siltstone. Here, plant fossils are very isolated and dispersed, preserved on the bedding planes in the basal 10–15 cm of only two bed sets just above the lower contact (3rd-order bounding surface). Preservation of small (~10 cm long) *Glossopteris* leaves ranges from well-developed impressions to mere outlines, along with unidentifiable, fragmentary plant debris including axes (Figs. 5D, E). Detrital plant remains also are preserved isolated and dispersed on bedding planes of low-angle crossbeds.

The exposure at Ashtonvale Guest Farm, which is decimeters stratigraphically above the quarry site, differs in its sedimentological features and is similar to the Tradestore Donga locality, also in KwaZulu-Natal (Appendix, <<http://www.sepm.org/archive/index.html>>). At both of these sites, limited outcrop exposes a coarse-grained siltstone organized into dunal bedforms, in which bedded leaves occur in clustered intervals throughout each bedform (Figs. 5A, 6). The siltstone at Ashtonvale is leached

white, with leaf mats accentuated by alteration to an orange-beige/brown (iron-stained) color, whereas the Tradestore Donga siltstone is medium to dark gray with dark gray-black adpressions. Here, leaf mats are organized in a manner identical to the Ashtonvale assemblage. Dune thickness ranges from 25–40 cm at the crest, with wavelengths from 1.2–1.5 m. Bedforms are overlain by either rippled or parallel-laminated coarse-grained siltstone, or medium-bedded, low-angle coarse-grained siltstone (cm-scale) in which plant material also is preserved.

The plant taphonomic character of these three sites is virtually identical. Each assemblage is dominated by *Glossopteris* leaves ranging from 3.5–16 cm in length and 2–4 cm in maximum width, preserved within mats composed of 3–6 overlapping leaves (Figs. 5A, 6). The leaves in each cluster (or mat) are separated from one another by matrix less than 1 mm in thickness, and it is possible that clusters overlie one another vertically (depending upon their spatial position within the bedform). Hence, each cluster in vertical section may range over a stratigraphic distance of up to ~1 cm, with stacked clusters comprising up to 3.5 cm of section. Isolated, non-clustered leaves are intercalated between mats, and may be associated with small-scale ripple features; these intervals of dispersed leaves may be as thick as 4.5 cm. Isolated *Phyllothea* whorls also are present and dispersed within the matrix, or in association with *Glossopteris*. All leaves are preserved as impressions and are flat-lying, oriented parallel to bedding. Few exhibit laminar contortion; where this does occur, the tip or margin of the leaf is folded under itself. The distributions of leaves on individual bedding surfaces were examined, and vector orientation measured and assessed in both localities. Although several leaves may be aligned parallel to one other, the data sets from both localities (at the individual-bed and combined-bed level of analysis) exhibit no preferred orientation (Fig. 7A, B). Hence, there is no evidence to support an interpretation of abiotic arrangement or reworking of leaves during or after emplacement at the sediment-water interface.

Loskop, Clouston Farm, and Colenso

These three localities in KwaZulu-Natal Province record fluvial channel complexes that were wide and deep, and situated stratigraphically higher than the previous localities. The roadcut in Colenso at the R74/R103 intersection exposes a point or lateral-accretion bar that is >1 km in length, whereas the channel deposits measured and mapped on the Clouston Farm are at least 25 m in total thickness (Fig. 4A). These sites are geographically extensive, with the fossil material preserved either in thick siltstone or silty mudstone. Fossiliferous lithologies are either underlain and overlain by fine- to very fine-grained sandstone (Loskop Quarry and Clouston Farm; Sims et al., 2004), or are within mudstone found at the top of bedforms in the barforms geometry (Colenso). To date, only plant and very rare insect fossils have been recovered from the Loskop and Clouston Farm localities, both of which represent abandoned channel fills, while both plants and tetrapods occur in the Colenso roadcut (Fig. 5B). *Lystrosaurus* remains have been recovered from a site 3.5 km east and approximately 80 m above the Loskop Quarry site.

Macrofloral assemblages are preserved in olive-gray

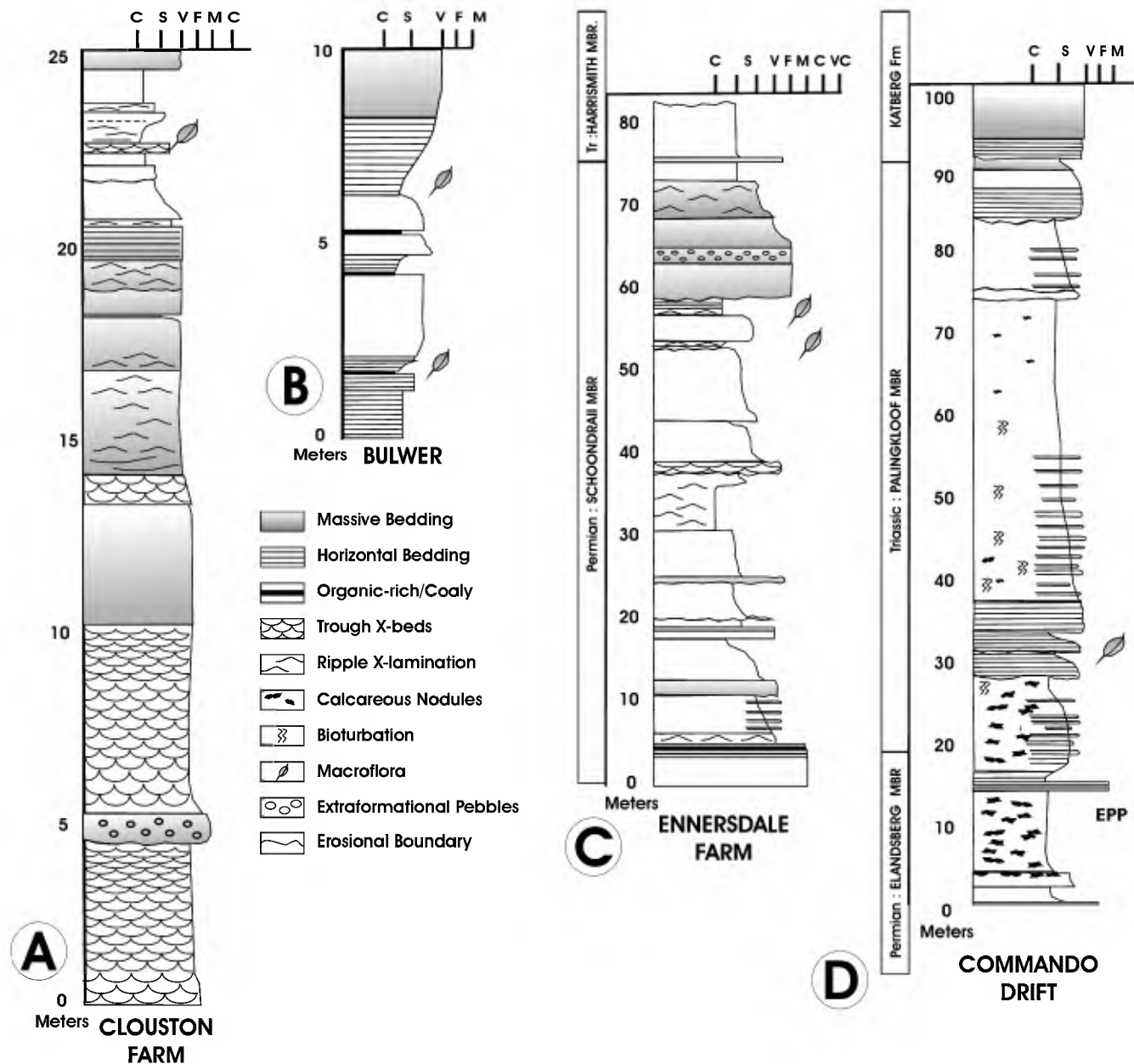
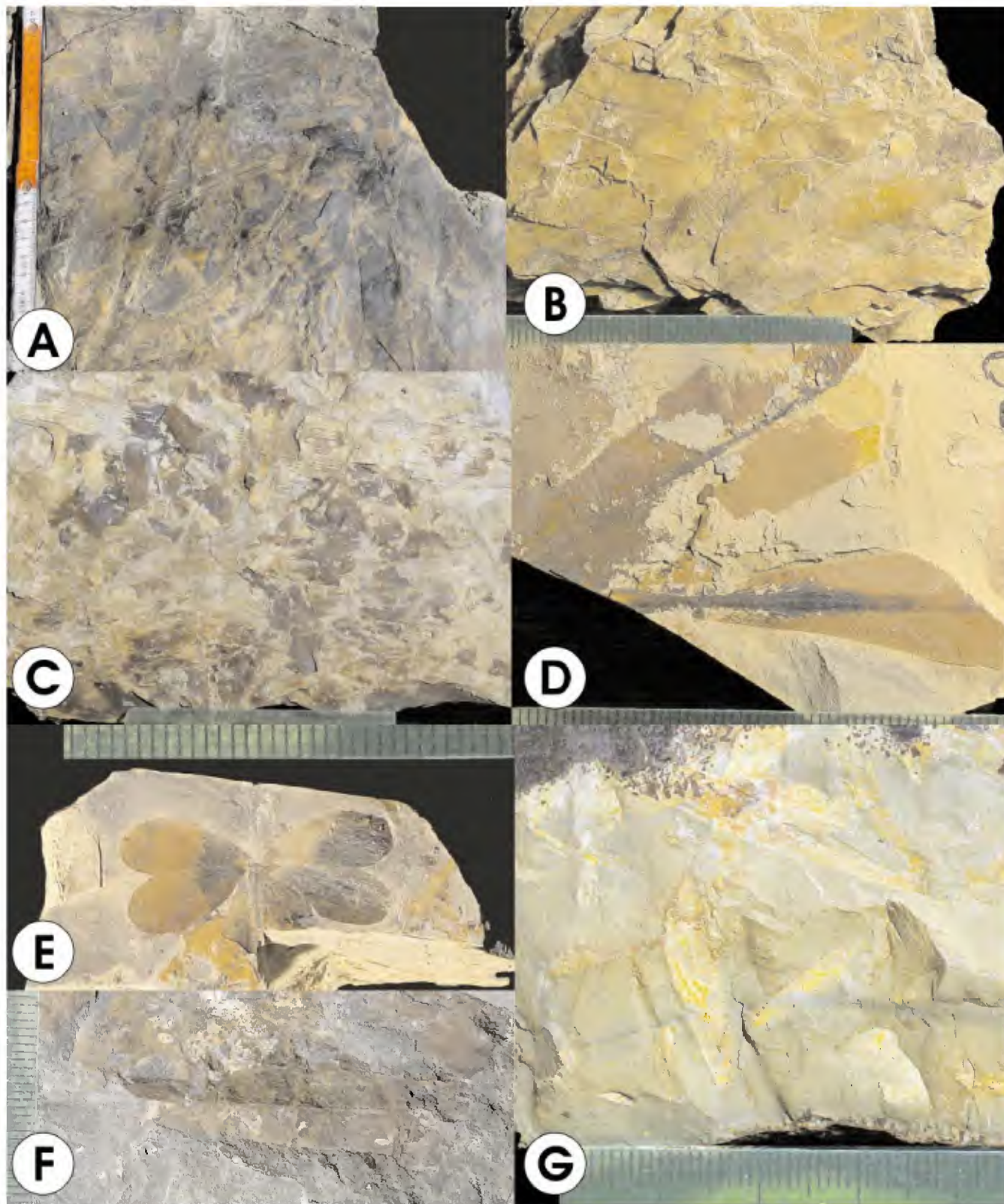


FIGURE 4—Measured Permian and Early Triassic stratigraphic sections (for details on localities, see Fig. 3 and Appendix, <<http://www.sepm.org/archive/index.html>>). (A) The donga exposure at Clouston Farm exposes a Late Permian channel-fill complex in which bedded leaf mats are preserved near the top of the fill sequence. Normandien Formation. (B) A quarry exposure at Bulwer preserves macrofloral elements on bounding surfaces and bedding surfaces of low-angle crossbeds. Normandien Formation. (C) The donga and outcrop sections at Ennersdale Farm cross the P/Tr boundary, although poorly preserved macrofloral remains only occur in siltstones beneath the boundary. (D) The P/Tr boundary is exposed at Commando Drift and poorly preserved fragmentary plant remains occur in coarse-grained siltstone above a carbonate-bearing interval interpreted as the EPP (End Permian Paleosol).

FIGURE 5—Parautochthonous and allochthonous plant-fossil assemblages from the Late Permian Balfour Formation, Karoo Basin; scales in mm, except where indicated. (A) Bedding-plane exposure of *Glossopteris*-dominated leaf mats at Tradestore Donga outcrop. Leaf mats are preserved in megaripple structures (dunes) composed of siltstone. Identified taxa include several *Glossopteris* morphotypes, *Eretmonia natalensis*, scale leaves, and sphenophyte axes. Scale in cm and dm. (B) Bedding-plane exposure of *Glossopteris*-dominated leaf mats in lateral-accretion bar, Colenso Roadcut. Taxa identified from this site include several *Glossopteris* morphotypes, fine rootlets, unidentified seeds, and



sphenophyte axes. (C) Bedding-plane exposure of *Glossopteris*-dominated leaf mats in channel-fill sequence (oxbow lake) at Loskop Quarry. (D) Dispersed *Glossopteris* leaves on bedding planes within accretionary barforms, Bulwer Quarry. Plant fossils preserved as impressions within siltstone. (E) Isolated whorl of *Trizygia speciosa*, preserved as an impression, from Bulwer Quarry. (F) Isolated, poorly preserved impression of *Glossopteris* leaf from Wapadsberg Pass. (G) Isolated, dispersed impressions of poorly preserved *Glossopteris* leaves and debris from siltstone megaripples (dunes) at Ennersdale Farm.

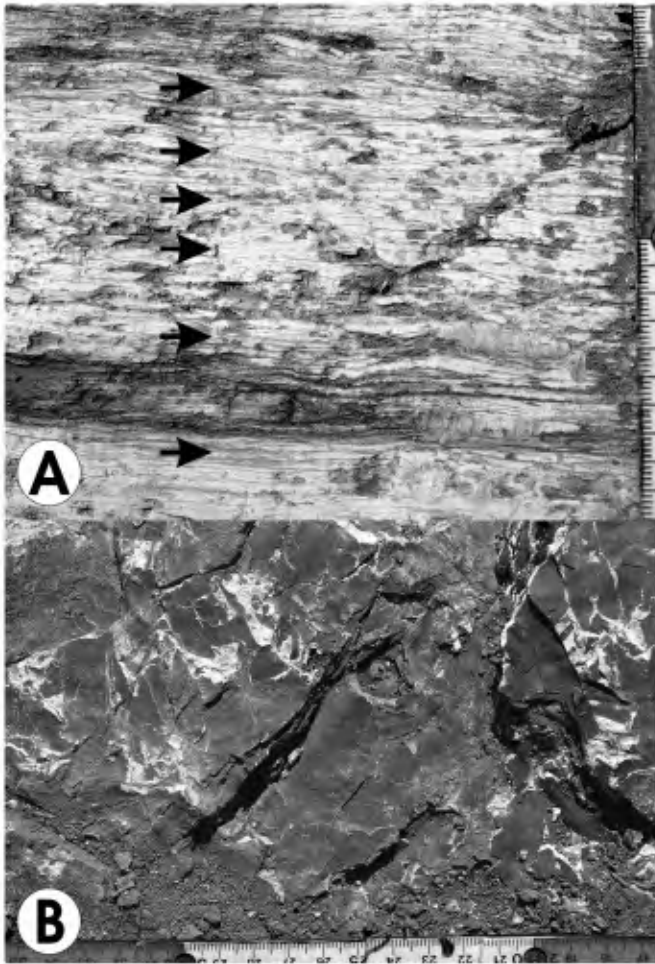


FIGURE 6—Typical arrangement of plant beds in Late Permian fluvial deposits in the lower part of the Balfour and Normandien Formations. Photograph taken at Ashtonvale Guest Farm. Scale in millimeters. (A) Successive concentrations of *Glossopteris* leaves (at arrows), separated by intervals in which leaves are dispersed, that characterize accumulations in siltstone megaforms and oxbow-lake deposits. (B) Bedding-plane surface of one matted interval on which *Glossopteris* leaves are overlapping and oriented randomly.

siltstone and extend over a stratigraphic thickness of 2.5 m at Clouston Farm and at least 1 m in the Loskop Quarry (Fig. 5C). At the Colenso roadcut, the fossiliferous olive-gray siltstone is restricted vertically and laterally, with a maximum observed thickness of 30 cm. A heteromeric mixture of leaves, axes, and reproductive structures are preserved as impressions in clustered intervals (Fig. 5B), similar to the plant-fossil distribution at Ashtonvale Farm and Tradestore Donga. Each cluster at Clouston Farm consists of randomly distributed (Fig. 7C–F), overlapping plant parts, each of which is separated by matrix less than 0.5 mm thick. Clusters may be up to eight leaves thick, and stratigraphically successive clusters are separated by up to 4 cm of matrix in which parts are isolated and unordered. Most debris consists of individual *Glossopteris* leaves oriented parallel to bedding, indicative of physiological loss, whereas only a few specimens in which *Glossopteris* leaves remain attached to small, ultimate branches are present. These specimens indicate transfer of bio-

mass via traumatic processes (Gastaldo, 1994). Contorted leaves are encountered rarely, and are associated either with small-scale ripples (overlying the primary structure) or microtopographic relief on the original channel bottom. Leaves range in length from 3–15 cm, with a mean length of ~8 cm (Fig. 8), although fragments of larger leaves (> 20 cm in length) have been encountered. Sphenopsid axial casts often are mixed with *Glossopteris* and are filled incompletely (Gastaldo et al., 1989). Axes may be up to 4 cm in width with a cast of only a few millimeters in thickness. Cast sediments may display small-scale cross stratification indicating bedload transport of sediment through the axis, or the fill may be homogenous.

Ennersdale, Commando Drift, Wapadsberg Pass, Bethulie, and Carlton Heights

The Permian–Triassic boundary is exposed at each of these localities and defined operationally as the stratigraphic disappearance of the *Dicynodon* Assemblage Zone fauna (Smith, 1995). The Bethulie section on the Bethel farm generally is recognized as the type area for the P/Tr boundary in the Karoo (Smith, 1995; MacLeod et al., 2000; Ward et al., 2000). Plant-bearing lithologies below the boundary at all localities are gray-green or blue-green siltstones of the Harrismith Member of the Normandien Formation or the Elandsberg and Palingkloof members of the Balfour Formation (Fig. 2; Appendix, <<http://www.sepm.org/archive/index.html>>). These are interbedded with fluvial deposits of fine-grained sandstone that display megaform/dunal structures and centimeter-scale planar beds, interpreted to represent low-sinuosity, unconfined channels. Above the boundary, plant assemblages also are preserved within coarse-grained siltstones and very fine-grained sandstones of the Palingkloof Member (Balfour Formation) and Katberg Formation, the latter of which has been interpreted as braided fluvial deposits (e.g., Hiller and Stavrakis, 1984; Ward et al., 2000). The plant taphonomic character of assemblages in these sites is different from those lower in the section (Figs. 4, 9).

Ennersdale: One plant locality at Ennersdale occurs in a weathered exposure of green-gray siltstone just below the red siltstones of the Harrismith Member (Fig. 4C; Appendix, <<http://www.sepm.org/archive/index.html>>). Bedding surfaces in the siltstone indicate that these sediments were deposited in low-angle crossbeds within a fine-grained channel system. Fine-grained sandstones occur as single-storied bodies, with intervening thicker siltstone deposits into which the sandstones have eroded. The plant-bearing interval is restricted spatially and stratigraphically, with a maximum thickness of 20 cm. Plant debris is highly fragmented, dispersed on bed surfaces, and poorly preserved as impressions (Fig. 5G). There is no apparent order or arrangement to isolated leaf fragments, sphenopsid axes, and possible reproductive structures; all remnants are small (generally <5 cm in length).

Commando Drift: A new plant locality above the P/Tr boundary at Commando Drift in the Palingkloof Member occurs in a green-gray, coarse-grained siltstone that exhibits low-angle cross-bedding (Fig. 4D; Appendix, <<http://www.sepm.org/archive/index.html>>). Here, siltstone fills scour-and-fill structures left behind on the upper surfaces of thin, fine- and very fine-grained sandstone bodies.

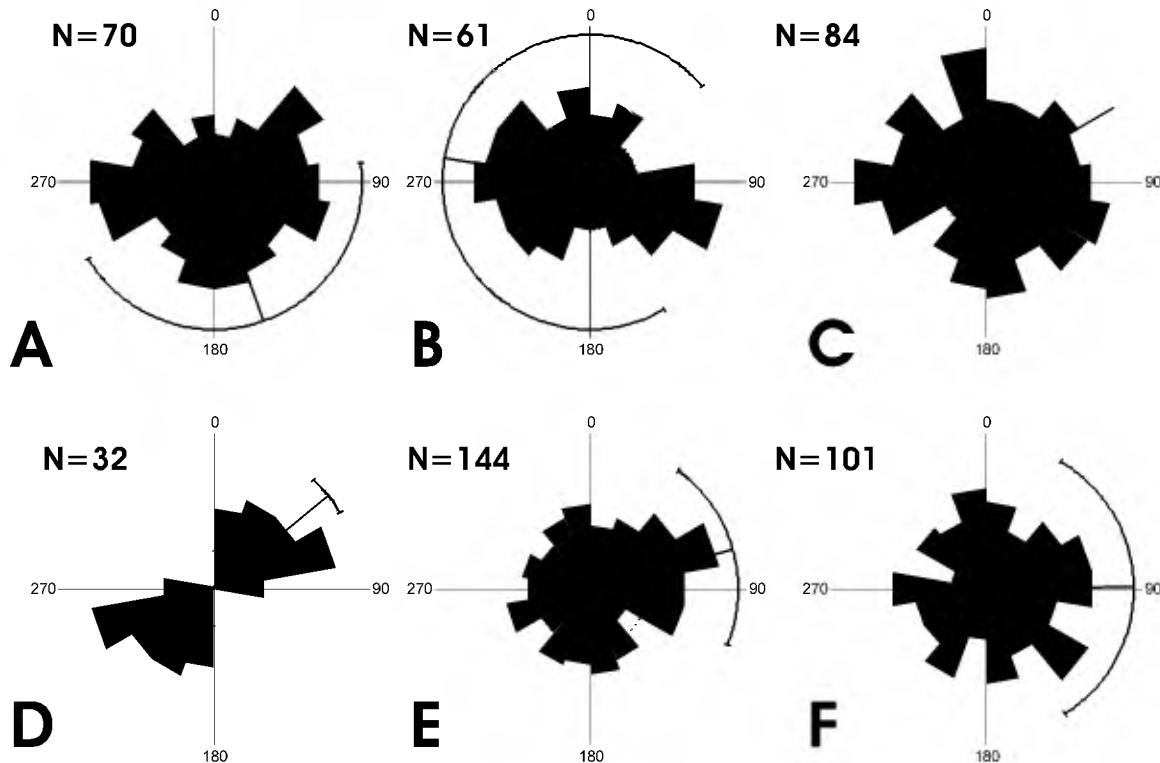


FIGURE 7—Rose diagrams of *Glossopteris* leaf and *Phyllothea* stem orientations with the 95% confidence interval calculated using Oriana v. 2.02. (A) *Glossopteris* leaf orientations from the 35-cm bed level at Ashtonvale Farm ($n = 70$). Leaves are oriented randomly, failing the Rayleigh Test of Uniformity ($Z = 1.03$; $p = 0.357$). (B) *Glossopteris* leaf orientations from Tradestore Donga ($n = 61$). Leaves are oriented randomly, failing the Rayleigh Test of Uniformity ($Z = 0.144$; $p = 0.443$). (C) A composite plot of all *Glossopteris* leaf orientations from Bed i in the Clouston Farm donga ($n = 84$). Leaves are oriented randomly, failing the Rayleigh Test of Uniformity ($Z = 0.078$; $p = 0.925$). (D) Orientations of compressed and siltstone-cast *Phyllothea* axes in Bed ii in the Clouston Farm donga ($n = 33$; $Z = 27.792$; $p = 6.65 \times 10^{-12}$). (E) *Glossopteris* leaf orientations from Bed ii in the Clouston Farm donga ($n = 144$). A composite plot of leaves from all bedding planes evaluated; leaves are not oriented randomly, passing the Rayleigh Test of Uniformity ($Z = 4.335$; $p = 0.013$). (F) *Glossopteris* leaf orientations from Bed iii in the Clouston Farm donga ($n = 101$). A composite plot of leaves from all bedding planes evaluated; leaves are oriented randomly, failing the Rayleigh Test of Uniformity ($Z = 1.806$; $p = 0.164$).

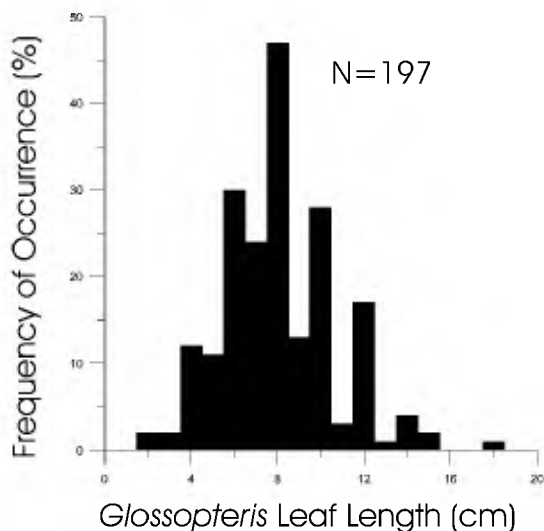


FIGURE 8—Histogram of leaf-size distribution of *Glossopteris* at Clouston Farm ($n = 197$).

Sandstones generally are less than 2 m in thickness and lenticular in geometry, suggestive of sand-wave bedforms. Basal, planar beds are ripple laminated at their upper contact and overlain by low-angle crossbeds in which mud clasts and plant debris occur. Cross-bed thickness is millimeter to centimeter in scale, and isolated, fragmentary, very poorly preserved impressions of axes and ?seeds occur on bedding surfaces (Fig. 10G). Channel deposits are interbedded with gray-red coarse-grained siltstone and green-gray to olive green fine-grained siltstone, which may be erosionally scoured.

Wapadsberg Pass: The Permian at Wapadsberg Pass (Smith et al., 2002) consists of thin, cross-bedded and rippled sandstones overlain by thicker green-gray or olive siltstone of fining-upwards cycles wherein there is a change from high-sinuosity to low-sinuosity fluvial systems (e.g., Ward et al., 2000; Fig. 9A). Five and a half meters below the noduliferous siltstone (P/Tr boundary; Smith et al., 2002) is a greenish gray, coarse-grained siltstone in which at least two *Glossopteris* taxa and sphenophyte axes are preserved. Horizontal and dense, cylindrical, lined, sandstone burrows are preserved as hyporeliefs in the base of the channel-fill sequence, which lies in sharp contact with an underlying siltstone. This channel-fill sequence consists of three upwards-fining units with fine,

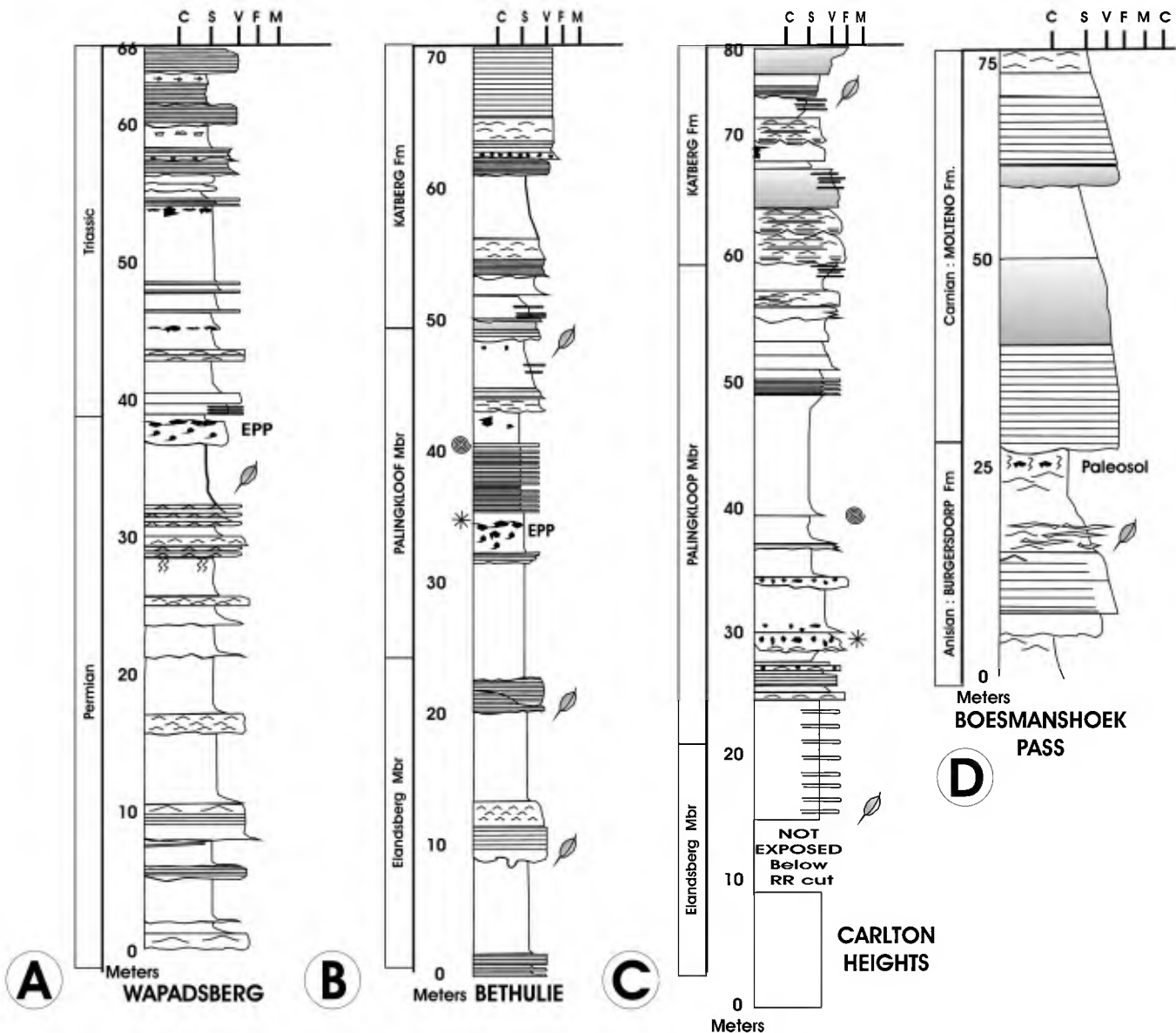


FIGURE 9—Measured Permian and Early to Middle Triassic stratigraphic sections (for details on localities, see Fig. 3 and Appendix <<http://www.sepm.org/archive/index.html>>). (A) Donga and roadcut section at Wapadsberg, with poorly preserved *Glossopteris* leaves beneath the EPP in a fining-upwards channel-fill sequence. Outcrop exposure is very limited, preventing assessment of rock-body geometries. (B) Partial section at Bethulie spanning the P/Tr boundary in which *Glossopteris*-bearing assemblages are preserved below the EPP, and a fragmentary assemblage was found in the Early Triassic. The exact placement of the P/Tr boundary at this section is contentious. Ward et al. (2000), Smith and Ward (2001), and Ward et al. (2005) placed the boundary at the top of the carbonate-nodule bearing paleosol (EPP; at asterisk) below the laminated event beds. Retallack et al. (2003) placed the P/Tr boundary at the top of the laminated event beds, based on the presence of the Late Permian therocephalian *Moschorhinus* (at spiral). Although unstated, Ward et al. (2005) considered the extended range of *Moschorhinus* and *Tetracynodon* into the earliest Triassic laminated event beds as indicative of survivor taxa (see Ward et al., 2005, and data therein). (C) Exposures in a donga, railway, and roadcuts in which the P/Tr boundary reportedly is exposed at Carlton Heights. Ward et al. (2005) placed the boundary at the carbonate-nodule bearing horizon below their laminated event beds, whereas Retallack et al. (2003, fig. 4) placed the boundary at the top of this sequence (i.e., laminites; at the spiral). No laminites were observed in either the donga or laterally equivalent strata at this locality (Gray et al., 2004). Poorly preserved fossil plants occur in the Katberg Formation; no fossil plants have been recovered from the Palingkloof Member, although very poorly preserved macrofloral remains were collected in the Elandsberg Member. Note that a complex stratigraphy exists in this section requiring a generalization of rock relationships in the diagram. (D) A Middle Triassic exposure of the Burgersdorp Formation at Boesmanshoek Pass exemplifies the relationship of plant-fossil assemblages within these fluvial systems.

greenish-gray sandstone overlain by similarly colored, coarse-grained siltstone. All plant fossils are preserved as fragmentary impressions with cm-scale debris in the uppermost siltstone (isomeric assemblage; Fig. 5F). Fragments are isolated and dispersed, without any spatial or-

dering. Sphenopsid axes, up to 4 cm wide and >20 cm long, may or may not be concentrated on the bedding.

Bethulie/Bethel Farm: The P/Tr section examined at Bethulie is the same as that used by Smith (1995), MacLeod et al. (2000), Ward et al. (2000), Retallack et al.

(2003), and Ward et al. (2005). Below the boundary are green-gray siltstones in which there are both ribbon sandstones and a few, thick, multistoried, fine-grained sandstone bodies. Two plant-bearing sites have been identified within this part of the section (Fig. 9B). The lowest plant bed is ~31.75 m below the P/Tr boundary and is preserved in an altered, red-gray siltstone within a channel-sandstone sequence. Yellowish-gray, fine-grained sandstone is organized in stacked megaforms, each of which has an amplitude of 40 cm and wavelengths of a few meters. A fossiliferous, dark, greenish-gray, coarse-grained siltstone is interbedded within this sandstone. Well-defined, isolated plant impressions occur on bedding planes of thin siltstone beds, 3–5 mm in thickness. There is no apparent order to, nor concentration of, the plant debris, which is dominated by axial remains. The original thickness of the interval is unknown because of an erosional upper contact with the overlying fine-grained sandstone bedforms.

The second locality, ~17.25 m beneath the EPP, also is found within fluvial deposits. Here, two fossiliferous intervals occur in close stratigraphic proximity to each other. Sandstone sheets, exhibiting *en-echelon* stacked barforms and ball-and-pillow structures, are overlain by thick, greenish-gray siltstone in which bounding surfaces are identifiable. Long, thin, narrow *Glossopteris* leaf impressions, along with sphenopsid axial remains, occur either isolated or in mat-like arrangements, 3–4 leaves thick, at the top of one siltstone interval (Fig. 10A, B). Leaves and axes may be oriented parallel to each other, as in some instances, or divergent without apparent orientation. All plant parts are of approximately equal size, with a maximum-length dimension of 10 cm. Overlying the siltstone are fining-upwards sequences consisting of thin, planar-tabular sandstone sheets or offset lenticular structures (waveforms) overlain by coarse-grained siltstone. Here, the siltstone is suspension-load fill within a scour structure. Poorly preserved, isolated impressions of *Glossopteris* leaves and sphenopsid axes occur on bedding surfaces, with venation and axial ridges visually prominent. The remains are similar in size to those noted above.

A channel-scour structure above the P/Tr boundary in Bethulie also preserves plant material in coarse-grained siltstone. The site is placed ~8 m above the P/Tr boundary, and is identified by the occurrence of *Moschorhinus* (Retallack et al., 2003, fig. 4) preserved in a nodule layer at the top of the laminated event-bed interval (MacLeod et al., 2000; Ward et al., 2000; Smith and Ward, 2001; Gray et al., 2004; Ward et al., 2005). Presently, this megafossil assemblage is thought to be within the Palingkloof Member below the Early Triassic Katberg Formation (Fig. 10C, D). This interval falls between rocks that are recognized as Palingkloof or Katberg, and bears characteristics of both. Here, three upwards-fining cycles of very fine-grained sandstone overlain by coarse-grained siltstone, in turn, are overlain by a thick sandstone unit consisting of stacked sheet sandstones. This uppermost sandstone is typical of the Katberg. Tracing the Palingkloof–Katberg contact within the area is difficult due to lateral interfingering of facies. Hence, the stratigraphic assignment to the Palingkloof is made based on the higher proportion of green-gray siltstone as opposed to a predominance of yellow-gray sandstone. This Early Triassic horizon consists of impressions of highly fragmented axes and fern pin-

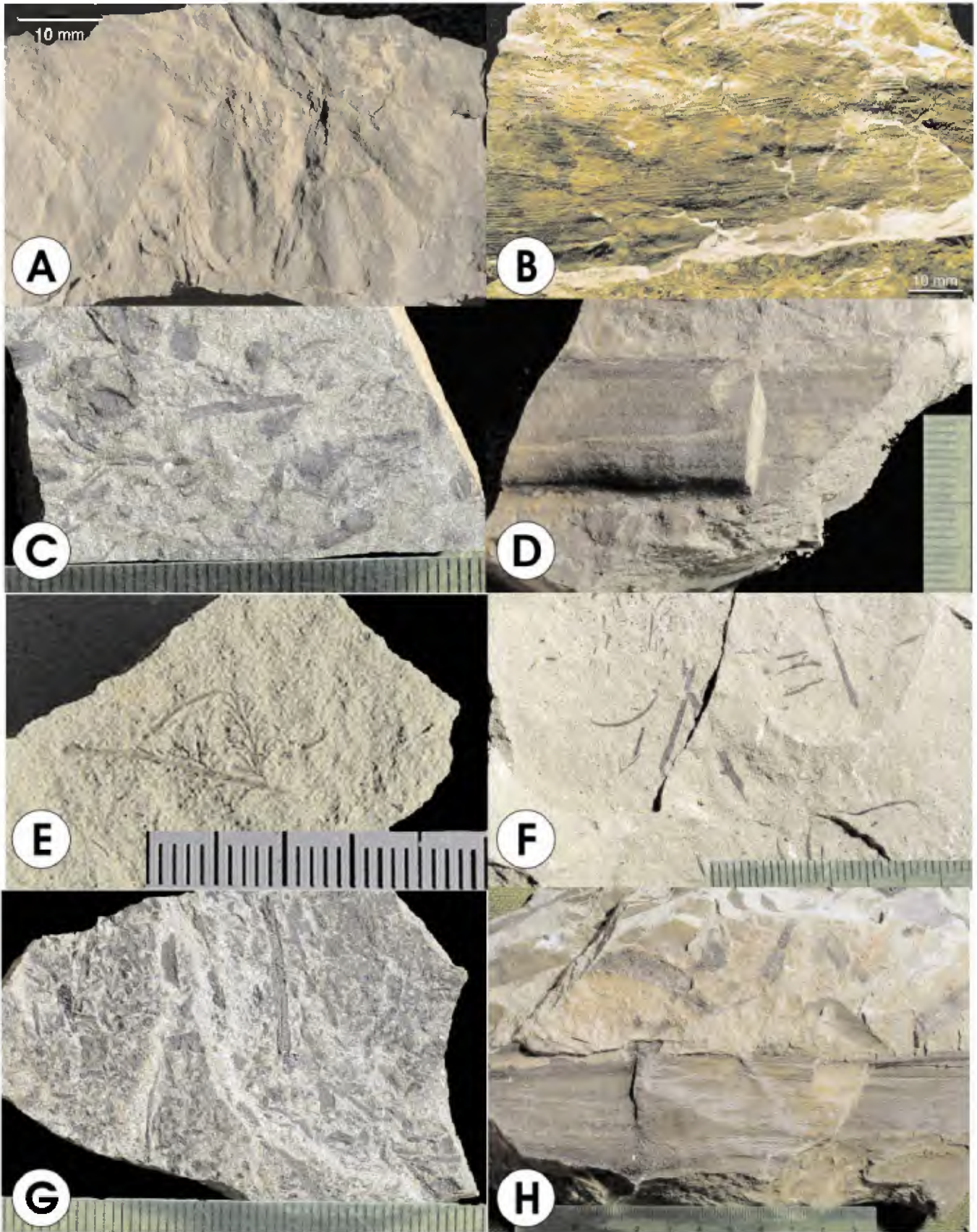
nules, along with seeds and possibly other reproductive structures (Fig. 10C, D). Most material is less than a few centimeters in overall dimensions, although axial fragments may be a decimeter in length. Debris may be concentrated or isolated in the matrix, and there is no indication of plant-part alignment. All material is poorly preserved.

Carlton Heights: To date, no macroflora has been identified in Upper Permian rocks in the Carlton Heights section, although palynological assemblages have been recovered and assessed (Steiner et al., 2003). However, a new earliest Triassic assemblage has been recovered from the base of the Katberg Formation at this site (Fig. 9C; Appendix, <<http://www.sepm.org/archive/index.html>>). Here, the Katberg is a multistoried, fine-grained, gray to white, sandstone-channel system overlying a heavily bioturbated, coarse, greenish-gray siltstone. Basal contacts within the fluvial regime are erosional, with lenses of intraformational mudstone pebbles and pedogenic carbonate-nodule conglomerate. The sandstone exhibits both horizontal and large-scale trough stratification, along with soft-sediment deformational features and small-scale mudcracks. Isolated, poorly preserved plant remains occur in a very fine-grained, rippled sandstone that infills a megaripple trough. There is no apparent order to the assemblage, with most fragmentary debris on the order of 5 cm in maximum dimension. Impressions of sphenopsid axes, dispersed fern pinnules, and reproductive structures, including a possible peltasperm, occur scattered in the matrix (Fig. 10E, F).

Lady Frere and Boesmanshoek

There is a dearth of Lower Triassic plant-fossil localities in the Karoo Basin, and a considerable gap exists from the Induan (Early Triassic, 251–249.7 Ma) to the Anisian (Middle Triassic, 245–237 Ma). Plant fossils occur in Middle Triassic fluvial complexes of the Burgersdorp Formation, which overlies the Katberg Formation. Hancox (1998, 2000) demonstrated that this unit can be subdivided into lower, middle, and upper intervals (corresponding to his informal subzones A, B, and C) based on paleontological and sedimentological criteria. There is a change in paleoclimate indicators from the lowermost Burgersdorp Formation, a semi-arid fluvial regime, to the top, where a more humid fluvial landscape predominates. Only poorly preserved, fern-like fragments have been found in the lowermost Burgersdorp Formation (Hancox, pers. comm., 2003), but a better plant record is known from the middle and upper parts of the formation.

The site at Lady Frere (previously located in the Transkei) occurs within the middle Burgersdorp interval, and was documented first by Brown in unpublished journals (1859–1920) and later by Anderson and Anderson (1985). This stream-cut and hillside exposure (Appendix, <<http://www.sepm.org/archive/index.html>>) consists of very fine- to fine-grained lithic arenites overlain by grayish red siltstone, some of which has undergone pedogenic alteration. A medium- to coarse-grained, poorly sorted, wedge-shaped lithic arenite exposed in the stream cut is overlain by a coarse-grained siltstone and very fine-grained sandstone-trough fill in which plant fossils are preserved. This fossiliferous interval is overlain by low-angle, lateral-accretion



beds of fine-grained sandstone in which plant axes are preserved on internal bedding surfaces. A heteromeric assemblage, consisting of compressed ginkgophyte (*Sphenobaiera*), cycadophyte, pteridosperm/conifer (*Heidiphyllum*), and taeniopterid foliage (identification based on Anderson and Anderson, 1985), along with robust axes and ?conifer shoots, seeds, and reproductive structures, is restricted to a 0.5-m-thick interval (Fig. 10H). As noted by other authors, this assemblage is similar to that found in the overlying Molteno Formation. Plant parts, including leaves, may be parallel, perpendicular, or at some angle to bedding, indicating that the leaves were turgid at the time of emplacement. The leaves are not highly fragmented, probably due to their coriaceous (robust) character. Additionally, sandstone-cast axes are parallel to bedding, indicating some residence time at the sediment-water interface before burial. There is no apparent order to the debris, nor are the plant parts concentrated in beds. Each leaf or axis is isolated in the matrix, with little to no overlapping of parts.

A similar taphonomic signature is evident in the Burgersdorp C interval, based on a new collection at Boesmanshoek Pass (Fig. 9D; Appendix, <<http://www.sepm.org/archive/index.html>>). Plant impressions are preserved in coarse-grained siltstone interbeds up to 50 cm thick, within very fine-grained sandstones deposited in a large fluvial system. Well-preserved leaves of *Heidiphyllum*, fern pinnules, and ?sphenophytes are densely concentrated on bedding surfaces, with both axial material and some specimens of *Heidiphyllum* parallel to subparallel in alignment. Accretionary sandstone in lateral barforms preserves impressions of axes, and these also may be aligned parallel to subparallel. Fragmentary plant debris is intermixed with better-preserved specimens.

PLANT TAPHONOMIC TRENDS

Hiller and Stavarakis (1984) first described the stratigraphic changes in fluvial systems of the Karoo Basin near East London (Fig. 3) in which the Upper Permian part of the Balfour Formation is characterized by sandy point-bar sequences of high-sinuosity rivers and fine-grained floodplain deposits. The change in fluvial style occurred with deposition of the Lower Triassic Katberg Formation, wherein low-sinuosity, braided river systems were attributed to tectonic rejuvenation in the Cape Fold Belt (Catuneanu and Elango, 2001). Sediment from this orogenic source continued to be deposited into the Middle Triassic (Burgersdorp Fm.) in which sand-dominated,

anastomosing and avulsing channels with aggradational floodplain deposits occur. Smith (1995), Ward et al. (2000), and Smith and Ward (2001) focused on the changes in fluvial character within the Balfour Formation at Bethulie and at sites east of 26°30' (Fig. 3). These authors affirmed previous interpretations and documented spatial heterogeneity across the basin in these facies (Fig. 11). They also interpreted a change from Late Permian, single-storied fluvial systems, characterized by low-angle, lateral-accretion surfaces, to a well-laminated, interbedded sandstone-siltstone interval underlain and overlain by sheet sandstones at the P/Tr boundary (Ward et al., 2000; Smith and Ward, 2001). The decimation of the terrestrial flora in response to the P/Tr extinction event was interpreted to have been the cause of the resultant change in fluvial regime.

The trend in fossil-plant assemblages parallels the change in fluvial style, as would be expected based on actualistic studies and deep-time data (e.g., Gastaldo et al., 1987; Gastaldo et al., 1989; Behrensmeier and Hook, 1992; Gastaldo et al., 1993; Gastaldo, 1994, 2001, 2004; Gastaldo et al., 1996; Gastaldo et al., 1998). Late Permian assemblages are characterized by stratigraphically successive mats of overlapping *Glossopteris* leaves, nodal whorls of *Phyllothea*, and other aerial debris (Fig. 12). These are well-preserved, entire leaves without evidence of skeletonization prior to burial (Gastaldo and Staub, 1999), and such mats dominate each bed or accumulation. Mats are preserved either in (1) fine-grained megaripples, where debris was emplaced within bedload deposits of channels of unknown geometries (Ashtonvale, Tradestore Donga; Fig. 5A); or (2) abandoned channel fills characteristic of oxbow lakes (Loskop, Colenso, Clouston Farm; Fig. 5B, C). These assemblages are parautochthonous and represent contribution from vegetation that grew in close proximity to the channels and/or lakes.

Latest Permian assemblages (Ennersdale, Commando Drift, Bethulie, Wapadsberg) differ in that they consist only of poorly preserved, fragmentary stem-and-leaf debris restricted to lateral-accretion and within-channel barforms. Although the assemblages also occur in coarse-grained siltstone, these fluvial channels are of a shallower character, as documented by previous authors. However, the distribution of plant-bearing intervals within close stratigraphic proximity at Bethulie indicates a somewhat deeper, silt-dominated regime. All latest Permian floras are allochthonous, with more robust sphenopsid axes dominating the assemblages, and intermixed with fragmentary leaf remains (Fig. 12).

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FIGURE 10—Allochthonous plant-fossil assemblages from the Late Permian and Early Triassic Balfour Formation, Karoo Basin. (A) Isolated, concentrated *Glossopteris* leaf impressions from the Late Permian section at Bethulie (from ~20 m below the proposed P/Tr boundary of Ward et al., 2005). Scale = 10 mm. (B) Concentrated, aligned sphenopsid axes in siltstone, Bethulie (from ~20 m below the P/Tr boundary of Ward et al., 2005). Scale = 10 mm. (C) Isolated, dispersed plant debris preserved as impressions in fine-grained sandstone approximately 12 m above the P/Tr boundary (Ward et al., 2005) at Bethulie. Scale in mm. (D) Isolated, poorly preserved, sand-filled axis of undetermined affinity in fine-grained sandstone (BS4 level) occurring ~12 m above the P/Tr boundary. Sandstone-cast axis indicates residency time of hollowed stem at the sediment-water interface prior to burial (Gastaldo et al., 1989). Scale in mm. (E) Isolated, degraded, impression of a partial fern pinna on which the venation patterns of the pinnules are preserved in a fine-grained sandstone, Katberg Sandstone, Carlton Heights; scale in mm. (F) Impressions of isolated, unidentified axial and leaf fragments in fine-grained sandstone, Katberg Sandstone, Carlton Heights. Scale in mm. (G) Concentrated, macerated debris preserved as impressions or adpressions on crossbed surfaces above the P/Tr boundary at Commando Drift Farm. Scale in mm. (H) Early Triassic axial-dominated assemblage of impressions and adpressions from Lady Frere. Axes may be sandstone casts or impressions preserved in fine-grained sandstone. Scale in cm.

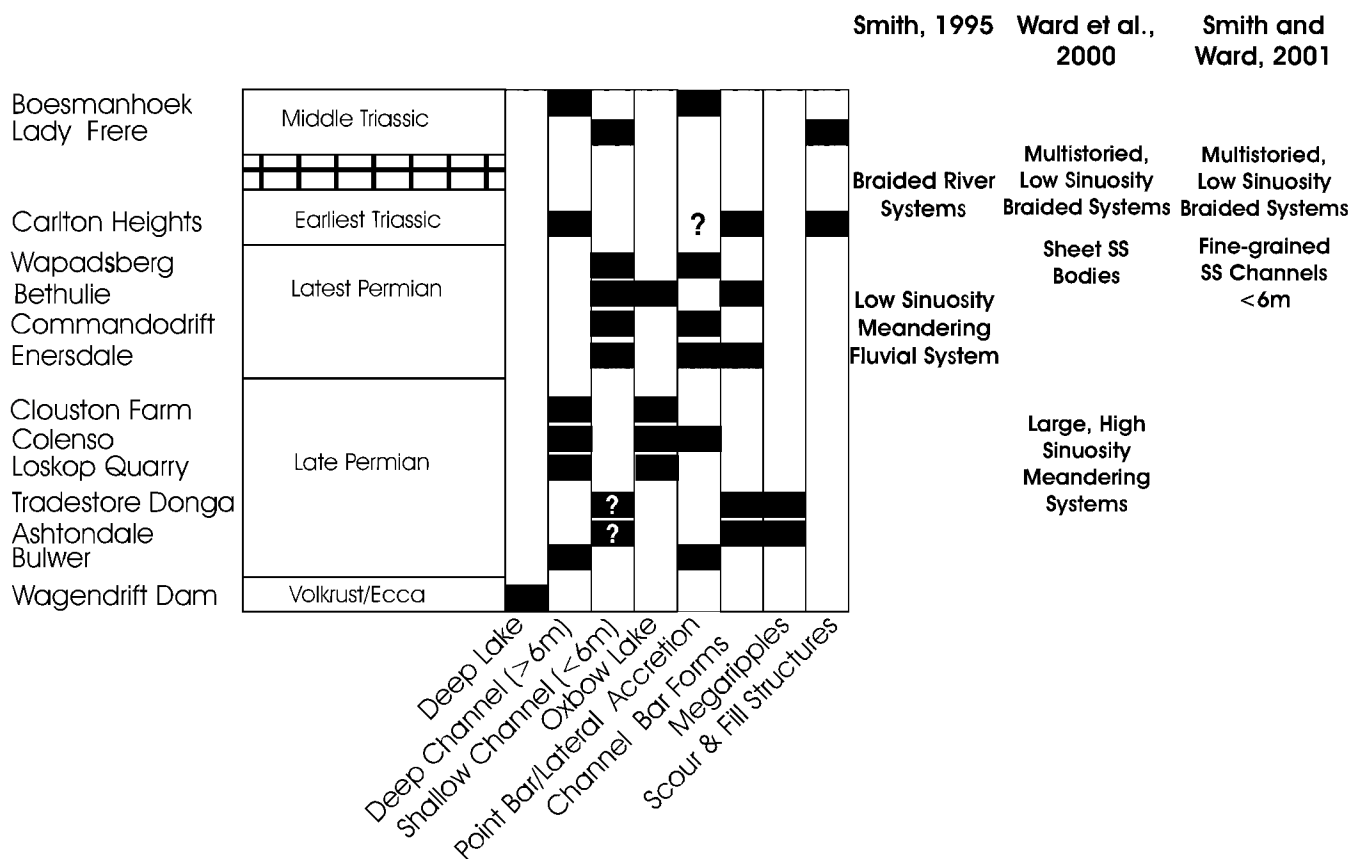


FIGURE 11—Diagram showing stratigraphic order of localities used in this study plotted against depositional environment and sites therein at which plant fossil assemblages were recovered. The generalized change in fluvial style from the Permian to Triassic within the Karoo Basin provided here is based on Smith (1995), Ward et al. (2000), and Smith and Ward (2001).

The earliest Triassic assemblages from a scour-and-fill structure in the Katberg Sandstone at Carlton Heights and in the Palingkloop Member at Bethulie continue the latest Permian trend. Here, isolated and dispersed debris consisting mainly of axial material with a small admixture of fragmentary leaves also indicate allochthonous assemblages (Fig. 12). By the time plant fossils are encountered in the Middle Triassic Burgersdorp Formation, more than 6 million years later, the assemblages consist of a higher proportion of leaves owing to the more coriaceous or robust nature of the taxa. Still, these Anisian deposits represent accumulation of allochthonous aerial debris. It is not until the Late Triassic Molteno Formation when parautochthonous assemblages again are encountered in the Karoo Basin (e.g., Cairncross et al., 1995).

DISCUSSION

The analysis and interpretation of biodiversity trends over space and time shape our understanding of events in Earth history. This is particularly true when assessing the global biological response at critical intervals, such as the Permian-Triassic boundary extinction. Previous contentions assert that global, catastrophic loss of terrestrial vegetation (both in numbers and in diversity) paralleled the diversity crisis in the oceans (e.g., Retallack, 1995; Retallack et al., 1996; Ward et al., 2000). Such interpretations are based, in part, on the paleobotanical records in South-

ern Hemisphere continental deposits, including those in the Karoo. To date, the taphonomic character of macrofloral assemblages above and below the boundary has been documented neither in Antarctica (Retallack and Krull, 1999) nor in Australia, or dismissed in the case of the latter's continental record (Retallack, 1995). Hence, the present study provides some insight into the terrestrial plant record of South Africa, the results of which may be applicable to other P/Tr continental records.

There is a distinctive change in plant taphonomic character in the Karoo Basin. Late Permian assemblages occur as well-preserved, complete leaves found in mat structures within mudrocks of fluvial channel-fill sequences. In contrast, dispersed, fragmentary, and rare, non-carbonaceous debris, impressed in fine-grained sandstones and coarse-grained siltstones of scour-and-fill, trough fills, and sand-wedge drapes, occur beneath and above the P/Tr boundary. This taphonomic imprint continues into the Middle and Late Triassic (Cairncross et al., 1995).

It is well established that preservation of leaves requires hydrological conditions that isolate them from biological or physical degradation (e.g., Gastaldo, 1994, 2001). These are some of the least-resistant plant parts, and they must reside within a geochemical environment that is conducive for preservation in order to be preserved (Gastaldo and Staub, 1999). Critical geochemical thresholds exist in terrestrial depositional environments that

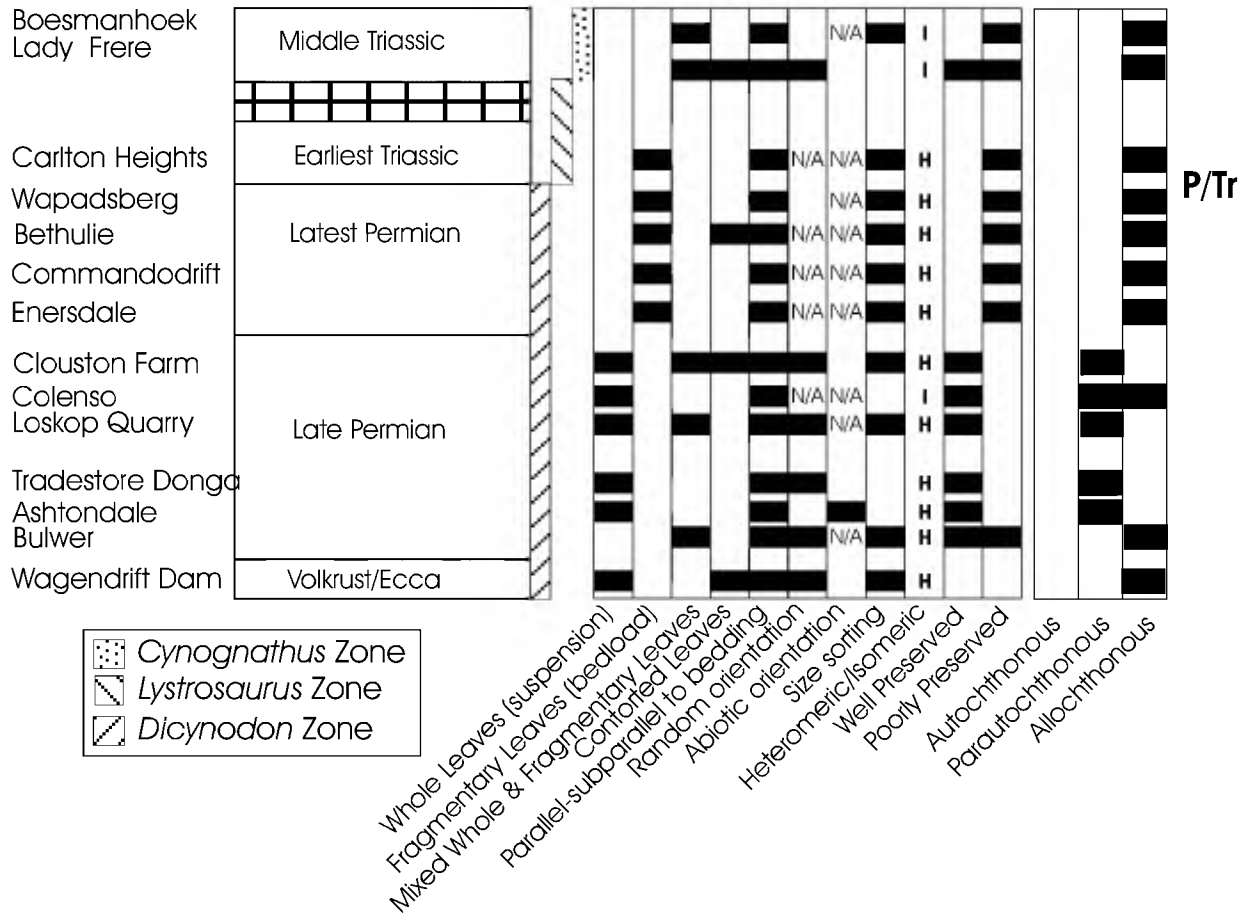


FIGURE 12—Diagram showing stratigraphic order of localities used in this study plotted with the taphonomic characteristics of the plant assemblages collected. A shift from allochthonous assemblages to parautochthonous assemblages in the Late Permian is evident. The latest Permian localities are characterized only by allochthonous plant accumulations, a depositional feature limited by prevailing hydrological conditions that continued into the Middle Triassic Burgersdorp Formation.

promote or retard rapid loss from the potential stratigraphic record. Such thresholds include oxygen levels, redox potentials, and cation availability for early diagenesis, all of which are related to climate. Conditions for plant preservation exist in wetter areas regardless of regional climate, and these spatially restricted sites provide an *a priori* bias towards plants that potentially can be preserved. In addition, leaves only have one chance for preservation in a state that allows for later systematic identification. Re-entrainment of saturated leaf material in a fluvial system always results in comminuted plant detritus because of interaction with bedload transport (Gastaldo et al., 1987; Gastaldo, 1994).

Put another way, preservation of plant debris as fossil is controlled by the level of the water table and the pore-water chemistries that exist in space and time at the site of burial (Gastaldo, 1994). This is particularly true for the preservation of any and all plant parts composed of parenchymatous (soft) tissues. Leaves, reproductive structures, roots, and non-woody axes undergo decay within weeks to years, and the rate depends upon the prevailing climate (Gastaldo and Staub, 1999). Burial, in and of itself, does not promote fossilization of these parts. Rather, plant parts must be maintained in subsurface, fully saturated sediment following burial where there are sufficient

pore waters, and the correct pore-water chemistries, to retard and/or prevent microbial decay. Internal cellular breakdown will occur even under these conditions, but the residual carbon and/or outline of the part will be retained and recognizable. Under fluctuating pore-water conditions, where oxygenated water and/or atmospheric gas are introduced to the sediment (natural rise and fall of ground-water table, including short-term drought conditions), the chances of preservation are reduced to nil. Therefore, in any continental basin where a change in depositional regime is recorded wherein fluvial systems become more braided or bedload dominated (either due to a change in bedload grain size, landscape gradient, or the temporal distribution pattern of rainfall to a more episodic and flashy discharge), the prevailing hydrological conditions prevent or minimize the potential for plant-part preservation. Under these conditions, it is difficult, if not impossible, to find a macrofloral record that actually records the vegetation that existed at that time. This also is true of palynological assemblages.

Therefore, it is of no surprise that a shift in fluvial style results not only in a change in the quality and quantity of plant material in any section, but also in its taxonomic diversity. The predominance of robust axes (sphenopsid stems) interspersed with bits and pieces of indeterminate

leaf remains and impressions of fern pinnules within the P/Tr boundary interval is a natural consequence associated with a change in the river systems. Hence, the apparent loss in terrestrial floral diversity may reflect the available sample, and not the catastrophic demise of the vegetation-landscape as has been proposed (Ward et al., 2000; Smith and Ward, 2001; Retallack et al., 2003). Palynological preparations from these Karoo sections now are being processed and evaluated. These data may provide an independent test on the extent of terrestrial plant loss at and across the boundary (if preserved; see caveat above).

The terrestrial plant-fossil record, *in toto*, is controlled by the prevailing basinal landscape. In turn, this landscape is controlled by regional, hemispherical, and/or global climate. Fully continental basins react to climate change in a variety of ways. Regional or localized generation of new accommodation through tectonism, wherein shifting depocenters are associated with an increase in stratigraphic resolution over time by allowing for more localized sediment accumulation, controls the overall stratigraphic resolution. It is understood and acknowledged that the development of mini-basins and/or spatially restricted sub-basins (flexural provinces) will result in a stratigraphic mosaic within any complex basin, such as the Karoo (Catuneanu et al., 1998). Correlation between these areas is essential to understand the landscape response at a basinal scale. To date, there is no high-resolution basin model in the public domain upon which such a correlation can be made.

The Permian–Triassic Beaufort Group was deposited in a foreland/retroarc-foreland basin during a phase of overfill (Catuneanu et al., 1998; Catuneanu and Elango, 2001). In their research on the Balfour Formation, Catuneanu and Elango (2001) recognized six 3rd-order fluvial sequences, each of which is reported to be capped by subaerial unconformities (SU). Unfortunately, most contacts between sequences are cryptic along the Grahamstown to Queens-town Road (R67, pers. obs., 4/2005). For example, no criteria are provided in Elango (1999) to identify SU #1 in the field, making recognition of this boundary difficult. Subaerial Unconformity #2 occurs stratigraphically between two road-cut exposures and is not visible, whereas photo-mosaics of SU #6 in Elango (1999) do not match the outcrop exposure figured in Catuneanu and Elango (2001, fig. 13). Each unconformity is reported to be regionally extensive, associated with truncation and fluvial incision, with abrupt lithofacies changes above and below the unconformities. Only fluvial facies are identified within each 3rd-order sequence, and paleosols are encountered rarely within any sequence (Catuneanu and Elango, 2001). It is probable that paleosols may occur at one or more of these unconformities (unless removed by degradational processes; see below). But, no paleosol features could be found in those outcrops where subaerial unconformities correlated with published observations (i.e., SU #4; Catuneanu and Elango, 2001, p. 296). The amount of time represented within each sequence is unknown because there is no credible chronometric control within this part of the Permian.

Sedimentary sequences within entirely continental basins are the consequence of a balance and interchange between aggradational and degradational processes (Bull, 1991). The results of aggradational processes are found within stratigraphic sequences and fluvial architectures,

whereas those of degradational processes are marked by the bounding unconformities that exist between fluvial sequences. The plant-fossil record is preserved in such aggradational sequences and not at the bounding surfaces. Bounding unconformities form by the processes of relative base-level fall and erosion, periods of minimal or no deposition, or some combination or succession of both (Demko et al., 2004). During intervals of landscape degradation (e.g., drainage-system incision, mass wasting, etc.), previously deposited sediment (and the potential fossil material therein) is removed from the surface (or shallow subsurface) and transported away, or is subject to pedogenesis in response to the effects of fluctuating water tables. The degree of pedogenesis and the depth to which alteration occurs at the unconformity depends upon the amount of time during which the landscape surface was exposed, as well as the prevailing or changing climate conditions during the exposure interval. Erosion and/or pedogenesis of sediments at and below a regional unconformity will result in the degradation and loss of underlying plant accumulations as oxygenated ground waters interact with the organic matter (e.g., Gastaldo et al., 1998). Rapid sedimentation associated with the subsequent aggradation of the landscape surface (the overlying fluvial sequence) will result in a well-preserved plant-fossil record (Demko et al., 1998). It is within this context, then, that the plant-fossil record of the Karoo must be assessed.

Catuneanu and Elango (2001) agreed with previous interpretations that temperate to humid conditions prevailed throughout accumulation of Lower Beaufort cycles, with a distinct change beginning somewhere at or below the Katberg Sandstone. Absence of color change (Smith et al., 1998), presence of a consistent paleontological record (Rubidge, 1995), and the asymmetrical nature of the fluvial sequences throughout the Lower Balfour are used to support this inference. The character of the plant taphonomic record presents a different image. Because the conditions required for maintaining highly labile organic remains (leaves, roots, etc.) are very restricted, the change in plant taphonomic character within the Lower Balfour truly indicates a change through time in preservational potential that is related to the landscape and, ultimately, climate. Hence, the onset of very poorly preserved, fragmentary plant-fossil assemblages decimeters below the P/Tr boundary (at least Sequence 'F'; Catuneanu and Elango, 2001) that are confined to sand waves, scour-and-fill, and trough fills within crossbeds, indicates fluctuating groundwater conditions within the landscape that probably were the result of sporadic rainfall and discharge events. These conditions are in stark contrast to the plant-fossil assemblages encountered lower in the Lower Beaufort where the sandstone:mudstone ratio is lower. The inferences on groundwater levels and geochemical constraints for preservation based on the plant taphonomy also are reflected in the distribution of carbonate concretions/nodules found in the End Permian Paleosol (De Kock and Kirschvink, 2004; P/Tr boundary of Ward et al., 2000, and Smith and Ward, 2001), although the stratigraphic relationship of this paleosol to the bounding unconformities identified by Catuneanu and Elango (2001) is unknown at present. A reasonable hypothesis would place the EPP at the upper boundary of their sequence 'F' (SU #7), which occurs just below the Katberg Formation.

CONCLUSIONS

A change in plant taphonomic character that occurs within the Lower Beaufort Group of the Karoo Basin is related to changing fluvial regimes and, hence, climate-controlled landscapes. The basalmost exposure examined in this study near Escourt, KwaZulu-Natal Province, preserves well-sorted, allochthonous, small leaves of *Glossopteris* and *Phyllothea* whorls in turbidite deposits of the Eccia Group (Selover and Gastaldo, 2005). The fluvial systems of the Lower Beaufort Group are characterized by leaf-mat assemblages of well-preserved aerial plant parts either in silt-dominated bedload regimes of deep channels or within oxbow-lake fills. All assemblages are parautochthonous. Within decameters below the P/Tr boundary, only poorly preserved, fragmentary allochthonous assemblages are preserved in barforms of a relatively shallow fluvial nature. Similar assemblages, which are found across the boundary in the lowermost Triassic, also typify the Middle Triassic, where plant debris is isolated within scour-and-fill structures. The presence of plant fossils in the Early Triassic Palingkloof Member and Katberg Formation indicates that the landscape was stabilized by a variety of vegetational architectures, providing evidence to negate previous claims that a regional extinction/extirpation of plants resulted in a change in fluvial style in the Karoo basin (e.g., Ward et al., 2000).

Preservational styles throughout the Balfour reflect prevailing hydrological and geochemical conditions at the time of burial, as well as diagenetic overprinting. Loss of preservation potential as the result of landscape unconformities generated by tectonism and climate has played a significant role in the plant-fossil record available for analysis of diversity trends throughout this critical interval in the Karoo and, potentially, elsewhere in continental Gondwana sequences. Without a full understanding of the processes responsible for the generation and preservation of the data set used to interpret the response of the terrestrial ecosystem to the P/Tr boundary event, care should be taken in its application. Of course, this conclusion is less desirable than one where this study's results could address directly the questions and hypotheses on the response of vegetation to the P/Tr boundary event (e.g., Ward et al. 2000; Smith and Ward, 2001; Retallack et al., 2003). But, the results presented here record the outcome of the physical, chemical, and biological processes that operated within the Karoo basin during, and subsequent to, the Late Permian. A more complete record is desirable, but compromised by nature itself.

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