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Portrait of a Gondwanan ecosystem: A new late Permian fossil locality from KwaZulu-Natal, South Africa

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ABSTRACT

The Clouston Farm locality, assigned to the Lopingian Epoch and occurring within the Normandien Formation of the northeastern Karoo Basin, provides evidence for a community of diverse vascular plants occupying riparian woodland. The depositional environment is interpreted as an abandoned trunk channel that preserved a megaflora in slack-water phases punctuated by overbank deposits from rare flood events. Of 9772 plant specimens tabulated from an unbiased census of all fragments greater than ~ 1 cm^2, there are 51 distinct organ morphotypes, including glossopterids, sphenopsids, and ferns, collectively represented as foliage, axes, fructifications, and dispersed seeds. Of the 11 most abundant morphotypes 10 are glossopterid morphotypes or variant subtypes, in addition to a sphenopsid. Glossopterid morphotype dominance also is reflected in the palynoflora. Palynological data indicate a Wuchiapingian age for the locality. A specimen of the dicynodont '*Oudenodon,*' found in a nearby stratigraphically equivalent outcrop, is attributable to the *Dicynodon* Assemblage Zone, assigned a younger Changhsingian age. A rich record of plant-insect associations demonstrates an elevated frequency of external foliage feeding by mandibulate insects and lower incidence of oviposition by palaeodictyopteroid and odonatopteroid taxa. Evidence for piercing-and-sucking and galling is rare. The most abundant plant taxon (glossopterid morphotype C2a) is the most intensively herbivorized, overwhelmingly by external feeding and ovipositing insects. Insect damage on this host is beyond that predicted by floristic abundance alone. This specificity, and high herbivory levels on other glossopterid taxa, demonstrates extension of the Euramerican pattern toward the preferential targeting of pteridosperms. The Clouston Farm site provides a glimpse into a late Permian ecosystem of primary producers, herbivores, and insectivores—a prelude to the crisis that engulfed life at the end of the period.

KEYWORDS: Permian, Lopingian, South Africa, Karoo, *Glossopteris* flora, herbivory, plant-insect interactions, palynology, palaeoecology.

1. INTRODUCTION

Pangaea during the late Permian was partitioned into several major biogeographic provinces, each characterised by elevated levels of endemic taxa. Cathaysia consisted of the isolated North and South China Terranes, major land masses that had not docked with eastern Pangaea proper. The other, major contiguous realms were a high-latitude, northern Angaran Realm (Meyen, 1987), an Euramerican Realm that extended as far south as northern Gondwana, but was separated from it by the Central Pangaean Mountains and associated with a major subtropical arid belt, and Gondwana, which occupied the greatest land mass and consisted of several major basins (Ziegler, 1990; Kutzbach and Ziegler, 1993; Ziegler et al., 1997, 1998; Rees et al., 2002) that preserved a distinctive record of plants, insects, and vertebrates (Anderson and Anderson, 1985; Schlüter, 1990; Lucas, 1998). Evidence from South America, southern Africa, Antarctica, India, and Australia indicates that the late Permian (Lopingian) was associated with a global greenhouse climate (Gastaldo et al., 1996a). The vegetation within the Gondwanan province varied spatially but generally was dominated by species of glossopterid gymnosperms (pteridosperms) and common to rare lycophytes, cordaitaleans, sphenophytes, and ferns (Maheshwari, 1976; Rösler, 1978; Anderson and Anderson 1985; Rohn and Rösler, 1986b; Taylor and Taylor, 1990; McLoughlin 1992; Cúneo et al., 1993; McLoughlin 1994a,b; Archangelsky, 1996; Pant, 1996; McLoughlin et al., 1997; Retallack and Krull, 1999; Retallack et al., 2005; Adami-Rodrigues and Iannuzzi, 2001). Despite the extensively documented distribution of Permian fossil-plant localities in the South African Karoo Basin, much remains unresolved regarding the systematic affinities of these taxa, their stratigraphic and geographic ranges, and their palaeoecological relationships (Lacey et al. 1975; Anderson and Anderson 1985; Kovács-Endrödy 1991; Adendorff et al., 2002, 2003).

In this paper, a new Upper Permian fossil-plant locality from the KwaZulu-Natal province of South Africa is detailed (Fig. 1). The site consists of extensive lateral exposure with several mudrock intervals containing well-preserved foliage, reproductive organs, and axes deposited in a deep, abandoned channel system. Most of the primary biological data consist of megafloral, wood, palynofloral, and isolated insect and vertebrate remains. Although few insect body-fossils have been recovered from the site, to date, more ecologically important are the significant insect-plant associations that are evidenced by a broad range of insect damage types preserved on leaves and, to a more limited extent, on stems. Integration of these varied sources of palaeontological information from the Clouston Farm locality provides an opportunity to evaluate multiple trophic levels in a late Permian floodplain ecosystem. In addition to the biotic evidence, taphonomic and sedimentologic analyses provide critical contextual information on the depositional environment and preservational filters that affected this system. The high quality of preservation and extent of outcrop suggest that future work at this, and other Permian sites, will provide additional insights on the morphology, taxonomy, organ associations, and insect associations of these and other plants. The intent of the current paper is to detail the locality and to summarize our current knowledge principally of the depositional environment, macroflora, palynoflora, fauna, and plant-insect associations.

2. THE CLOUSTON FARM LOCALITY

The Clouston Farm site at S28.758^{o} E29.797^{o} (accuracy = 5 m based on the WGS 84 datum) is located approximately 26 km north of the town of Estcourt in the province of

KwaZulu-Natal, South Africa (Fig. 1). The fossiliferous siltstone crops out along both sides of a small, seasonally-dry stream bed (donga) running roughly southeast to northwest on the Clouston family's farm (labeled as 'Varkens Fontein' 1138 on the 1:50 000 topographical map of Colenso 2829DD). The locality is accessed from road R103, 1.4 km north of the entrance to the Clouston Garden of Remembrance, and 2.3 km south of the intersection of roads R103 and R74 in the town of Colenso. The fossiliferous beds occur between a small brick dam and a barbed wire fence that cuts diagonally across a gully and marks the northeastern property line of the Clouston Farm.

2.1. Stratigraphic Context

During the Pennsylvanian to Middle Jurassic, the sedimentary record of the Karoo Basin in South Africa is characterised by aggradational and degradational phases within a retroarc foreland basin situated in southern Gondwana (Smith et al., 1993; Johnson et al., 1997). Within the Karoo Supergroup (Fig. 2), the Beaufort Group has the most extensive aerial outcrop distribution and represents fluviatile deposition spanning the late Permian to Middle Triassic. The Clouston Farm locality is situated in the northeastern exposures of the Beaufort Group which are presently assigned to the Normandien Formation (Adelaide Subgroup, Beaufort Group, Karoo Supergroup) (South African Committee for Stratigraphy, 1980), now the officially recognised name for the previous Estcourt Formation (South African Committee for Stratigraphy, 1980; Johnson, 1994).

Lindström (1973) introduced the term Estcourt Formation for the laminated carbonaceous shales that crop out above the dark grey shales of the Volksrust Formation in northwestern KwaZulu-Natal. At the same time, Theron (1972) preferred the name Mooi River Formation for these rocks, but subsequent workers (Botha and Lindström, 1978; South African Committee for Stratigraphy, 1980) favoured the name Estcourt Formation. According to work by Botha and Lindström (1978), the Estcourt Formation stratigraphically and sedimentologically separates the open shelf to lacustrine deposits of the Volksrust Formation (Ecca Group) from the fluviatile sandstones of the Triassic Katberg Formation (Beaufort Group). Unfortunately, the upper and lower boundaries of the Estcourt Formation are poorly defined and the unit incorporates widely differing rock types and depositional environments in different parts of the basin. As a result, the Estcourt Formation shows characteristics of both the Ecca (Selover and Gastaldo, 2005) and Beaufort Groups. The South African Committee for Stratigraphy evaluated the Estcourt Formation in 1980 and concluded that initially it should not be grouped with either the Ecca or Beaufort Groups until their stratigraphic relationships have been clarified (South African Committee for Stratigraphy, 1980).

Groenewald (1984, 1989), working to the northwest of the Clouston Farm, made a significant contribution towards the resolution of these stratigraphic problems by proposing a new stratigraphic nomenclature for exposures distal to the center of the Beaufort Group. After Groenewald's work (1984, 1989), the Estcourt Formation was incorporated into the Normandien Formation of Groenewald (Johnson, 1994; Johnson et al., 1997, pers. comm., 2007; Rubidge, pers. comm., 2003). In addition, the Normandien Formation was considered by Groenewald to be correlated with the uppermost exposures of the Adelaide Subgroup in the southern region of the Karoo Basin. This correlation is supported by the documented occurrence of vertebrate fossils of the *Dicynodon* Assemblage Zone (Rubidge et al., 1995) in the greyish-green siltstones of the Normandien Formation (Groenewald, 1984, 1989), below the uppermost Harrismith

Member. This is suggestive of a latest Permian age (MacLeod et al., 2000; Smith and Ward, 2001).

During the course of the current investigation, a skull of the dicynodont '*Oudenodon*' (specimen CGP/1/875) was recovered from the Colenso Roadcut locality, on R103 approximately 2.5 km northeast from, and roughly equivalent stratigraphically to, the fossil plant beds at the Clouston Farm locality. This taxon is unique to only two Assemblage Zones in the Karoo, an early late Permian (Wuchiapingian) *Cistecephalus* Assemblage Zone and a younger late Permian (Changhsingian) *Dicynodon* Assemblage Zone (Kitching, 1977, 1995; Rubidge, 2005). Although both zones are restricted to the Beaufort Group, the *Cistecephalus* Assemblage zone is restricted to the southern and southwestern parts of the basin and is absent from KwaZulu-Natal, whereas the *Dicynodon* assemblage Zone extends circumbasinally and is present in KwaZulu-Natal (Kitching, 1995; Smith and Keyser, 1995; Rubidge and Hancox, 2002). Consistent with this age assignment is palynological evidence from the Clouston Farm site, reported below, that indicates a Changhsingian age.

Historically, palynological (Anderson, 1977; Aitken, 1993), palaeobotanical (Lacey et al., 1975; Anderson and Anderson, 1985), and palaeoentomological (Riek, 1974, 1976a) assignments were cited as evidence in favour of a late Permian age for the Normandien Formation. Currently, lithostratigraphic, palynologic, and vertebrate palaeontologic evidence support referral of the Clouston Farm locality to the Wuchiapingian or Changhsingian Stages of the Lopingian Series. However, the presence of '*Oudenodon*" indicates a Changhsingian age assignment. Further work on the biostratigraphic zonation and lithostratigraphic definitions of the Karoo likely may provide refinement of this assignment in the future.

2.2. Local Stratigraphy and Sedimentology

The exposure at the Clouston Farm locality extends for an ~ 425 m transect along a dry stream bed (Fig. 3) and dips at a low angle, which allowed for a continuous stratigraphic section of more than 25 m to be measured and described (Fig. 4). Overall, this section fines upwards from medium- to fine grained sandstone at the base to a 3–4 m thick, interbedded siltstone, to a macrofossil-bearing shale that caps the channel-fill sequence. The basal ~ 12 m of the channel-fill is composed of very fine- to medium-grained, dusky yellow (5Y6/4; 5Y5/4) arkose which consists of moderately sorted, subrounded clasts. Scanning electron microscopy revealed the mineralogical composition of this lithofacies to contain 70% quartz, 18% plagioclase, 4% K-feldspar or rutile, 6% illite/smectite, and 2% mica fragments.

Trough cross-stratified beds, bounded by sharp and erosional bounding surfaces and ranging from 0.5–1.0 m in thickness (Plate I, 1), predominate within the main channel sandstone. Individual troughs in the lowermost 3 m of section display trough widths of 6–7 m and bed thicknesses of 1.0–1.25 m, indicative of high energy flow conditions. Rare ripple cross-stratification uncommonly drapes individual trough crossbeds, indicating decrease in flow rate at time of formation. A coarse-grained, cross-stratified sandstone bed was recorded at a level of 2.6–3.3 m in the section. The individual troughs of this 0.7 m thick bed are similar (5.0–6.5 m wide) to those lower down in the section, but differ in a coarser grain size and the presence of small quartzose and feldspathic (< 8 mm in diameter), and intraformational siltstone (< 15 mm in diameter) clasts (Plate I, 2). Trough cross-stratification predominates in the overlying fine-grained sandstone. These rocks display a gradual upwards decrease in average bed thickness (1.0–0.5 m) and trough width (5 – 1.9 m), while ripple cross-stratification shows a concomitant increase over the same interval. Beginning at 13.8 m in the section, smaller troughs (1.9 m wide) in the sandstone are filled with in-phase ripples (Plate I, 3, 4). The fine to very fine grained sandstone grades upwards into stacked ripple cross-stratified beds, 10–50 cm thick, that generally drape steeply dipping, upwards-concave bounding surfaces (Plate I, 5). Thin (< 1 cm), fine- to medium-grained siltstone in some cases separates individual ripple cross-stratified beds.

The general upwards-fining trend is continued with dusky yellow (5Y6/4) ripple cross-stratified sandstone that grades upsection into a > 1 m thick interval of massive and ripple cross-stratified, light olive (10Y5/4) siltstone. An erosional contact separates the latter from a light olive grey (5Y5/2), 3.3 m thick unit consisting of stacked, thin (12–40 cm) intervals of siltstone, shale, and thin claystone (Fig. 4). It is within the thicker shale intervals that the plant macrofossils are preserved. Several distinct beds, delimited by abrupt bounding surfaces or rare gradational contacts, have been recognised in the shale. These are commonly separated by thin (1–5 cm), laterally extensive, brownish black (5YR2/1) or yellowish grey (5 Y 7/2) clay horizons (Plate I, 6, 7).

Due to their lateral extent, some clay layers, which display fairly uniform thicknesses when traced laterally, have been used as marker horizons. In most instances the clays are bounded by undulating (Plate I, 6), abrupt surfaces at the base; but, in some cases, (especially directly below and above Plant Bed A) the clays drape erosional surfaces that erode as much as 10 cm into the underlying shales. These bounding surfaces are indicative of infrequent high-discharge events. Very thin, horizontal laminae are atypically visible in unweathered exposures of the clay.

Within the thicker shale intervals, grain size is uniform, although rare upwards-coarsening trends (see Plant Bed C) have been documented. In general, horizontal and low amplitude in-phase ripple stratification prevails in the shale (Plate I, 7). Massive siltstone predominates towards the top of the sequence. Restricted slickensides, probably syndepositional in origin, occur at the base of the fine-grained sequence and the basal 10 cm of Plant Bed B, and represent the only evidence of desiccation recorded in this sequence.

The majority of plant fossils originate from three discrete intervals of finely laminated shale. The lowermost bed (Plant Bed A) is a light olive grey (5Y5/2) shale containing dark yellowish orange (10YR6/6) nodules and displaying moderate brown (10YR5/4) and dusky yellow (5Y6/4) staining on the bedding planes. This bed is exposed as a 20–35 cm thick unit and contains dense mats of well-preserved leaf impressions. Internally, ripple cross-stratified shale drapes steeply dipping surfaces, which in some cases may mimic the shape of small troughs (Plate I, 8). Thin, restricted lenses of carbonaceous shale atypically are found in the floor of these depressions (Plate I, 8).

The middle bed (Plant Bed B) consists of light olive brown (5Y5/4) shale that displays horizontal to very low in-phase ripple stratification and ranges from 17–60 cm in thickness. Numerous, well-preserved macroplant impressions occur throughout the unit. By contrast, the uppermost bed (Plant Bed C) is located at the base of a 32–48 cm thick unit that coarsens upwards (from fine to coarse siltstone). It displays greater lateral variation than the other plant-bearing beds, with finely laminated shale grading laterally into massive siltstones. The rocks display general light olive grey (5Y5/2) to olive grey

(5Y5/4) colours. Plant fossils are restricted to the lower 10 cm of the bed and include sparse, but well-preserved plant impressions. This latter unit is succeeded by light olive grey (5Y5/2) shale (14–24 cm thick), which is characterised by prominent moderate reddish brown (10R4/6) and blackish red (5R2/2) staining. Only isolated plant remains have been recovered from this layer.

2.3. Depositional Environment

With the exception of the lowermost Frankfort Member, a meandering fluvial model is envisaged for the Normandien Formation (Groenewald, 1984, 1989). Grain-size trends, grading from medium- and fine-grained trough cross-stratified sandstones, at the base, to shale and claystone at the top, together with a concomitant change in observed sedimentological structures, indicate an upward decrease in flow energy. The overall thickness of the channel fill and the trough cross-stratification of the lowermost sandstone bedsets indicate deposition in deep, fluvial channels, with the lower sandstones probably representing channel sandbars.

The meandering fluvial model proposed for most of the Normandien Formation (Groenewald, 1984, 1989) is supported by the partial exposure of a pointbar deposit, with a lateral extent of more than 500 m, recorded at the Colenso Roadcut locality. The proximity of this deposit, together with the size of the channel-fill exposed at the Clouston Farm locality, supports a general meandering, fluvial setting. Exposure was insufficient for adequate numbers of palaeocurrent readings to be taken, but the available data points (11°, 340°, 352°, 345°) measured from the trough crossbeds at the base of the channel fill, indicate that channel flow at this point was towards the N-NW. The ripple cross-stratified, very fine-grained sandstone dissected by steeply dipping bounding surfaces occur above a height of 18 m in the section, is interpreted as representing deposition on the upper reaches of a pointbar.

The general upwards-fining trend of the channel-fill reflects waning flow and suggests shutoff from bedload transport that may be due to progressive channel migration and ultimate abandonment. Fine grain size, the presence of low amplitude in-phase and out-of-phase ripples, and rich accumulations of plant material in the uppermost strata indicate that deposition occurred in slow moving or standing water. The overall thickness, the documentation of several discrete sediment packages (representing distinct depositional events), and the paucity of any desiccation features indicate that deposition occurred in a semi-perennial water body which existed over an interval of time. Therefore, it is likely that the plant material accumulated in the relatively slack water conditions of an abandoned channel meander or oxbow lake.

2.4. Taphonomy and Preservation of Vegetation

Glossopteris A. Brongniart 1828 leaves and sphenophyte axes are the most common plant parts encountered in the channel fill. The fossiliferous beds consist of multiple sequential horizons in which thin beds of siltstone are overlain by concentrated aerial detritus. These concentrated assemblages are characterised by plant parts either overlapping one another on a single bedding surface, over sequential, closely spaced bedding surfaces of less than 1 mm thickness, or are isolated from each other on the bedding surface with intervening matrix. Plant assemblages in Bed A occur on the top of small-scale, fining upwards sequences consisting of millimetre-thick very fine to fine sandstone laminae overlain by several millimetres of siltstone. Assemblages in Beds B and C occur on the top of siltstone laminae that range from a few millimetres to 1 cm in thickness; no sandstone laminae are found. These assemblages higher in the channel fill are associated only with fine sediments, with one thin siltstone bed overlain by another. Sequential bedding surfaces upsection alternate between concentrated assemblages and those in which there is more matrix between plant parts.

Leaves and stems show little or no signs of decay prior to deposition and burial, although individual leaves were fragmented during extraction due to splitting along closely-spaced planes of weakness defined by surrounding plant parts. Leaves range in length from ~ 3 to 20 cm, with most in the 6–10 cm range (Fig. 5). Venation is prominent on most leaves. Insect-plant associations are commonly well defined, with no evidence for degradation of the areas affected following emplacement of the leaves at the sediment-water interface. Axes have been recovered up to 50 cm in length and as wide as 6 cm, preserved either as impressions or as pith casts. Siltstone casts of sphenopsid axes are found at several stratigraphic horizons, and some display small-scale imbrication indicating some transport of sediment along the sediment-water interface prior to burial. Cast axes do not exceed 4 mm in thickness, indicating a minimal duration of sediment fill (Gastaldo et al., 1998). In Bed B, a few rare examples of apparently in situ, upright to slightly inclined sphenophyte axes (with diameters of less than 1 cm) were found spanning several bedding planes. These examples may represent post-burial regeneration of displaced axes (Gastaldo, 1994). Evidence for traumatically-introduced axes is found in Bed A, associated with the preservation of glossopterid leaves attached to a small branch. However, in most instances glossopterid leaves are isolated from axial material probably through physiological loss (Gastaldo, 1994).

Sphenopsid axes and glossopterid leaves in each bed show a range of orientations.

Sphenopsid axes from Beds A and C are omitted from palaeocurrent analyses because of (1) low numbers on the assessed bedding surfaces, and (2) their limited use in such analyses (Gastaldo, 2004). Overall, palaeocurrent results on composite leaf data from each fossiliferous interval (leaf orientation measured towards the leaf apex) indicate that *Glossopteris* leaves in Bed A and Bed C do not show any preferential orientation (Table 1; Rayleigh test: p=0.21, p=0.16, respectively). Leaves in these intervals are uniformly distributed and exhibit a wide variance in orientation (Fig. 6A, 6D). Leaves in Bed B show a predominant orientation to the NE with a mean vector of 59° (failed Rayleigh test: p=0.00, Table 1), which is paralleled by the sphenopsid axes from this interval (Fig. 6B, 6C). When individual bedding planes are assessed, though, there may or may not be a preferential leaf orientation to the dataset (Table 1). This condition occurs on only a few bedding surfaces and is due most probably to a near uniform distribution with no statistical variance.

In summary, the fossil-bearing sequence consists of a compositionally diverse mixture of large, robust axes, microphyll leaf size, and isolated reproductive structures. These are concentrated on bedding surfaces on top of small-scale fining-upwards sequences in the basal part and on overlying millimetre-to-centimetre scale mudstone beds in the middle and upper parts of the channel fill. Individual planar beds can be traced along the outcrop, and plants are not concentrated in lenticular structures. Bedding surfaces are characterised by both overlapping leaves and axes, up to 5 plant parts in thickness, or by isolated organs with intervening siltstone matrix that may be up to 3 leaves in thickness. Axes may be dynamically ordered, with orientations changing throughout the duration of channel fill, whereas glossopterid leaves are disordered. These features are characteristic of parautochthonous assemblages (Gastaldo et al., 1996b) originating from riparian vegetation adjacent to abandoned channels (Gastaldo et al., 1989).

3. MACROFLORA

The Clouston Farm macroflora (Table 2; Fig. 7) appears to be typical of the late Permian of South Africa (Table 3), as evidenced by the close similarities to floras from other Normandien Formation sites described from the KwaZulu-Natal Midlands (Lacey, 1974, 1978; Lacey et al., 1975; van Dijk, 1981; van Dijk et al., 1977; Anderson and Anderson, 1985). These assemblages are all dominated by glossopterid leaf types, with hygrophilous plants such as sphenophytes and ferns apparently playing a subsidiary role in the flora.

3.1. Systematic Palaeobotany

Division Sphenophyta
Class Sphenopsida
Order Equisetales
Family Schizoneuraceae
Schizoneura Schimper and Mougeot 1844

***Schizoneura gondwanensis* Feistmantel 1876** (Plate II, 5). Only a single foliar fragment of this sphenophyte was found. The multiple, long narrow leaves, each with a single midvein and fused into a foliar lobe with a slightly asymmetrical base, are typical. The fragment represents the proximal section of a lobe, bearing characteristic commissural lines that are broader and more prominent than the midribs of the individual leaves. The 13 to 14 mm broad foliar lobe comprises at least 11 fused leaves, each approximately 1.3 mm in breadth. These dimensions fall well within the ranges observed by Benecke (1977) in more complete specimens of this taxon.

Schizoneura gondwanensis is a rare but typical element of the Normandien Formation, and has been found at several other localities in KwaZulu-Natal, including Bergville, Kilburn, Estcourt, Mooi River, Mount West, and Inhluzani (Du Toit, 1932; Plumstead, 1969; Benecke, 1977; Anderson and Anderson, 1985). It is known from the Upper Permian of South Africa, India, Brazil and Australia (Feistmantel, 1880; Etheridge, 1903; Du Toit, 1932; Benecke, 1977; Anderson and Anderson, 1985; Rohn and Rösler, 1986a; McLoughlin, 1992), although its range apparently extends back into the middle Permian of India (Singh, 2000).

Family Phyllothecaceae

Phyllotheca Brongniart 1828 emend. Townrow 1955

***Phyllotheca australis* Brongniart 1828 emend. Townrow 1955** (Plate II, 3, 4, 6).

A few, rare examples of leaf whorls also were recovered from the site. All comprised narrow, strap-shaped leaves with tapering, pointed apices and a single midvein, their bases fused to varying degrees into a funnel-shaped sheath. The specimen (Plate II, 6) has a narrow sheath with approximately 12 leaves in a half-circumference. Although the distal portion is incomplete and poorly preserved, the sheath appears to be approximately 3 mm deep and 13.1 mm wide. In one specimen (Plate II, 3), the leaves are fused into a sheath for approximately half of their length. These leaves are over 15 mm long and taper towards the apex from a width of 1.4 mm at the sheath margin. The sheath is at least 7.8 mm deep, with midveins and lines of leaf fusion clearly defined. Seventeen leaves are apparent in the incomplete whorl, suggesting that over twenty were present in the living plant. Some leaf whorls exhibit an unusually high degree of leaf fusion (Plate II, 4). Only narrow (0.3 mm wide), pointed, 1.4 mm long apical portions of the leaves are free from the disk-like sheath which measures at least 6.4 mm deep. Midveins are visible on the sheath, but lines of leaf fusion are not well-defined. Approximately 6 leaves are present in a quarter-circumference, suggesting a total number in the region of 24 leaves within the complete whorl.

Lacey et al. (1975) described a similar range of leaf-sheath morphologies from the Upper Permian Mooi River locality. They considered the possibility that there may be two species of *Phyllotheca* present at the site. Smaller (diameter 4 to 9 mm), more funnel-shaped sheaths with 14 to 22 leaves and whorls of 28 to 32 mm, were assigned to *Phyllotheca australis*. Those specimens showing greater fusion of the leaves, with a sheath of 12 to 19 mm in diameter, bearing 28 to 32 leaves, and with a whorl width of 26 to 36 mm, were compared to *Phyllotheca etheridgei* Arber 1905. *Phyllotheca etheridgei* apparently represents an intermediate form between *P*. *australis* and species of the genus *Raniganjia* Rigby 1963 (McLoughlin, 1992). The latter taxon exhibits a high degree of leaf fusion and leaves that bear transverse striae. No such striae were apparent in any of the specimens recovered from Clouston Farm. In light of the intergrading morphologies observed in the Clouston Farm leaf whorls, all are considered here to conform to *P. australis* as defined by Anderson and Anderson (1985). A range of intraspecific variation is accommodated within the concept of this taxon as regards size and degree of leaf fusion.

In addition to the Mooi River site, *P*. *australis* has been recorded at other Upper

Permian localities in KwaZulu-Natal, including Wagondrift quarry, Bulwer Quarry, Bergville, Loskop, Lidgetton, Estcourt, and Emakwezini (Benecke, 1977; Anderson and Anderson, 1985; Selover and Gastaldo, 2005; Gastaldo et al., 2005). *Phyllotheca australis* is distributed broadly across Gondwana throughout the Permian (Pant and Kidwai, 1968; McLoughlin, 1992).

Paracalamites Zalessky 1932 (Plate II, 1, 2)

Sphenophyte axes of *Paracalamites* were preserved as impressions and internal pith casts. The majority were devoid of attached foliage, although a few examples were found in association with *Phyllotheca* sp. leaves. *Paracalamites* is a broad form genus for unidentifiable equisetalean stem fragments from Late Palaeozoic, Gondwanan deposits that have ribbing which is opposite at each node (Rigby, 1966; Plumstead, 1969). As discussed by McLoughlin (1992), articulate axes from the Permian of Gondwana exhibit little diversity, and most can be accommodated within *Paracalamites australis* Rigby 1966.

Axes at the Clouston locality reached widths of over 60 mm, with lengths well in excess of 500 mm. The ratio of internode length to stem width ranged from 0.3:1 to >6:1, with the broader stems typically producing smaller ratios. Approximately 15 to 25 ribs were present across the axes (one half circumference; Plate II, 1, 2); and these were longitudinal, parallel and opposite at the nodes. Ribs were 2 to 3 mm apart and bore fine, longitudinal striations. Rarely, circular to elliptical branch scars were present at nodes. Some of the axes, particularly the broader specimens, bore dense clusters of adventitious roots at the nodes (Plate II, 2). These root-bearing articulates are very similar to those described by Gordon-Gray et al. (1976; p. 49, pl.1, figs. 1, 5) from Lidgetton. Gordon-

Gray et al. (1976) suggested that the broadest stems they examined (in excess of 4 cm wide) had short internodes relative to stem width, were curved and lacking leaves, and represented rhizomes rather than aerial stems. An abundance of these broad rhizome-like axes were observed in Beds B and C.

Class ?Lycopsida (Plate III, 1)

A single fragment of what may be a lycopsid axis was found. The fragment is 26.4 mm wide and 20 mm long, and bears what appear to be widely spaced leaf scars on its surface. The scars are broadly falcate to hemispherical, 4 mm wide and 1.8 mm deep, and are spaced approximately 7 mm apart. The surface of the axis is smooth and featureless between the leaf scars, becoming longitudinally rugose towards the center, although this latter feature may be an artefact of preservation. As discussed by Lacey et al. (1975), the presence of alternating or spirally arranged scars on a stem is not restricted to the Lycopsida, and this specimen may conceivably be a member of the Coniferophyta. It is also possible that the stem fragment represents a section of a glossopterid long shoot, from which the leaves have been shed.

Lycopods have been found in abundance in Lower Permian localities in South Africa, but they appear to be very rare in the Upper Permian Normandien Formation. Lacey et al. (1975) described a few ‘axes with leaf cushions’ from the Mooi River locality which they considered very likely to be lycopod in origin. The leaf cushions varied in size from 1 to 3 mm wide and 0.3 to 1.5 mm deep. The Clouston specimen does not exhibit the transverse wrinkles or striations described for the Mooi River specimens, and the leaf cushions are larger and do not appear to bear circular scars. Anderson and Anderson (1985) did not document any lycopod occurrences from the Upper Permian of South

Africa. In addition, the absence of lycopod spores in the palynological samples collected during this study casts doubt on the lycopod affinities of this specimen.

Division Filicophyta

Class Pteropsida

Order Filicales

Sphenopteris (Brongniart 1822) Sternberg 1825, ex Sternberg 1820-1838

***Sphenopteris alata* (Brongniart) Brongniart 1822 (Plate II, 7, 8).** Several fragments of fern were recovered, with the best preserved specimen representing the apical portion of a fertile frond. The frond is bipinnate, with pinnae alternate on the rachis. Pinnae are lanceolate, 9 to >20 mm long. Bases of pinnae are contracted and decurrent, creating a narrow flange or wing along the sides of the rachis. Pinnules are well developed, 2 to >5 mm long, alternate, with approximately 7 lobes (one terminal) along the margin, ranging from gentle undulations to very well developed, rounded and, in some cases, bicuspid lobes. The pinnule apex is obtusely rounded whereas the base is contracted and slightly asymmetrical. Pinnule bases are decurrent along the rachilla, creating a flange or wing. Each pinnule has a persistent, flexuous midvein and bifurcating secondary veins extending into each lobe. Sporangia are small (approx. 0.2 mm diameter), circular, and are positioned irregularly on ultimate veins, 0.3 to 0.5 mm from the pinnule margin (Plate II, 8).

The Clouston material is very similar to specimens from Mooi River described by Lacey et al. (1975) as *Sphenopteris alata*, on the basis of Du Toit’s (1932) interpretation of the species. Anderson and Anderson (1985) later transferred these specimens to *Sphenopteris lobifolia* Morris 1845. According to Du Toit (1932), both species have an alate rachis with pinnae set at a fairly wide angle to the rachis. However, in *S. lobifolia* the pinnae become opposite in the apical portion of the frond and the pinnules have fewer lobes than in *S. alata*. The Clouston specimens have alternate pinnae to the apex, conforming more closely to the diagnosis for *S. alata*.

Division Pinophyta

Class Pteridospermopsida

Order Glossopteridales

Glossopterid fertile structures

A range of generally well-preserved fertile and related structures were found, including pollen organs, isolated capituli, scale leaves, and dispersed seeds.

***Eretmonia natalensis* du Toit emend. Lacey et al. 1975** (Plate II, 10, 11). This fertile structure is generally considered, on the basis of strong associative evidence, to be the pollen organ of a *Glossopteris* plant. Typically, *Eretmonia* bears one to two pairs of pedicellate microsporangial clusters in opposite ranks near the base of a scale leaf of variable shape (Lacey et al., 1975; Anderson and Anderson, 1985). The Clouston specimens fall within the range of variation cited by Lacey et al. (1975) for this species. The scale leaves have a lamina that varies in shape from rhombohedral to obovate with an acuminate apex, and tapers at the base into a long, narrow petiole that is 1.0–2.7 mm wide at the base (Plate II, 10, 11). Overall, scale-leaf dimensions range from 6.8 to 10.5 mm wide, and 14.3 to over 25 mm long. One to two pairs of sporangial clusters are present near the base of the lamina, although details of pedicel attachment to the petiole have not been preserved. The longitudinally striated, elliptical to falcate sporangial bodies borne by *Eretmonia* regularly were found in isolation or detached clusters. Isolated bodies of this type are referable to the genus *Arberiella* Pant and Nautiyal, 1960. *Eretmonia natalensis* is abundant in the fossiliferous beds of the Normandien Formation of KwaZulu-Natal, in many cases with multiple specimens occurring in close proximity on a common bedding plane (Plate III, 2).

***Lidgettonia africana* Thomas emend. Lacey et al. 1975** (Plate III, 3). Several isolated capituli of the ovuliferous glossopterid fructification *Lidgettonia* were found. The 4.8 x 5.6 mm specimens with pointed lobes are typical of *L. africana* (Thomas, 1958; Lacey et al., 1975; Anderson and Anderson, 1985). In more complete examples of this species, multiple pedicellate capituli are attached in opposite ranks to the petiole of a scale leaf. This genus is found predominantly in strata of the Upper Permian Normandien Formation of KwaZulu-Natal, although specimens also have been found at Lawley, near Johannesburg, in a deposit of uncertain age but which currently is thought to belong to the Volksrust Formation (Middle Permian) (Rayner and Coventry, 1985; Anderson and Anderson, 1985). *Lidgettonia* also has been found in the Upper Permian of India and Australia (Surange and Chandra, 1974; White, 1978; Holmes, 1990).

Glossopterid scale leaves (Plate III, 4, 5). Numerous isolated scale leaves occur. These sterile structures, identical to the scale leaves of *Eretmonia* and *Lidgettonia* spp., are common elements in the Permian floras of South Africa (Anderson and Anderson, 1985), and elsewhere in Gondwana.

Isolated Seeds (Plate II, 9). Several platyspermic, samaropsoid seeds (~ 4 x 5 mm wide) were recovered. The seeds have an ovate to elliptical sclerotesta (~ 4 x 3 mm), and a sarcotesta that is contracted at the micropyle and hilum, flanked by two rounded, laterally expanded wings. The wings taper towards the hylar end of the seed, but are slightly broader distally (1 mm), forming a rounded lobe on either side of the micropyle. The seeds resemble those produced by *Lidgettonia africana* and *Rigbya arberioides* Lacey et al. 1975, and are probably glossopterid in origin.

***Glossopteris* leaves**

Glossopterid plants dominated the flora across most of the Gondwanan supercontinent for the entire Permian and yet, despite the efforts of many workers over the years, there is still much disagreement with regard to the taxonomy of this group. *Glossopteris* and *Belemnopteris* (Feistmantel) Lacey et al. 1975 are the only two glossopterid leaf forms reported from the Upper Permian of South Africa (Lacey et al., 1975; Anderson and Anderson, 1985), and only leaves assignable to the former were found at the Clouston Farm locality. Previous workers have emphasised different suites of characters when distinguishing between species of *Glossopteris* leaves. And, in many cases, workers have either shoehorned specimens into a few existing taxa or have created numerous species on the basis of small differences that reasonably could be accounted for in terms of natural variation within a population. As a result, the literature on *Glossopteris* is notoriously subjective, and contradictory, as has been discussed at length by many authors (Plumstead, 1962; Maheshwari, 1976; Banerjee, 1978; Lacey et al., 1975; Kovács-Endrödy, 1976, 1991; Anderson and Anderson, 1985; McLoughlin, 1993, 1994a, 1994b; Singh, 2000). In addition, accumulating evidence for a high degree of provincialism within the *Glossopteris* floras of Gondwana, particularly with regard to the ovulate fructifications of this group, has contributed to a sense of diminished confidence in the broad application of species names for glossopterid leaves from different parts of the supercontinent (Chandra and Surange, 1979; Anderson and Anderson, 1985; McLoughlin, 1993, 1994a, 1994b). In an attempt to unify associated glossopterid fertile organs and leaves, and to create a taxonomic system that took cognizance of population dynamics and variability, Anderson and Anderson (1985) applied their palaeodeme concept to the group. (A palaeodeme is a local assemblage of genetically related individuals.) Their classification relied very heavily on associative evidence and, in light of our limited knowledge of the *Glossopteris* flora, it is an approach not supported here.

We propose the use of a morphotyping system, restricted to leaves found at the Clouston Farm locality. In conjunction with detailed descriptions and comparisons with existing taxa, this taxonomically sensitive approach removes the clutter of potentially redundant species, while maintaining a high level of morphological discrimination (e.g., Leaf Architecture Working Group, 1999, for angiosperms). The morphotypes reflect discrete morphological trends in character suites, which may approximate species-level differentiation of the leaves. This approach has allowed for a rapid assessment of the morphological diversity of the leaves in the collection, and is seen as the first step towards a more formal identification of species. Only non-cuticular features have been considered, as all leaves examined were impressions. Comparisons with existing characterisations of *Glossopteris* leaf types have been restricted to those from other South African localities.

Glossopterid morphotypes were distinguished using some of the criteria adopted by McLoughlin (1994a). It should be noted that the midrib of *Glossopteris* is not considered here to be a true midvein, but rather a medio-longitudinal concentration of veins, which may be emphasized by the presence of supportive tissues. Marginal vein density was measured parallel to the leaf margin. Vein angles were measured relative to the midrib, in the medial portion of each leaf, in three parts of the lamina: (1) near the midrib in the proximal third of the lamina; (2) the mid-laminar region, and (3) adjacent to the margin. Mesh characteristics and number of anastomoses from midrib to margin also were assessed along the medial part of the leaf, in the mid-laminar region.

Each morphotype was numbered (C1–C7), and sub-types (a-c) were assigned to indicate subtler differences within some morphotypes (e.g., C2b), which later may be attributed to intraspecific variation. This system has allowed for a flexible and expressive preliminary classification. Seven morphotypes of *Glossopteris* leaf, incorporating five subtypes, were identified (see Table 4 for major defining characters of each morphotype), and their observed relative frequencies noted (Fig. 7).

Clouston Morphotype C1 (Plate IV, 3, 4; Plate VII). Morphotype C1 is a fairly broad grouping of small leaves with moderately open meshes. The only comparable leaves, in terms of size, shape and venation pattern, that have been reported previously from South Africa are a few examples included by Anderson and Anderson (1985) in *Lidgettonia lidgettonioides* from Mooi River (pl. 127, figs 9, 10, 11, 13, 14).

Subtype C1a (Plate IV, 1; Plate VII). This is a variable leaf type that is typically obovate, with broad meshes at a steep angle to the midrib. These leaves are among the smallest at the Clouston Farm locality.

Subtype C1b (Plate IV, 4; Plate VII). These rare leaves are distinguished from C1a mainly on the basis of their slightly narrower, denser, more linear meshes, and more moderate vein angle. They are also broader, more elliptical, and with a bluntly pointed, as opposed to rounded, apex.

Clouston Morphotype C2 (Plate IV, 3–9; Plate VII). This morphotype is by far the most common at the locality. These are generally long and narrow and exhibit fine, dense venation that diverges from the midrib at a steep angle and curves gently to the margin. Three, apparently intergrading subgroups have been identified. Anderson and Anderson (1985) linked similar leaf types, by association, to the glossopterid ovulate fructification *Lidgettonia*.

Subtype C2a (Plate IV, 3–5; Plate VII). Morphotype C2a is the most common, with leaves that are typically long and strap-shaped with fine, dense, steeply inclined, gently arching venation. In terms of shape, size, vein density and vein angle, this leaf form closely resembles those assigned by Anderson and Anderson (1985) to the *Lidgettonia africana* and *L. inhluzanensis* palaeodemes at other Upper Permian sites in KwaZulu-Natal.

Subtype C2b (Plate IV, 6; Plate VII). Morphotype C2b tends to be larger and more elliptical in shape than C2a, and has venation at a more moderate angle to the midrib. The meshes also tend to be slightly larger near the midrib, whereas in C2a they are consistently fine from midrib to margin. These leaves are comparable in venation style, size, and shape to some of those from Mooi River associated by Anderson and Anderson (1985) with *L. lidgettonioides* (particularly the larger specimens, in pl. 126, figs. 2-5, 13; pl. 127, figs 1, 3).

Subtype C2c (Plate IV, 7–9; Plate VII). Members of this subgroup are oblanceolate as opposed to the more ligulate forms seen in C2a and C2b. The venation also tends to be less dense (broader meshes) and has an angle of inclination intermediate between that seen in leaves of C2a and C2b. Leaves of morphotype C2c resemble, in shape, venation style, and size to examples from Bulwer, Bergville and Mooi River that were included within the *L. lidgettonioides* palaeodeme of Anderson and Anderson (1985; pl. 127, figs 6; pl. 128, figs 15-20; pl. 130, figs 1-7).

Clouston Morphotype C3 (Plate V, 1, 2; Plate VII). The long, narrow, linear, generally sinuous lamina and very prominent, broad and persistent midrib make this morphotype one of the most distinctive at Clouston Farm. Anderson and Anderson (1985) figured leaves from the Mooi River locality that are virtually indistinguishable from C3, and assigned them to their *Lidgettonia elegans* palaeodeme. These leaves are also very similar to those from Mooi River that were assigned by Lacey et al. (1975) to the species *G. angustifolia* Brongniart. However, C3 does not accord with Kovács-Endrödy's (1981, 1991) detailed account of *G. angustifolia* from Hammanskraal, in which she clearly described the leaf as having an obtuse apex and venation that is 'arched evenly in a steep and slight curve to the margin.' This variation in *Glossopteris* leaf morphology within the Karoo Basin provides an important basis for conducting similar, morphotype-based assessments across other spatiotemporally varied Gondwanan basins.

Clouston Morphotype C4 (Plate V, 3, 4; Plate VII). Morphotype C4 is a rare but distinctive morphotype, with characteristic broad-meshed venation inclined at a steep angle to the midrib, and following a straight path across the lamina. This morphotype is closely similar to leaves attached to *Plumsteadia gibbosa* (Benecke 1976) Anderson and Anderson 1985 from the Upper Permian Loskop Quarry site in KwaZulu-Natal (Benecke, 1976; Anderson and Anderson, 1985).

Clouston Morphotype C5 (Plate V, 5; Plate VII). Although only a single fragment of this leaf type was found, the venation is distinctive and very different to any other morphotype. The meshes are fairly broad, elongate polygonal to trullate, and become narrower towards the margin. Leaves with comparable venation have been reported from the Loskop locality by Anderson and Anderson (1985, pl. 98), who placed them within their very loosely defined *Estcourtia vandijkii* palaeodeme.

Clouston Morphotype C6 (Plate V, 6, 7; Plate VI, 1–3; Plate VII). Morphotype C6 was created for a common leaf type with dense, fine, linear venation at a moderate angle to the midrib. The meshes are narrow, linear and parallel, and are of approximately consistent width across the lamina. These represent the largest leaf-type found at the site. They are comparable in size, shape, and venation features to leaves from the Mooi River locality described by Lacey et al. (1975) as *G. indica* and *G. ampla*, and to examples from various Upper Permian sites in KwaZulu-Natal assigned by Anderson and Anderson (1985) to *G. symmetrifolia*.

Subtype C6a (Plate V, 6, 7; Plate VI, 1, 2; Plate VII). Members of Morphotype C6a are narrower and more strap-like than leaves of C6b, and have venation that generally is less steeply inclined and follows a straighter path across the lamina. Only incomplete specimens have been found. These leaves are very similar to *G. symmetrifolia* from Estcourt and Inhluzani, as figured by Anderson and Anderson (1985; pls. 140, 141). In some cases, venation is almost perpendicular to the midrib, and the first row of meshes is slightly larger. These variants are reminiscent of *G. taeniopteroides* (Anderson and Anderson, 1985; Kovács-Endrödy, 1991), and appear to represent end-members of a morphological continuum with those displaying more moderate mid-laminar venation angles of approximately 60°. The vein angle decreases significantly in the apical portion of the more taeniopteroid forms, and venation in the apices of Morphotypes C6a and C6b is indistinguishable.

Subtype C6b (Plate VI, 3; Plate VII). Although the vein characters are similar to C6a, subtype C6b is a larger, broader form with a more elliptical lamina. Meshes are of even width from midrib to margin, and the venation arches across the first third of the lamina before following a straight path to the margin. Morphotype C6b is similar in size, shape, and venation features to the Mooi River leaf types Lacey et al. (1975) found comparable to *G*. *ampla*. Morphotype C6b also resembles some of the *G*. *symmetrifolia* leaves from Mooi River, as figured by Anderson and Anderson (1985; pl. 138, fig 1), although the apex is more acute in the Mooi River specimens.

Clouston Morphotype C7 (Plate VI, 4, 5; Plate VII). Morphotype C7 is one of the more easily recognised leaf types, and is moderately common. The fairly broad meshes, the alterative vein course, and the retuse apex are diagnostic features. The distinctive recurving of the veins near the margin becomes progressively more pronounced towards the apex of the leaf, and may be difficult to detect in the basal region. We are confident that the retuse apex of C7 is a consistent feature and not an artefact, because a number of specimens with complete apices were recovered from the site.

The only leaf recorded by Anderson and Anderson (1985) as having a retuse apex is a single specimen they placed within their *E*. *vandijkii* palaeodeme (p. 271; pl. 96, fig. 5). They included a wide range of variation in leaf morphology within this group associated with the ovulate glossopterid fructification *E*. *vandijkii*. Leaf bases vary from cuneate, as seen in C7, to sagittate, and the apices have a retuse to acute point. The shape of the leaves is generally elongate-elliptical. The venation, although broad meshed in all cases, varies considerably. It is possible that several leaf species have been accommodated within their concept of a single population. Members of C7 are comparable to those specimens with cuneate bases and more steeply inclined venation, although there are no specimens figured by Anderson and Anderson (1985) that precisely conform. In particular, none of the specimens exhibits the progression towards more linear meshes from midrib to margin, which is a typical feature of C7. Morphotype C7 would therefore appear to be a new taxon for the late Permian of South Africa.

3.2. Comparison with other Normandien Formation floras

Occurrences of floral elements found at Clouston Farm (Table 2) have been plotted for all major Normandien Formation plant-fossil localities previously documented in South Africa (Lacey et al., 1975; Anderson and Anderson, 1985; van Dijk, 2000) (Table 3). The degree of similarity between the floras is influenced partially by the size of the collections made at each locality, but even small collections provide a means of comparison among the more common elements present at these sites. Mixed levels of endemism occur within the *Glossopteris* morphotypes (Table 3), with some highly localised occurrences such as C7 contrasted with the almost ubiquitous C2 morphotype complex. Morphotype complex C2 is present at all except two of the localities listed in Table 3, with C2b the most broadly occurring morphotype, followed by C2a. Morphotypes C1a, C1b and C7 represent new taxa that have not been recorded previously in South Africa.

Corresponding occurrences of other floral elements also support the broad correlation of the Clouston Farm flora with those of the Normandien Formation, particularly the presence of *Schizoneura gondwanenesis* and *Lidgettonia africana*. *Phyllotheca australis* is a very typical element of late Permian South African floras, although it may not be restricted to these floras. *Sphenopteris alata* is a rare but consistent element of late Permian floras in South Africa, but also has been recorded from the early Permian (Anderson and Anderson, 1985). The Upper Permian locality with the strongest overall similarity to Clouston Farm is the Mooi River National Road site, with eight glossopterid morphotypes and seven other elements in common. This was also the most extensively sampled site (7500 specimens), which no doubt resulted in representation of a greater proportion of rare elements and, hence, provided a broader basis for comparison. The Loskop locality, which has provided five *Glossopteris* morphotypes and other elements in common with Clouston Farm, represents the locality with the second highest similarity, despite the fact that it was assessed on the basis of fewer specimens than many of the other sites. These similarities are not unexpected: the Clouston Farm and Loskop localities probably have a similar stratigraphic position, and were deposited in similar environments. These are abandoned channel fills associated with deep, wide fluvial channel complexes (Gastaldo et al., 2005). The Loskop locality also is closest geographically to Clouston Farm, of all the Normandien Formation sites listed in Table 3. Unfortunately, no comparative geological or taphonomic information is available from the Mooi River National Road locality, which was destroyed during road construction about 30 years ago.

Surprisingly, broad-meshed glossopterid leaf forms are almost absent from the Clouston Farm flora. Morphotype C5 is the only one that could be referred to as broad-meshed, and only a single fragment was recovered. This leaf type, and similar forms attributed by Anderson and Anderson (1985) to their *Estcourtia* palaeodemes, is abundant at many of the late Permian, Dicynodont Zone assemblages in KwaZulu-Natal, including the Loskop and Mooi River National Road localities. Also absent from Clouston Farm, but present at Loskop, Mooi River National Road, and other Normandien Formation sites, is *Rigbya arberioides* and the narrow, broad-meshed leaf type commonly found in association with this ovulate glossopterid fructification. These patterns reinforce the concept of a floral mosaic, comprising patchy distributions of taxa with ranges exhibiting different degrees of overlap, resulting in variable community compositions even at sites with apparently similar habitats and depositional environments. This phenomenon requires that some caution be exercised when attempting to place glossopterid morphotypes within a biostratigraphic framework. Suites of morphotypes rather than individual forms should be employed.

4. FOSSIL WOOD

Fossil gymnosperm woods are common in the Palaeozoic but seldom have been integrated into floral studies. Reasons for this omission include the difficulty in preparing woods for study, the complexity of their taxonomy, and the difficulty in associating the wood with other macroplant morphotaxa (Bamford, 2004). In contrast to Mesozoic woods, some Palaeozoic woods have a central pith, a feature that is not always preserved. Consequently, there are two nomenclatural protocols. Where the central pith is preserved, it is the primary diagnostic character and the secondary wood becomes of ancillary significance. Typically, only the secondary wood is preserved and there is a range of genera for such ‘tracheidoxyl’ woods (sensu Creber, 1972), also known as homoxylous woods. The Clouston Farm woods are homoxylous.

Dadoxylon is probably the best known genus of late Palaeozoic woods, characterised by very distinctive araucarian tracheidal pitting ranging from alternate and contiguous to compressed. However, *Dadoxylon* is an invalid name (Philippe, 1993). Some authors have used *Dadoxylon* Endlicher 1847 for Late Palaeozoic woods and *Araucarioxylon* Kraus 1870 for Mesozoic woods, but this distinction for taxa based solely on age is unacceptable. In a comprehensive review of Gondwanan wood taxa, Bamford and Philippe (2001) proposed that *Agathoxylon* Hartig 1848 be the form genus for homoxylous gymnospermous woods possessing tracheidal pitting of the araucarian type. These are characterised by an absence of thickenings on tangential walls of ray cells, and cross-field pits that are araucarian or taxodioid. It should be stressed that araucarian tracheid pits occur in many Late Palaeozoic woods and are associated with several plant groups—Cordaites, Voltziales, Glossopteridales, Coniferales, and the extant Araucariaceae—although this does not imply a close phylogenetic relationship between these groups.

Small pieces of silicified wood were recovered from the dry stream bed on Clouston Farm, albeit these fragments eroded from the sediments and were not recovered *in situ*. Thin sections cut in the standard three planes (transverse, radial-longitudinal and tangential-longitudinal), and approximately 40 μm thick, were studied under a petrographic microscope and compared with fossil woods from the Bernard Price Institute fossil wood database.

Although not well preserved, the Clouston Farm woods are identifiable as typical Palaeozoic gymnospermous woods of *Agathoxylon africanum* (Bamford) Bamford and

Philippe 2001 and *Agathoxylon karooensis* (Bamford) Bamford and Philippe 2001. The woods are similar in their anatomical characteristics, are of unknown phylogenetic affinity (Bamford 2004), and are assigned to taxa that historically have been attributed to differing age ranges (Bamford 1999). In transverse section, the woods appear the same with square to rectangular outlines of tracheids. The rays also are the same in tangential-longitudinal section, being uniseriate with smooth walls and heights ranging from 10 to 15 cells. The most useful section is radial-longitudinal, which exhibits the tracheid pitting and cross-field pits. Specimen BP/16/1492 is *Agathoxylon africanum* with biseriate araucarian (alternate and contiguous), 10 µm wide, tracheidal pitting on the radial walls, uniseriate rays 2–18 cells high, and 2–7 araucarian pits per cross-field (6–8 µm in diameter) (Plate VIII, 1–3). Specimen BP/16/1493 is *Agathoxylon karooensis* with triseriate araucarian, 10 µm wide tracheidal pitting on the radial walls, uniseriate rays 9–18 cells high, and 2–4 araucarian pits per cross-field (7.5–10 µm in diameter) (Plate VIII, 4–6).

Agathoxylon africanum occurs in the Lopingian and Triassic of southern Africa, whereas *A. karooensis* occurs only in the Lopingian. The several species of *Agathoxylon* display subtle differences, but commonly are confined to particular regions and time ranges (Philippe et al. 2004). Although Lopingian woods of southern Africa lack distinctive growth rings, it is still unknown whether this absence is attributable to an aseasonal climate or the genetics of plant biology. The Clouston Farm woods are no exception, as only indistinct and somewhat distorted growth rings are observable (Plate VIII, 1).

5. PALYNOFLORA

Rock samples were collected from the Clouston Farm and Colenso Roadcut localities for palynological analyses. Eighteen samples were taken from the plant beds and the dark grey to black clay layers that separate the beds at the main locality. Palynomorphs were extracted following standard palynological techniques, using HCl (30%), HF (40%) and $ZnCL_2$. Six of these samples were productive, which are three samples from plant Beds B and C, and the clay layer below Bed A and overlying Bed C, the latter preserving heavily oxidised palynomorphs. Only one sample, originating from a very thin purple-blue clay layer 0.5 cm below the clay layer overlying plant Bed C, contained a sparse but relatively well preserved palynological assemblage. Palynomorphs from this assemblage were counted quantitatively up to 800 specimens, of which more than 300 palynomorphs were identified at the generic or species level (Table 5). Additional slides were screened for rare species. The sample from the Roadcut section was barren. Photographs were taken with a Nikon DSM1200F digital camera mounted to a Nikon Eclipse 80i microscope. Extended depth-of-field images were generated for specimens of variable height. A series consisted of images taken at focal planes from set intervals, after which MediaCy Image Pro software was used to extract the separate images for creation of a composite image. The stacking of images in some cases generated visual artefacts. Sample residues and slides are housed in the Paleobotanical Collections of the University of California Museum of Paleontology, Berkeley, CA, under the under the UCMP catalogue numbers 398620–398633. These numbers also are cited in the figure captions.

5.1. Represented Taxa

The palynological assemblage (Plate IX; Table 5) has a relatively low diversity. It is characterised by taeniate bisaccates (67%) with *Protohaploxypinus* and

Striatopodocarpites being most frequent (Plate IX, 8–12), and *Striatoabieites multistriatus* (Balme and Hennelly) Hart 1964 (Plate IX, 13) and *Lunatisporites* sp. common. The majority of the taeniate forms are difficult to differentiate at the generic level because the grains have damaged or detached sacci. The original relative frequency of taeniate bisaccates was probably higher; one-tenth of the assemblage consists of indeterminate bisaccates. Nontaeniate bisaccate pollen grains are less abundant; *Chordasporites waterbergensis* MacRae 1988, *Falcisporites*, and cf. *Alisporites ovatus* (Balme and Hennelly) Jansonius 1962 are rare. The taeniate asaccate pollen taxon *Weylandites lucifer* (Bharadwaj and Saluhja) Foster 1975 is common. A considerable portion of the assemblage (19%) consists of simple trilete spores, of which *Granulatisporites papillosus* Hart 1965 (Plate IX, 7), *Lophotriletes novicus* Singh 1964 (Plate IX, 6), and *Horriditriletes tereteangulatus* (Balme and Hennelly) Backhouse 1991 (Plate IX, 5) are common; and *Calamospora plicata* (Luber and Waltz) Hart 1965 (Plate IX, 1), cf. *Cyclogranisporites gondwanensis* Bharadwaj and Salujha 1964 (Plate IX, 2), cf. *Apiculatisporis cornutus* (Balme and Hennelly) Høeg and Bose 1960 (Plate IX, 3), and *Horriditriletes ramosus* (Balme and Hennelly) Bharadwaj and Salujha 1964 are rare elements. In addition, the assemblage also contains well-preserved gymnosperm tracheids of the morphogenus *Agathoxylon* (Plate IX, 14).

The pollen record of Clouston Farm reflects a glossopterid dominated woodland with an understory of sphenophytes and pteridophytes, and various other gymnosperms (peltasperms, corystosperms and conifers) as either subsidiary or non-local elements. Several morphogenera of dispersed taeniate saccate and asaccate pollen are associated with Gondwanan glossopterids (e.g. Balme, 1995). Species of the dispersed morphogenera *Protohaploxypinus* and *Striatopodocarpites* have been found together in situ within sporangia of several species of *Arberiella* (Zavada, 1991), which are morphologically similar to those attached to glossopterid pollen-producing organs *Eretmonia* DuToit 1932 and *Glossotheca* Surange & Maheshwari 1970 (Pant and Nautiyal 1960; Rigby and Chandra, 1990; Lindström et al., 1997). The taeniate asaccate taxon *Weylandites* has the least strong association with glossopterids, and is known from the synangium of *Rugatheca*, which has only a possible *Glossopteris* affinity (Pant and Basu, 1977; Balme, 1995). Nontaeniate *Alisporites* and taeniate *Lunatisporites* pollen was likely produced by extrabasinal peltasperms and conifers that are not represented in the macrofossil record (Balme, 1995). Other seed-plant affiliations include alete bisaccate pollen that has been found in a range of Permian conifers and pteridosperms, and other alete forms such as *Falcisporites* and *Alisporites* that seem to represent peltasperms or corystosperms in Gondwanan floras (Zavada and Crepet, 1985; Balme, 1995; Lindström et al., 1997). Incomplete tracheids of *Agathoxylon* also occur, but can not be identified at the species level. Most likely these tracheids are from *Agathoxylon africanum*. As for pteridosperms, acavate trilete spore types, such as *Cyclogranisporites*, are characteristic of ferns (Balme, 1995), and *Calamospora* is known from equisetalean fructifications (Grauvogel-Stamm, 1978). Cavate spores characteristic of lycopsids were not found in this assemblage. The parent plant of *Chordasporites* is unknown.

5.2. Inferred Age

For an age assessment in terms of standard chronostratigraphic classification, this local Karoo assemblage has to be compared with palynostratigraphic zones in Australia, one of the few areas in Gondwana where palynological records have been calibrated against adequately dated marine invertebrate zones (Foster and Archbold, 2001). The Australian zones are for a large part based on the first or consistent appearance of spore and pollen taxa in western (e.g., Mory and Backhouse, 1997) and eastern Australian basins (e.g., Price, 1997). As none of the Australian indicator taxa were recorded in the impoverished Clouston assemblage, comparisons have to rely on overall species associations and the relative proportions of major spore/pollen categories.

In general, assemblages dominated by taeniate bisaccates such as *Protohaploxypinus* and *Striatopodocarpites* are characteristic of late Permian sediments in Gondwana. In Australia the transition of codominance of nontaeniate and taeniate bisaccates to full dominance of taeniate bisaccates takes place within the *Dulhuntispora parvithola* Zone (Mory and Backhouse 1997) and the APP5 zone (with subzones APP5001-5006); leading to dominance in APP5004 (Price, 1997). In addition, Price (1997) described distinct decline of monosaccate pollen starting in subzone APP5001. These patterns strongly resemble the changes in abundance described from the Karoo Basin (Anderson, 1977) and the adjacent Waterberg and Pafuri basins (MacRae, 1988), and also from areas such as the Prince Charles Mountains, Antarctica (Lindström and McLoughlin, 2007). The *D. parvithola* Zone is late Wordian to Wuchiapingian in age based on ammonoid and brachiopod evidence (Foster and Archbold, 2001).

The youngest late Permian biozones in Australia are the *Protohaploxypinus microcorpus* Zone (Mory and Backhouse, 1997) and the APP6 zone (Price, 1997). It is within these zones that the drastic change from characteristic late Permian dominance of taeniate bisaccates to assemblages rich in cavate spores and alete bisaccates such as *Falcisporites* is recorded. The assemblages at the base of the APP601 subzone still contain high abundances and diversity of taeniate bisaccate pollen grains (e.g., *Protohaploxypinus limpidus*). The difference with the preceding APP5 and *D. parvithola* zones are the first occurrences of several taxa of acavate and cavate spores and the consistent presence of distinctive pollen taxa of *Guttulapollenites hannonicus* Goubin 1965. Late Permian assemblages similar to the oldest APP6 assemblages are those from the McKinnon Member of the Prince Charles Mountains, Antarctica (Lindström and McLoughlin, 2007), and at the base of the Buckley Formation, Graphite Peak, Antarctica (Collinson et al., 2006). The *Klausipollenites schaubergeri* zone recognised by Steiner et al. (2003) at the Carleton Heights section, southern Karoo Basin, is correlative with younger assemblages in the *P. microcorpus* and the APP6 zones. The base of the APP6 zone has been correlated to the upper Chhidru Formation in the Salt Range, Pakistan, which has independently been dated as early Changhsingian (Foster et al., 1997).

In conclusion, because of the absence of monosaccates, and the absence of characteristic Changhsingian pollen taxa such as *Guttulapollenites*, the Clouston assemblage is likely to correspond to the subzones APP5004–5006 of Price (1977) and the upper part of the *D. parvithola* Zone (Mory and Backhouse, 1997). This correlation supports a Wuchiapingian (early Lopingian) age estimate that is in accordance with the megafloral and vertebrate fossil record of this locality.

6. PLANT-INSECT ASSOCIATIONS

Based on the palynological evidence above, the Clouston Farm locality represents one of the latest Permian occurrences of insect herbivory from any documented flora worldwide. The other coeval sites include, in eastern Australia, the Newcastle Coal Measures from the Sydney Basin of northern New South Wales and southern Queensland

(Beatty, 2007), and the Rangal coal Measures of the Bowen Basin, of central Queensland (McLoughlin, 1994a, 1994b). The close stratigraphic proximity of the Clouston Farm locality to the P-T boundary provides a rare snapshot of insect herbivore activity during the Lopingian. In this substudy, we characterised all plant organs, overwhelmingly leaves, but also axes, seeds and fructifications, for the presence or absence of insect-mediated damage. Herbivory was established by single or multiple presences of four explicit criteria (Labandeira, 1998, 2002). First was the presence of plant response tissues such as callus; second was evidence for micromorphological features of the attacked leaf margin such as veinal stringers, necrotic tissue flaps, or removed surface tissues; third was the expression of damage as a stereotyped pattern not attributable to known types of physical damage; and last was the expression of particular types of damage patterns on selected host-plant morphotypes. When present, each occurrence of damage was assigned to a distinctive and defined damage type (DT), as outlined by previous studies throughout the Phanerozoic plant-insect associational record (Beck and Labandeira, 1998; Labandeira et al., 2002; Wilf and Labandeira, 1999; Wilf et al., 2005; Adami-Rodrigues et al., 2004b; Labandeira and Allen, 2007). These data are recorded as presence-absence occurrences from slabs containing impressions or compressions of leaves and other plant organs larger than approximately 1 cm^2. Presence-absence data allow for multiple occurrences of the same DT on a single leaf, although frequency data was not recorded for each leaf. Data from Clouston Farm, and other of mid-Permian to Late Triassic floras from the Karoo Basin, will constitute an integrated study of plant-insect associations across a 50 m.y. interval.

6.1. Patterns of Insect Feeding

There are 22 distinctive damage types, or DTs, on 137 of the total 9772 plant organs scored. This damage was caused overwhelmingly by insect or possibly rare mite feeding on live plant tissues, and one or two interactions attributable to epiphyllous fungal colonization of leaf tissues (Table 6). Of those DT's not attributable to plant pathogens, four insect functional feeding groups are represented: external foliage feeding, piercing-and-sucking, galling, and oviposition. Because of its abundance in time and space (Labandeira, 2002; Béthoux et al., 2004), oviposition herein is treated functionally as a type of 'feeding,' even though it represents the insertion of eggs by a female abdominal structure, the ovipositor, that is analogous to piercing-and-sucking mouthparts borne by the insect head (Mickoleit, 1973). These DTs occur on 23 plant-host morphotypes, including categories for undiagnosable glossopterid foliage and other plant fragments, which represent specimens that could not be referred to other existing morphotypes (Table 6, Fig. 7). Of the 23 plant morphotypes with damage, 14 are glossopterid leaf morphotypes or subtypes and 9 represent nonglossopterid, axes, foliage and roots.

A striking pattern of this host-plant use is the targeting of glossopterid host Morphotype C2, including subtypes C2a, C2b, C2c and C2 unassignable to subtype. This host morphotype constitutes 56.2 % (77/137) of all associations, and undoubtedly is supplemented by some of the associations on unidentifiable glossopterid foliage, which probably accounts for a significant portion of an additional 18.2 % of associations. This pattern of host use significantly surpasses the frequency (42.1 %) of Morphotype 2 in the flora (Table 2; Fig. 7). Importantly, while subtype C2a is the second most frequent taxon (20.5 %), ranking first in terms of identified plant morphotypes, it harbours 30.7 % (42/137) of the herbivory. The elevated frequencies of herbivory on Morphotype C2 and particularly subtype C2a strongly indicate preferential targeting of this host plant. By contrast, all of the other 10 glossopterid plant hosts were either not attacked (C4, C5, C6b) or bore evidence for 1 association (C1, C1b, C7) or at most three or four associations (C1a, C2c, C6, C6a).

The commonest associations are two types of external foliage feeding, cuspate margin feeding (DT12: 25/137, 18.2 %), and polylobate window feeding (DT30: 7.3 %, 10/137), as well as two types of oviposition. One type of ovipositional trace is typified by insertion scars on the leaf midrib (DT76: 20.4 %, 28/134), and the other type is characterised by randomly distributed scars on the leaf lamina (DT101: 9.7 %, 13/134). These four associations collectively account for 58.4 % of all herbivory occurrences. Examples of shallow to deep cuspate margin feeding (DT12), replete with distinctive edge-reaction tissue, a shelf of necrotic tissue, and veinal stringers, overwhelmingly occur on Morphotype C2 (Plate X, 6, 7), particularly subtype C2a (Plate X, 1, 3, 8–10, 12), but also on an unidentified glossopterid (Plate X, 11). Other occurrences on Morphotype C2, subtype C2a are trenched feeding (DT15), a more intensive form of margin feeding (Plate X, 4, 5, 13, 14), and hole feeding (DT2). As for oviposition, the targeting of midrib vascular tissue (DT76) is best developed on Morphotype C2, including subtypes C2a (Plate XI, 1, 2) and C2b (Plate XI, 3, 4, 9, 10), and an unidentified glossopterid (Plate XI, 5). Isolated, random occurrences of oviposition also occur on glossopterid blades (DT101), particularly C2a (Plate XI, 6–8; Plate XII, 7–10). A third type of oviposition occurs as insertions on the leaf margin parallel to venation (DT102), exemplified by extensive arrays on Morphotypes C2a (Plate XII, 1, 2, 4–6) and C2 (Plate XII, 3). More enigmatic, leaf-mine like occurrences include elongate strip feeding (DT103) on

Morphotype C2a (Plate XIII, 1–4), the latter of which superficially resembles a leaf mine with sinusoidal frass, but clearly is a surface structure. V-shaped patches of necrotic tissue (DT75), bordered by distinctive reaction rims or fronts, occur on Morphotypes C2 (Plate XIII, 5) and C2b (Plate VIII, 11). Another damage type, possibly attributable to fungal damage, is DT103 on C2 (Plate XIII, 6, 7). Galls also are very rare at Clouston Farm, mostly consisting of small, hemispherical surface structures probably with single chambers (DT33) on Morphotype C2a (Plate XIII, 8–10). These associations represent the most diverse spectrum of insect damage on any examined Lopingian Permian flora.

Most of the DT's are attributable to an exophytic mode of feeding (62.0 %, 85/137) encompassed by external foliage feeding. Notably, the last 6 of the 22 DT's in Table 6 are endophytic in mode (38 %, 52/137), involving consumption or use of internal tissues rather than surface layers of the entire leaf, represented by oviposition, piercing-and-sucking, and galling. These associations have been documented in previous Gondwanan Permian floras, almost exclusively on glossopterid leaves, and particularly include various types of margin feeding (Plumstead, 1963; Amerom, 1966; Holmes, 1995; McLoughlin, 1994a, 1994b; Guerra-Sommer, 1995; Adami-Rodrigues, 2004a, 2004b); a few types of oviposition, previously misidentified as reproductive structures or fungal damage (Bunbury, 1861; pl. vii, figs. 1, 4; Plumstead, 1969, pl. xiv, fig. 4; Plumstead, 1970, p. 142; McLoughlin, 1990, pl. 2, fig. 7); or other types of insect damage (Adami-Rodrigues et al., 2004a) such as galling (Pant and Srivastava, 1995; Banerjee and Bera, 1998). Although two occurrences at the Clouston Farm site are suggestive (Plate XIII, 1–4), no definitive leaf mines were identified, currently supporting the absence of this functional feeding group during the Palaeozoic (Labandeira, 1998, 2002). The earliest leaf mining presently known is from the late Middle to early Late Triassic interval (Rozefelds and Sobbe, 1987; Zherikhin, 2002; Scott et al., 2004; Labandeira et al., 2005). Additionally, insect or mite borings were not observed in any permineralised wood, such as those described by Zavada and Mentis (1992) for a nearby Permian locality, and material documented from other Permian localities (Goth and Wilde, 1992; Weaver et al., 1997).

Insect herbivory from Clouston Farm indicates four major patterns. First, there was a relatively low level of herbivory. This herbivory disproportionately targeted a small but abundant selection of available glossopterid host morphotypes, comparable in intensity and preference to other analyzed Permian compression/impression floras (Beck and Labandeira, 1998; Adami-Rodrigues et al., 2004b; Labandeira and Allen, 2007). Second, the herbivory of particular glossopterid taxa, namely Morphotype C and its subtypes, particularly host C2a, was at a more elevated frequency than its occurrence in the bulk flora. Third, most of the herbivory occurred as external foliage feeding, particularly DT12, although a surprisingly high percentage of oviposition, especially DT's 76 and 102 that targeted midribs and margins, also was found on glossopterid leaves. Last, exophytic modes of feeding were dominant, although subdominant endophytic feeding types were represented mostly by stylet-like perforation of tissue. This latter pattern is in distinct contrast to the seed predation, leaf mining, and greater occurrence of galling occurring during the later Triassic (Labandeira, 2006).

Because of the highly fragmented nature of most of the specimens examined, our figures undoubtedly represent an underestimation of the actual amount of herbivory that took place, attributable to unavoidable taphonomic factors. Our figures are likely to be conservative. Relative abundance, assessed at a foliar surface-area basis, is unbiased, but overall abundance is under-represented. This is because, in most cases, a small proportion of leaf-surface area was examined for each leaf, reducing our chances of detecting other sites of damage. However, such bias also is true for other compression floras (Labandeira and Allen, 2007), and different biases characterise examination of modern herbivory as well (Coley and Barone, 1996).

6.2. Comparisons with Other Permian Localities

Although Permian data are sparse, the patterns of herbivory at Clouston Farm can be compared qualitatively and quantitatively to earlier Gondwanan, Euramerican, and Cathaysian compression-impression localities (also see Labandeira and Allen, 2007). Quantitative patterns of herbivory, as measured by frequency of attack, are approximately analogous to four upper Lower and lower Middle Permian sites from the Paraná Basin of Rio Grande do Sul, in southeastern Brazil (Adami-Rodrigues et al., 2004b), both in terms of a similar general spectrum of associations, and also in the targeting of a particular glossopterid taxon (*Glossopteris browniana*) for the highest herbivory levels. Although the incidence of oviposition in the Brazilian data (misattributed as ‘galls’) is less than that of Clouston Farm, these sites represent considerably fewer examined plant organs, consisting of 352 total specimens examined compared to the 9772 of the present study; additionally, the Brazilian floras represent significantly earlier floras probably originating from different physical settings. Qualitative comparison of the Clouston Farm locality to late Permian sites of the Sydney and Bowen basins of New South Wales and Queensland, Australia, based on published damage (McLoughlin, 1994a, 1994b; Holmes 1995) and personal communication (R. Beattie) indicate even lower incidences of oviposition than that of southeastern Brazil, and comparatively greater predominance of external foliage feeding, almost entirely as leaf-margin damage. The qualitative data from the Middle Permian of India are less clear (Chauhan et al., 1985; Srivastava, 1988, 1996). The presence of margin feeding and limited oviposition has been documented, and seemingly a higher proportion of galling is present than at Clouston Farm (Banerjee and Bera, 1998), probably attributable to a lack of detailed, quantitative analyses of Indian floras.

By contrast, some data from the Euramerican and Cathaysian Realms reveal significant differences from Clouston Farm and other Gondwanan localities. Data from two Lower Permian localities of Euramerican north-central Texas—Taint of Sakmarian age (Beck and Labandeira, 1998) and Coprolite Bone Bed of Artinskian age (Labandeira and Allen, 2007)—indicate the virtual absence of oviposition, although some eastern Euramerican floras have considerable oviposition on sphenopsid stems (e.g., Roselt, 1954). At the Texan sites there is the near complete dominance of external foliage feeding, characterised by a greater proportion of hole feeding over margin feeding, and the presence of a unique conifer gall. This pattern parallels that of Western Europe (Florin, 1945; Geyer and Kelber, 1987). For Cathaysia, namely the North China Block, one qualitative study reveals a significant degree of external foliage feeding, predominantly in the form of hole- and margin feeding on gigantopterid pteridosperms (Halle, 1927; Glasspool et al., 2003), similar in style to analogously constructed foliage from the Early Permian Taint locality of Texas (Beck and Labandeira, 1998). After careful examination of Gondwanan (especially Clouston Farm), Euramerican, and Cathaysian localities, it is evident that pteridosperms, a paraphyletic group of variously related seed-plant clades, principally the Medullosales, Peltaspermales, Gigantopteridales and Glossopteridales (Hilton and Bateman, 2006), overwhelmingly exhibit the most varied and highest levels of herbivory from the several habitats in these floras (Labandeira, 2006; Labandeira and Allen, 2007). Coexisting taxa, such as sphenopsids, ferns, cordaites, conifers and cycadophytes, remain virtually unherbivorized, though this is not true for some Permian floras (Beck and Labandeira 1998, Beatty 2007; Labandeira and Allen, 2007). Subsequently, those seed-plant clades that survived the end-Permian crisis, as well as those that originated during the Triassic, were colonised by mostly new clades of insect herbivores that re-evolved the same functional feeding groups as those occurring among Permian floras (Labandeira, 2006).

7. INSECT BODY FOSSILS

The Permian insect fauna of South Africa is known mainly from insect-wing impressions (Riek, 1973, 1976b), although rare examples of more complete body fossils have been recorded (Riek, 1974, 1976a, 1976b, 1976c; van Dijk, 1981, 1998; van Dijk and Geertsema, 1999; Geertsema et al., 2002). Below, two fossil insect specimens that are accommodated under taxa described for the late Permian of South Africa are discussed and figured.

7.1. Neopteran Wing

A single, fragmentary insect-wing impression was found in Bed B (Plate XIV, 1, 2). This wing consists of the distal third of a probable hindwing, and preserves predominantly major veins, and a few costal veinlets between the costa and subcosta; no significant crossveins are present. The radius (R) appears to be 2-branched, although the basal branch is not evident. The media (M) appears 3-branched and the basal bifurcation similarly is missing. The Cubitus (Cu) minimally has three branches; possible additional branches are missing because of the absence of the posterior wing margin. The maximum length of the wing, diagonally from the anterior-proximal to posterior distal aspect, is 14.5 mm. This specimen is assigned the accession number of BP/2/29893 and is housed in the Bernard Price Institute of the University of the Witswatersrand, in Johannesburg.

This wing is tentatively assigned to the Grylloblattida (sensu Storozhenko, 2002), which subsumes most taxa formerly included under the ‘Protorthoptera,’ “Paraplecoptera,” and “Protoperlaria.” Further definitive assignment to a subclade is not possible, although it resembles the family Liomopteridae. The systematic status of Palaeozoic Grylloblattida is probably paraphyletic, as no distinctive synapomorphies have been determined that link these fossil taxa to the modern clade (Engel and Grimaldi, 2006). Extant grylloblattodeans have a relictual distribution and inhabit cold habitats in northern North America and Eurasia (Vršansky et al., 2001), and are commonly known as rock crawlers.

7.2. Sternorrhynchan nymphs

As discussed by Geertsema et al. (2002), fossils of immature insects are particularly rare. Hence, the discovery of two adjacent nymphs, or alternatively, a single nymph and its newly shed exoskeleton, is an important find. Although plecopteroid nymphs are known from the Permian of South Africa (Riek, 1976c), the only comparable specimens are from two Upper Permian localities in the KwaZulu-Natal Midlands. The first is an immature sternorrhynchan hemipteran, *Aleuronympha bibulla*, described by Riek (1974) from the Mooi River locality, an additional specimen from this locality of which was described by Riek (1976a), and the second is an example of what van Dijk (1981) described as a late nymphal instar comparable to *Aleuronympha*, from the Lidgetton locality.

The two contacting specimens (Plate XIV 3, 4) are conspecific hemipteran nymphs, possibly assignable to the Sternorrhyncha. The specimens possess the abdominal doublure that is absent in *Aleuronympha* but present in many extant sternorrhynchans. Six, possibly seven, abdominal segments are present in both specimens. The cephalic and thoracic regions, as well as appendages and ornamentation, are not evident. The midbody axial lengths of the specimen positioned at the top are 2.4 mm, and the specimen oriented to the lower-right is 2.2 mm. This specimen is assigned the accession number of BP/2/30000 and is housed in the Bernard Price Institute of the University of the Witswatersrand, in Johannesburg.

8. VERTEBRATE OCCURRENCES

Dicynodont therapsids are the most common group of fossil tetrapods from the Beaufort Group in terms of specimen numbers and inferred biomass. Thus, it is not surprising that vertebrate material discovered at the Colenso roadcut, near the Clouston Farm locality (Fig. 1) is assigned to this group. The collected fossil material includes a partial basicranium and associated left jugal arch, in addition to a few postcranial elements. Based on the preserved basicranium, it is estimated that the complete skull was approximately 28 cm in length. The specimen compares favourably with the larger *Oudenodon* Owen 1861 skulls housed in the fossil collection of the Council for Geoscience (Pretoria, South Africa) in terms of both size and cranial outline. This specimen has an interpterygoid vacuity that is poorly preserved, but apparently reaches the anterior margin of the palatine elements. The presence of a narrow and blade-like vomerine plate, postcaniniform crests, and the absence of upper canines support assignment of this specimen to *Oudenodon* (Angielcyzk, 2001).

An abundant and varied amphibian and therapsid fauna has been described (Kitching, 1995; Smith, 1995) from the *Dicynodon* Assemblage Zone. Several gorgonopsian, therocephalian, and cynodont genera occupied various carnivore niches, whereas dicynodont taxa dominated herbivorous niches within this faunal assemblage. Dicynodont herbivores display great variation in body size, but anatomically are conservative with long, barrel-shaped bodies and short legs. The upper and lower jaws of dicynodonts incorporated a horizontal (or shredding) component in their masticatory mechanism, in addition to the vertical (crushing) action, presumably to improve digestive efficiency (Crompton and Hotton, 1967; King, 1981, 1990; Cox, 1998). By comparison, *Oudenodon* was a medium-sized dicynodont and, based on its anatomy, King (1990) considered it to have pursued a medium-height feeding strategy of consuming plants in a zone 20–100 cm above the ground. This contrasts to forms such as *Dicynodon* and *Diictodon* which King (1990) interpreted as feeders that targeted substrates as low foliage croppers and forms consuming roots and tubers.

9. DISCUSSION

There are three important implications of this study. These aspects are presented in the broader context of changes in the physical environment and ecosystem structure in the Karoo Basin from the late Guadalupian, through the P-T boundary interval, and well into the Triassic. The most salient aspects of the Clouston Farm site for understanding these changes are (1) the depositional setting; (2) macrofloral, especially glossopterid, physiognomy; and (3) animal trophic structure, such as plant-insect associations.

Although this geographically restricted site represents one time slice in a succession of biotas throughout an interval that have been, and are currently, under examination (Bamford, 1999; 2004; Adendorff et al., 2002, 2003; Neveling, 2004; Neveling et al., 2005; Gastaldo et al., 2005; Labandeira et al., 2005), it does provide a Lopingian baseline from which younger, particularly Early Triassic biotas can be compared and assessed.

9.1. Depositional Setting

The plant-fossil assemblage preserved within the fine-grained clastic interval, superposing a thick sequence of trough crossbedded sandstone, is characteristic of an abandoned, meandering channel system within the Normandien Formation. Hiller and Stavrakis (1984) first described these fining-upwards sequences in which trough crossbeds, ranging from a few to tens of meters in thickness, are complemented by ripple cross-lamination. Sandstone bedsets were ascribed to point bar deposits, although such bedload accumulations may represent any number of barforms within meandering fluvial regimes that accrete within aggradational sequences (Miall, 1996). Lateral accretion barforms are a common feature in these channels (e.g., Smith, 1987; Gastaldo et al., 2005), but restricted outcrop at Clouston Farm moderates such an interpretation for the trough crossbed sets described herein. The majority of Normandien lithologies are siltstone in which primary structures range from horizontal to ripple lamination, with fossiliferous meso-scale bedforms (Gastaldo et al., 2005). Thick plugs of mudrock are interpreted as abandoned channel fills in slack-water sites (Hiller and Stavrakis, 1984; Smith, 1995), and typically preserved as aerial plant detritus. Such landscape conditions have been attributed to the prevalence of temperate and humid climatic conditions throughout the accumulation of the Lower Beaufort (Hiller and Stavrakis, 1984; Smith, 1995; Ward et al., 2000; Catuneanu and Elango, 2001).

The nature of the fossil-plant assemblage within the siltstone interval is consistent taphonomically with actualistic data from equivalent hydrological regimes (Gastaldo et al., 1989, 1996b) and other deep-time deposits (Gastaldo et al., 1998). Channel abandonment progresses over time from meander loops to ultimate isolation from normal discharge, receiving sediment only during high flow events. In oxbow systems that, at present, remain partially open, such as the Macareo River of the Orinoco delta, Venezuela (Gastaldo et al., 1996b), sediment distribution ranges from fine sand adjacent to the downstream, open end of the meander to clay at the upstream, closed end. Where fine-grained clastics prevail, aerial plant parts (axes, leaves, fruits and seeds) are found stratified throughout cores, and bedded litter characterises shallow-water sites. Here, all well-preserved leaves originate from the riparian gallery forest adjacent to the standing water body, whereas allochthonous elements introduced through transport into Macareo Lake consist of decomposed and unidentifiable taxa. The presence of rippled siltstone in the fossil-bearing interval attests to bedload transport and genesis of primary structures under low flow conditions. Whether these conditions were related to flow into an incompletely closed meander loop or resuspension and reworking at the sediment-water interface in response to high winds associated with storms is uncertain. But, the presence of traumatically induced aerial detritus attests to the influence of storms in the genesis of the plant beds at this locality.

Once a meander has been isolated from the main fluvial channel, a thick sequence of interbedded mud and aerial debris can accumulate. These sequences consist of clusters of dense leaves that are interbedded with intervals of less dense plant material. In modern, temperate regimes, these intervals consist of stratified leaf clusters 3-5 leaves in thickness, separated by a thin interval of fine clastics, such as those documented for the Alabama River (Gastaldo et al., 1989) and Tensaw River (Gastaldo et al., 1996b) in Alabama, USA. Such clusters represent coordinated leaf fall associated with a change in climate, such as temperature or water stress, that are interbedded with fine-grained clastics, indicating overbank deposition. In general, leaf apices show no preferred orientation in these assemblages suggesting that water movement within the channel has no effect on assemblage characteristics. Due to the logistics of acquiring data from woody axes at the sediment-water interface in modern abandoned channels, trends in orientation can be inferred from leaf litters in adjacent swamps and from within active channels (Gastaldo, 2004). When both of these settings are evaluated, there is no evidence for alignment of wood branches preferentially with channel orientation. Hence, the fact that woody debris in the Clouston Farm channel shows preferred orientation within each fossil horizon may be the result of low sample numbers, a preferential orientation established prior to axial sinking (in response to prevailing wind direction across the oxbow lake), or possible reworking at the sediment-water interface in response to currents established within the lake system. It is not possible to identify one mechanism responsible for all of the observations.

Aerial debris preserved within an oxbow lake represents contribution from the plants living directly adjacent to the body of water, representing a parautochthonous assemblage (Gastaldo, 1994; Gastaldo et al., 1996b). From the limited data available in modern settings, it appears that both Gaussian and log-normal distributions of leaf size occur in lake deposits. Gaussian distributions are attributed to sun- and shade leaf contributions from vegetation next to the site (Gastaldo et al., 1996b), whereas log-normal distributions appear to be characteristic of allochthonous leaves found in areas where fluvial channels debouch into standing bodies of water (Spicer, 1981). The presence of a Gaussian leaf-size distribution at Clouston Farm also supports direct contribution from plants that grew along the margins of the waterway.

9.2. Characterising the Macroflora

The high quality of macrofossil preservation and the extensive exposure of fossiliferous sediments at the Clouston Farm site provide a unique window into a Gondwanan terrestrial ecosystem from the late Permian of South Africa. While the Normandien Formation of KwaZulu-Natal previously yielded an abundance of plant fossils from more than 20 localities (Lacey et al., 1975; Lacey, 1978; Benecke, 1976; Anderson and Anderson, 1985; Gastaldo et al., 2005) (Table 3), documentation of these sites has been largely restricted to classical descriptions of the floral elements, with little consideration of palaeoecology. This paper represents the first detailed assembly of evidence provided from geologic, taphonomic, and micro- and megafloral studies of a single South African Permian plant locality.

The use of morphotypes in portraying the diversity of glossopterid leaves at the Clouston Farm site represents an important first step in the correlation of Upper Permian floras of South Africa. Future expansion of this study to other localities, with the application of similar taxonomic methodologies, will provide a platform for the objective assessment of glossopterid diversity in South Africa in both a temporal and spatial context. The absence of formal specific designations has imparted a degree of flexibility to the process, allowing taxonomic concepts to keep pace with our understanding of inherent degrees of variability observed in glossopterid leaf populations. This approach also serves to remove any biostratigraphic preconceptions that may be associated with inaccurately applied taxonomic titles from earlier studies.

The Clouston Farm locality, with its seven *Glossopteris* morphotypes and suite of subtypes, corroborates the work of Cúneo et al. (1993), who studied diversity patterns of Antarctic glossopterid floras in southern Victoria Land and the Central Transantarctic Mountains. They noted that assemblages associated with abandoned channel deposits showed the highest diversity of leaf morphotypes (8 to 22), with floodplain and lacustrine taphocoenoses yielding a significantly lower diversity of leaf forms (1 to 4).

The lack of accompanying geologic and taphonomic information in nearly all previous studies of late Permian plant fossil localities in South Africa has impeded our ability to make ecologically meaningful comparisons with floras from these sites. It seems, on the basis of our preliminary investigations, that late Permian autochthonous floras are a rarity in South Africa, with many of the floras documented to date indicative of parautochthonous or allochthonous assemblages (Gastaldo et al., 2005). This may offer an explanation for the paucity—and gross under-representation as reflected by the palynological data from Clouston Farm—of hygrophilous elements in the late Permian megafloral fossil record of South Africa (Anderson and Anderson, 1985). These elements tend to be delicate, do not easily survive the rigors of transportation, and are typically only introduced into the channel system during relatively rare traumatic events such as bank collapse, storms, and extensive herbivory. Glossopterid leaves and fertile structures, however, appear to have been abscised from the plant in great numbers, ensuring their adequate representation in most environments conducive to the formation of plant fossils.

The Clouston Farm leaf morphotypes fall mostly within the microphyll leaf size category as defined by Webb (1955), with ranges of three of the morphotypes extending into the notophyll category. This appears to be a trend for all Upper Permian deposits of South Africa, which exhibit a predominance of smaller leaves (microphyll to notophyll classes), whereas much larger leaves (mesophyll to macrophyll) form a major component of Lower Permian, Vryheid Formation floras, such as those from the Vereeniging and Hammanskraal localities. This may be a reflection on the broad-scale climatic changes that occurred during the Permian, with an increase in temperature and decrease in humidity favouring the persistence of smaller-leaved glossopterid forms. However, it should be borne in mind that the two temporally and spatially separated floras grew in very different habitats. The large-leaved floras of the earlier Permian are found in the fluvio-deltaic deposits associated with coal deposits in the northern parts of the Karoo Basin, whereas the floras typical of the Normandien Formation appear to have derived from riparian forests and floodplain vegetation associated with meandering river systems (Gastaldo et al., 2005).

Although lycopsids formed a conspicuous component of early and middle Permian floras in South Africa, there is only tentative evidence for the presence of this group in the late Permian deposits of the Normandien Formation. This is of importance, as lycopsids are widely considered to have been a dominant component of floras following the end-Permian crisis in the Northern Hemisphere, particularly the isoetalean *Pleuromeia* Corda ex Germar 1852 (Looy et al., 1999; Grauvogel-Stamm and Ash, 2005). Retallack (1995, 1997) reported a similar trend in Australia, and later in

Antarctica, which he subsequently extrapolated to South African floras (Retallack et al., 1996). Triassic evidence for a similar trend in South Africa comes from both the micro- and macrofossil record. Anderson and Anderson (1985) described *Pleuromeia*-like stems (*Gregicaulis dubius* (Seward) Anderson and Anderson) from the Burgersdorp Formation. Steiner et al. (2003) recorded a dominance of lycopsid spores in their Early Triassic *Kraeuselisporites*-*Lunatisporites* spp. assemblage from the Carleton Heights section, southern Karoo Basin. This supports the hypothesis that, also in South Africa, sparse lycopsid populations underwent profound niche expansion following the end-Permian crisis (Retallack, 1997; Looy et al., 1999).

Future expansion of this South African study will incorporate other plant communities preserved in different environments. We hope to better understand the relationships between diversity patterns and localised habitats within a circumscribed temporal framework.

9.3. Insect Herbivores, Food Webs, and the P-T Interval

Sedimentological and biological evidence at Clouston Farm supports riparian woodland dominated by a few taxa of glossopterid trees and including sphenophytes, ferns, and possibly lycopods. Within this community, tentative evidence supports a food web consisting of four herbivore functional feeding groups based mostly on plant-insect associational evidence. Less evidence supports the trophic regulation of these herbivores from above by odonatopteran dragonflies and, perhaps, vertebrates. The primary producers, mostly glossopterid taxa, hosted a functional feeding group of predominantly mandibulate insect herbivores feeding on leaf tissues, including the consumption of entire leaf-blade margins and the stripping of more specified foliar epidermal tissues. Suspected culprits for this type of plant damage were orthopterans and perhaps beetles. Two additional functional feeding groups, piercing-and-sucking and oviposition, had histological effects on deeper-seated vascular tissues, particularly glossopterid midribs and less commonly stems and other axes from a wider range of vascular plants. Piercing-and-sucking insects were represented by hemipteroid and palaeodictyopteroid taxa; ovipositing insects were represented principally by palaeodictyopteroid and odonatopteroid taxa, the latter clade which were obligate insect predators (Bechley, 1996). A rare, fourth guild of insect herbivores were gallers, producing small, hemispheroidal galls on surface tissues of glossopterid leaves. Taxa most likely responsible were mites, sternorrhynchan hemipteroids, perhaps related to the two nymphal fossils at Clouston, and early lineages of endophytic holometabolous insects (Labandeira, 2005).

The Clouston Farm locality documents the recurrence of a widespread insect-plant damage syndrome that characterises Permian floras worldwide. Specifically, it illustrates that exophytic leaf-resource use, a broad category of feeding in which plant tissues are consumed by herbivores positioned external to the leaf, was established overwhelmingly on pteridosperm leaves (Labandeira, 2006), in this case, glossopterids. This pattern of pteridosperm tissue use at Clouston Farm emphasized principally margin feeding and oviposition, and subordinately hole- and surface feeding and galling. This variety of Permian herbivory occurred at other Gondwanan sites (Plumstead, 1963; Srivastava, 1988; Holmes, 1995; Adami-Rodrigues et al., 2004a) and represented a continuation of earlier, Late Pennsylvanian to Guadalupian pattern of herbivory that was present in several environments from Euramerica (Müller, 1982; Scott et al., 1992; Labandeira and

Phillips, 1996, 2002; Beck and Labandeira, 1998; Rößler, 2000; DiMichele et al., 2004; Labandeira and Allen, 2007) and possibly Cathaysia (Glasspool et al., 2003). In addition to these Permian types of herbivory, there was the subsequent origination of Middle to Late Triassic plant-damage trends characterised by considerably more diverse, endophytic modes of plant tissue consumption, such as leaf-mining and seed predation, and more varied types of galling and piercing-and-sucking (Anderson and Anderson, 1989; Kelber and Hansch, 1995; Grauvogel-Stamm and Kelber, 1996; Ash, 1997, 1999; Scott et al., 2004; Labandeira et al., 2005). As for the functional feeding groups documented at Clouston Farm, tentative evidence indicates that they continued across the P-T boundary and also ecologically characterised Triassic biotas, though exhibiting a different spectrum of damage types. Importantly, there was significant taxonomic convergence as Triassic lineages of both plant hosts and their insect colonizers invaded new ecological settings (Labandeira, 2006).

10. SUMMARY AND CONCLUSIONS

1. *Locality*. The Clouston Farm locality, near the town of Colenso in central KwaZulu-Natal, contains a late Permian (Lopingian) deposit of Wuchiapingian (palynological assignment) to Changhsingian (vertebrate biostratigraphical assignment) age within the Normandien Formation (Lower Beaufort Group) of South Africa's Karoo Basin. This exposure consists of a stratigraphic sequence of fluvial deposits and accompanying sedimentological structures, and provides body- and trace-fossil evidence for a rich local community of plants, insect herbivores, vertebrates and their associations.

2. *Stratigraphy*. Three plant-bearing beds occur within the upper 3 to 4 meters of a 25

m thick section of predominantly medium- to fine-grained sandstone that represent an overall upwardly fining trend. This sequence is interrupted by thick and more vertically extensive sets of ripple and trough cross-stratification that represent channel infill. Toward the top, a shale-dominated interval contains three horizons of densely packed plants dominated by glossopterid leaves and other vascular plant organs.

3. *Depositional environment*. Toward the bottom of the stratigraphic sequence the environment of deposition probably was a channel bar deposit in a comparatively high-energy perennial river. Towards the top of the sequence, channel migration and abandonment and general shallowing indicate deposition of plant beds in finer-grained sediment under a relatively slack-water phase or in a standing body of water. Concentrated assemblages of dense but commonly fragmentary glossopterid leaves, robust axes, and other organs occur at the tops of several millimetre-thick layers of siltstone. The glossopterid leaves exhibit no preferred orientation, minimal decay prior to burial, and a modal microphyllous size distribution.

4. *Macroflora*. The flora consists of 9772 specimens attributable to 51 distinct types of vascular plant organs, but dominated overall by three categories of glossopterid leaves. Morphotypes C2, C2a, and C2b constitute 40.4 % of all plant occurrences. Seven, distinct glossopterid morphotypes are present, three of which bear a subtler range of variation, and some of which are similar to published descriptions from floras in other regions of Gondwana. Notable features of these glossopterids are their modest diversity and small size of glossopterid morphotypes when compared to older Karoo floras. Also included in this flora are sphenophytes (*Paracalamites*, *Phyllotheca*, *Schizoneura*), a possible lycopod, the fern *Sphenopteris*, a few types of seed-plant scale leaves, glossopterid

reproductive structures (such as *Arberiella*, *Lidgettonia*, *Eretmonia*), related but dispersed platyspermic seeds, and a wide range of unidentifiable axes.

5. Woods. Specimens of fossil wood at Clouston Farm were identified as *Agathoxylon africanum* and as *A. karooensis*. These taxa are of unknown taxonomic assignment, but are known to occur only in the Lopingian and Triassic of southern Africa.

6. *Palynoflora*. The palynoflora from Clouston Farm is nondiverse and in general proportion is taxonomically congruent with the macroflora. It is dominated by taeniate bisaccate taxa, particularly *Lunatisporites*, *Protohaploxypinus* and *Striatopodocarpites*, that typically are associated with glossopterid plants. There is a subdominant component of simple trilete spores, with an over-representation of fern-attributed taxa. The bulk of the evidence indicates a Wuchiapingian age.

7. *Plant-insect associations*. The insect herbivory patterns from the Clouston Farm site indicate a relatively low level of herbivory, an elevated degree of host specificity on glossopterid morphotype C2a, a surprisingly high percentage of oviposition on glossopterid leaf midribs and margins, and the overwhelming predominance of exophytic foliar feeding by mandibulate insects (62.0 % of all occurrences) over endophytic use by ovipositing, piercing-and-sucking and galling insects (38 %). This pattern changed with the emergence of many new types of endophytic feeding during the Triassic.

8. *Insect fauna*. Two insect body fossils, a fragmentary wing assigned to the Grylloblattodea *sensu lato*, comparable to the Liomopteridae, and two conspecific nymphal hemipteroids, assignable to the Sternorrhyncha, were present. The two taxa closely resemble other specimens described from the Lopingian of South Africa.

9. *Vertebrate fauna*. Earlier works (Kitching, 1977; Groenewald, 1984, 1989)

reported *Dicynodon* Assemblage Zone fossils from greyish-green siltstones of the Normandien Formation. Recovery of cranial material assigned to the herbivorous dicynodont *Oudenodon* from an adjacent and correlative locality is consistent with placement of the plant locality in the *Dicynodon* Assemblage Zone. This rich and diverse biozone has a global distribution with faunal correlatives from other Gondwanan localities as well as China, Russia, Laos, and Europe, where they are assigned to the late Permian Changhsingian Stage.

10. *Significance*. This study is a first attempt in integrating the depositional environment and all biotic features available for examination from a spatially circumscribed locality in the context of a local ecological community. This study, in conjunction with other similar ongoing and future studies across the P-T boundary of the Karoo Basin, will provide additional primary data for documenting environmental and biotic trends across the most important physical and biological event in the Phanerozoic history of terrestrial life.

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FIGURE CAPTIONS

Figure 1. Location of the Clouston Farm locality.

Figure 2. Gross stratigraphy of the Karoo Basin and location of the Clouston Farm locality.

Figure 3. Exposure of the donga at the Clouston Farm locality.

Figure 4. Generalised stratigraphic column of the Clouston Farm locality, with an expansion of the local, plant bearing interval. Abbreviations: **e**, erosional contact; **g**, gradational contact; **Fm**, massive siltstone; **RCB**, ripple crossbedding, **Sm**, massive

sandstone; **St**, trough-crossbedded sandstone; **TCB**, trough crossbedding; and **A**, **B**, and **C** adjacent to the leaves are the three plant-bearing beds referred to in the text.

Figure 5. Frequency histogram of glossopterid leaf length from Bed B.

Figure 6. Rose diagrams of *Glossopteris* leaf and sphenopsid axial orientations within the three concentrated, plant-bearing intervals. **A**, composite plot of *Glossopteris* from Bed C exhibiting a wide range in leaf orientation. Mean vector is 89° (N = 101), with individual bedding surfaces ranging from 25° to 196°, and no preferential orientation (see Table 1; Rayleigh test, p = 0.16). **B**, Composite plot of *Glossopteris* from Bed B exhibiting a narrow range in leaf orientation. Mean vector is 59° (N = 101), with individual bedding surfaces ranging from 50° to 312° (see Table 1; Rayleigh test, p = 0.00). **C**, Composite plot of sphenopsid axes from Bed B exhibiting a narrow range of variance in stem orientation. Mean vector is 57° (N = 33, see Table 1; Rayleigh test, p = 0.00). Circular statistical analyses conducted on axial orientations in the NE quadrat; rose diagram wedges translated to the SW quadrat. **D**, Composite plot of *Glossopteris* from Bed A exhibiting a wide range in leaf orientation, along with no preferential orientation. Mean vector is 256° (N = 32), with individual bedding surfaces ranging from 27° to 257° (see Table 1; Rayleigh test, p = 0.00).

Figure 7. Frequency of the 20 most common plant morphotypes at the Clouston Farm locality. The frequencies of the remaining 31 morphotypes constitute the last column.

PLATE CAPTIONS

Plate I. Detail of sedimentary lithology, structures, and interbed relationships at the

Clouston Farm locality. **1**, Sandstone bedsets with trough cross-stratification between 6–7 m wide predominate in the lower half of the study section. **2**, Extraformational clasts (principally quartz and feldspar) up to 8 mm in diameter drape individual laminae of a coarse-grained, trough cross-stratified sandstone bed. **3**, Individual trough size as well as grain size decrease upsection. **4**, Many troughs found towards the top of the channel fill (Fig. 6C) are filled with stacked sets of in-phase ripple cross-stratification. **5**, Steeply dipping, upwards-concave bounding surfaces in the uppermost channel sandstones are draped by 10–50 cm thick ripple cross-stratified sandstone. **6**, Thinly bedded packages of fossiliferous shales are separated by very thin, laterally extensive clay strata (arrow), some of which were used as marker horizons. **7**, Horizontal and low amplitude, in-phase ripple stratification predominate the very fine and clay-rich shales of the fossil-bearing beds. The arrow denotes the position of a yellowish-grey clay layer that separates thin-bedded shale units. **8**, Ripple cross-stratified shale of Plant Bed A drape undulatory and steeply-dipping surfaces, mimicking the shape of small troughs. Carbonaceous lenses (arrow) uncommonly are found in the "troughs" of these depressions. Length of entire scale is 20 cm.

Plate II. Clouston Farm sphenopsids (A-F), a fern (G, H), platyspermic seed (I), and *Eretmonia natalensis* (J, K). **1**, *Paracalamites* sp.; smaller specimen with a central node (BP/2/29902). **2**, *Paracalamites* sp.; larger specimen exhibiting three nodes with attached rootlets (BP/2/30068). **3**, *Phyllotheca* sp. leaf whorl and attached stem (BP/2/30018b). **4**, *Phyllotheca* leaf whorl next to a sphenopsid stem (BP/2/30053). **5**, *Schizoneura gondwanensis* (BP/2/30022a). **6**, Stem with *Phyllotheca* sp. leaves originating from a node (BP/2/30029). **7**, *Sphenopteris* sp. fern (BP/2/29896). **8**, Detail of (G), showing venational details of pinnules and sori. **9**, Platyspermic seed (“*Samaropsis*”) (BP/2/29939). **10**, The glossopterid pollen organ *Eretmonia natalensis* (BP/2/29943). **11**, Another specimen of *E. natalensis* (BP/2/30025b). Scale bars: stippled = 1 mm, striped = 5 mm, solid = 10 mm.

Plate III. A possible lycopod and glossopterid-associated reproductive structures from the Clouston Farm locality. **1**, Possible lycopod stem with leaf cushions (BP/2/30028b). **2**, The pollen organ *Eretmonia natalensis* (BP/2/30097a). **3**, The ovuliferous fructification *Lidgettonia africana* (BP/2/29947). **4**, Isolated scale leaf (BP/2/29945). **5**, Another isolated scale leaf (BP/2/29936b). Scale bars: stippled = 1 mm; striped = 5 mm.

Plate IV. Clouston Farm glossopterid leaf morphotypes: C1 to C2c. **1**, Morphotype C1a (BP/2/29719). **2**, Morphotype C1b (BP/2/29761). **3**, Morphotype C2a (BP/2/29784). **4**, Morphotype C2a (BP/2/29714). **5**, Morphotype C2a (BP/2/29808b). For C2a, also see BP/2/29713 on Plate XII, 7, 8. **6**, Morphotype C2b (BP/2/29685). **7**, Morphotype C2c (BP/2/29780). **8**, Morphotype C2c (BP/2/29644b). **9**, Morphotype C2c (BP/2/29844). Scale bars: striped = 5 mm, solid = 10 mm.

Plate V. Clouston Farm glossopterid leaf morphotypes: C3 to C6a. **1**, Morphotype C3 (BP/2/29879). **2**, Morphotype C3 (BP/2/29644). **3**, Morphotype C4 (BP/2/29710). **4**, Morphotype C4 (BP/2/29891). **5**, Morphotype C5 (BP/2/30051). **6**, Morphotype C6a (BP/2/30012). **7**, Morphotype C6a (BP/2/30011). Scale bars: striped = 5 mm, solid = 10 mm.

Plate VI. Clouston Farm glossopterid leaf morphotypes: C6a to C7. **1**, Morphotype C6a (BP/2/30012). **2**, Morphotype C6a (BP/2/29718a). **3**, Morphotype C6b (BP/2/29645b). **4**, Morphotype C7 (BP/2/30038). **5**, Morphotype C7 (BP/2/29715). Scale bars: striped = 5 mm, solid = 10 mm.

Plate VII. Summary of Clouston Farm glossopterid leaf morphotypes. Photograph tracings of specimens illustrated in Figures 12 to 14. Scale bar is 10 mm.

Plate VIII. Woods of the Clouston Farm locality. **1–3**: *Agathoxylon africanum* (Bamford) Bamford and Philippe (BP/16/1492). **1**, transverse section showing the more or less square outline of tracheids. Note the absence of axial parenchyma and canals. **2**, radial longitudinal section with alternate, biseriate, contiguous bordered pits on the radial wall (**bp**) and araucarian cross-field pits (**a**). **3**, tangential longitudinal section with low, uniseriate rays (**r**) between the vertical tracheids. **4–6**: *Agathoxylon karooensis* (Bamford) Bamford and Philippe (BP/16/1493). **4**, radial longitudinal sections showing several tracheids with triseriate, contiguous, alternate bordered pitting on the radial walls of the tracheids. **5**, transverse section showing the square to rounded tracheids. **6**, radial longitudinal section with the araucarian pits in the cross-field (**a**). Scale bars: slashed = 10 μm, quadrille = 100 μm, backslashed = 1000 μm.

Plate IX. Selected pollen and spores from the Normandien Formation deposit at the Clouston Farm locality. Scale bar is 10 μm. Specimen names are followed by UCMP specimen numbers, slide code, and England Finder graticule coordinates. **1**, *Calamaspora plicata* (UCMP 398620), SA-CA0.5-9. O49-2. **2**, Cf. *Cyclogranisporites gondwanensis* (UCMP 398621), SA-CA0.5-2, F38-4. **3**, Cf. *Apiculatisporis cornutus*, UCMP-398622, SA-CA0.5-5, M46-1. **4**, *Horriditriletes tereteangulatus* (UCMP 398623), SA-CA0.5-9, H37-4. **5**, *Horriditriletes tereteangulatus* (UCMP 398624), SA-CA0.5-2, Y40-2. **6**, *Lophotriletes novicus* (UCMP 398625), SA-CA05-5, E29-2. **7**, *Granulatisporites* sp. (UCMP 398626), SA-CA0.5-2, Y37-2. **8**, *Striatopodocarpites cancellatus* (UCMP 398627), SA-CA0.5-6, Q31-1. **9**, *Striatopodocarpites fusus* (UCMP 398628), SA-CA0.5-5, C44-3. **10**, *Striatopodocarpites cancellatus* (UCMP 398629), SA-CA0.5-6, F31-3. **11**, *Protohaploxypinus limpidus* (UCMP 398630), SA-CA0.5-7, P29-4. **12**, *Striatopodocarpites cancellatus* (UCMP 398631), SA-CA0.5-2, S48-1. **13**, *Striatoabietes multistriatus* (UCMP 398632), SA-CA0.5-2, E43-1. **14**, *Agathoxylon* sp. tracheid with alternate bordered pitting (UCMP 398633), SA-CA0.5-5, G42-3.

Plate X. Plant-insect associations: external foliage feeding. Note development of reaction rims, surface-tissue removal, veinal stringers, and growth deformities. **1**, Shallow cuspate margin feeding (DT12) and hole feeding (DT02) damage on Morphotype C2a (BP/2/29892). **2**, Enlargement of DT02 from (1), showing reaction rim. **3**, Enlargement of DT12 from (1), showing ovoidal hole and surrounding reaction rim. **4**, Trenched feeding at leaf midsection, without growth abnormality (compare to 13 and 14 below) on Morphotype C2a (BP/2/29738). **5**, Enlargement of (4). **6**, Deep cuspate feeding on Morphotype C2 (BP/2/29744). **7**, Enlargement of (6), showing foliar surface tissues removed between reaction front and chewed edge. **8**, Folivory on Morphotype C2a evidenced by DT12 along the leaf margin and DT14 extending to the midrib (BP/2/29654d). **9**, Enlargement of (8), showing veinal stringers. **10**, Folivory (DT14) on Morphotype C2a showing a distinctive type of continuous feeding, evidenced by inverted cuspules (BP/2/29641). **11**, Margin feeding (DT12) indicated by cuspules, on an unidentifiable glossopterid (BP/2/30136). **12**, Continuous margin feeding (DT12) indicated by adjacent cuspules, on Morphotype C2a (BP/2/30011). **13**, Trenched feeding (DT15) toward the leaf apex of Morphotype C4, forming a growth abnormality, indicated by an anomalous vein pattern (BP/2/29644). **14**, Enlargement of (13), showing details of damaged leaf margin. Scale bars: stippled = 1 mm; striped = 5 mm.

Plate XI. Plant insect associations: midrib oviposition (DT76) on glossopterids (1–5, 9, 10) and random occurrences (DT102) on the laminae (7, 8). Note elliptical to lenticular damage with surrounding scar and disrupted internal tissues. **1**, A single, lenticular oviposition mark, with peripheral scar on a midrib of Morphotype C2a (BP/2/29767). **2**, Enlargement of (1), displaying ridged outer scar and disrupted internal tissue. **3**, Five oviposition marks on Morphotype C2b, four of which are positioned on the midrib edge, and a narrower, elongate, fifth mark at top lodged in the midrib center (BP/2/29731). **4**, Enlargement of five midrib oviposition marks in (3). **5**, Four, equally-spaced oviposition marks, expressed as elliptical indentations, on a thick midrib from the leaf base of an unidentifiable glossopterid (BP/2/29821). **6**, Isolated oviposition mark near the midrib of Morphotype C2a, exhibiting continuity of four major veins but altered interveinal tissue (BP/2/30026). **7**, Another example of an isolated, lenticular oviposition mark on Morphotype C2a, as in (6), but lacking accentuated veins (BP/2/30017b). **8**, Enlargement of (7), showing a prominent reaction rim. **9**, A series of four, subequally spaced oviposition marks on a midrib of Morphotype C2b, appearing as raised areas (BP/2/29732). **10**, Enlargement of (9), with prominent encirclement of the oviposition mark by a granular reaction rim. Scale bars: stippled = 1 mm; striped = 5 mm.

Plate XII. Plant-insect associations: oviposition (DT101) on or adjacent glossopterid leaf margins (1-5), and random occurrences (DT102) on the lamina near the midrib (6-10). Note characteristic lenticular to ellipsoidal scars with surrounding callus tissue and internally disrupted tissue. **1**, Leaf with extensive oviposition marks, some overlapping, concentrated on the distal leaf margin on Morphotype C2a (BP/2/30036). **2**, Enlargement of oviposition marks in (1), showing distinctive, darkened, encircling reaction rims, infrequent coalescence, and orientation parallel to venation. **3**, A similar pattern of oviposition marks in (1, 2), but with preservation differentially enhancing the reaction rims, on Morphotype C2 (BP/2/29808d). **4**, Oviposition marks occurring adjacent but not on the leaf margin of Morphotype C2a (BP/2/30035). **5**, Enlargement of (4), showing the orientation of oviposition scar tissue, likely representing a single oviposition event. **6**, An example of a larger, robust, and more ovoidal oviposition scar, compared to (1-5), occurring on Morphotype C2a (BP/2/29836a). **7**, Two oviposition marks occurring at leaf midsection of Morphotype C2a, with mark at the leaf margin causing minor distortion of venation (BP/2/29714). See Plate IV-5 for source leaf. **8**, Isolated oviposition mark on Morphotype C2a (BP/2/29747a). **9**, A large oviposition scar with an uncommon shape, on Morphotype C2a (BP/2/29835a). **10**, Enlargement of (9), showing a central constriction that possibly is related to ovipositor insertion angle. Scale bars: stippled = 1 mm; striped = 5 mm.

Plate XIII. Rare types of external foliage feeding (DT103: 1-4), galling (DT33: 8-10), the effects of plant pathogens (DT97: 5, 11), and unknown surface tissue damage (DT106: 6, 7). **1**, A mine-like, parallel-sided feeding trace along primary venation on Morphotype C2a (BP/2/29752), representing a type of strip feeding (DT103) in which surface tissues are removed. **2**, Enlargement of (1), showing the lack of internal particulate frass that would indicate a mine. **3**, An enigmatic surface feature of sinusoidal or anastamosing ridges on Morphotype C2a (BP/2/30055), probably representing a linear surface feeding subparallel to venation (DT103). **4**, Detail of (3) above, showing surface texture. **5**, V-shaped necrotic tissue on Morphotype C2, surrounded by a distinctive, thick, granular reaction rim and extending toward a major vein midway between the leaf edge and midvein (BP/2/29685). This may represent epiphyllous fungal damage. **6**, Distinctive surface damage (DT106) of unknown origin, possibly attributable to epiphyllous fungi or other plant pathogens on the surface tissues of Morphotype C2 (BP/2/29849b). **7**, Enlargement of (6), showing pustulose surface and sporadic dark, organic material. **8**, A small, hemispherical gall (DT33) on a leaf lamina of Morphotype C2a (BP/2/29977). **9**, Leaf lamina with two galls (DT33) on Morphotype C2a (BP/2/29866), almost identical to (8). **10**, Enlargement of (9), showing similar diameters of both galls. **11**, Another example of possible fungal damage from a V-shaped necrotic region with a border of callus tissue, on Morphotype C2b (BP/2/29754). Note clear delineation of primary veins and parallel striae in enclosed region. A Scale bars: stippled = 1 mm; striped = 5 mm.

Plate XIV. Insect body fossils from Clouston Farm. **1**, Wing of grylloblattotean insect, possibly a liomopteran (BP/3/29893). **2**, Overlay drawing of (A). **3**, Abdomens of two hemipteran nymphs, attributable to the Sternorrhyncha (BP/3/30000). **4**, Overlay drawing of (C). Scale bars: stippled = 1 mm; striped = 5 mm.

TABLES

Table 1. Orientation data for Glossopteris leaves in the Clouston Farm section. Analyses conducted using ORIANA, version 2.02 (Kovach Computing, 2004).

Table 2. List of plant morphotypes occurring at the Clouston Farm locality.

Table 3. Comparison of the Clouston Farm flora with other floras of the Normandien Formation.

Table 4. Description of glossopterid morphotypes at the Clouston Farm locality.

Table 5. Semiquantitative abundance of pollen and spore taxa.

Table 6. Distribution of insect damage types on plant morphotypes at the Clouston Farm locality.

	Bed C (0.25m^2)	Bed B (0.32m^2)	Bed A (0.15m^2)	Bed A Axes
N	101	176	32	33
Mean vector μ	89.01°	58.86°	256.50°	57.30°
95% CI (-/+) for μ	30.18° * 147.85° *	39.84° 77.89°	193.95° 319.05°	42.28° 58.47°
Rayleigh test of uniformity (p)	0.16	0.00	0.21	0.00

Table 1. Orientation data for *Glossopteris* leaves in the Clouston farm section.

Each of the three plant-bearing intervals was evaluated on stratigraphically descending beds with the total area evaluated for each interval ranging from 0.15m^2 to 0.32m^2. Confidence interval values marked with (*) may be unreliable because of low concentration. The Rayleigh's test of uniformity calculates the probability of the null hypothesis that the data are uniformly distributed; values < 0.05 indicate that the data are not distributed uniformly, exhibiting a preferred direction. Analyses conducted using Oriana v. 2.02 (Kovach Computing, 2004).

Table 2. List of plant morphotypes occurring at the Clouston Farm locality. Glossopterid morphotype designations in bold; prefix "C" refers to the Clouston Farm site**.**

Rank	Floral element	Abundance	Frequency (%)
1	Unidentifiable glossopterid foliage	2599	26.60
2	Glossopterid morphotype **C2a**	2007	20.54
3	Glossopterid morphotype **C2**	1692	17.31
4	C-sphenophyte axis	470	4.81
5	C-scale leaf	456	4.67
6	Glossopterid morphotype **C6a**	411	4.21
7	Glossopterid morphotype **C6**	305	3.12
8	Glossopterid morphotype **C3**	260	2.66
9	Glossopterid morphotype **C2b**	252	2.58
10	Glossopterid morphotype **C7**	193	1.98
11	Unidentifiable fragment	166	1.70
12	Glossopterid morphotype **C2c**	161	1.65
13	Glossopterid morphotype **C1a**	137	1.40
14	*Arberiella* sp.	99	1.01
15	C-sphenophyte roots	95	0.97
16	Unidentifiable axis	95	0.97
17	Glossopterid morphotype **C1b**	72	0.74
18	Glossopterid morphotype **C4**	48	0.49
19	C-woody axis	44	0.45
20	C-sphenophyte foliage	30	0.31
21	Glossopterid morphotype **C6b**	29	0.30
22	Glossopterid morphotype **C1**	27	0.28
23	*Eretmonia natalensis*	22	0.23
24	*Sphenopteris* sp.	17	0.17
25	C-seed 2	15	0.15
26	*Lidgettonia africana*	12	0.12

27	*Lidgettonia* sp.	12	0.12
28	C-seed 1	10	0.10
29	Glossopterid morphotype **C6c**	9	0.09
30	C-rugose reticulate axis	4	0.04
31	C-axis with leaf scars	4	0.04
32	*Phyllotheca australis*	4	0.04
33	C-ovulate fructification	4	0.04
34	C-?lycopod axis	3	0.03
35	*Phyllotheca* sp.	3	0.03
36	Glossopterid morphotype **C5**	1	0.01
37	C-small scale	1	0.01
38	*Lidgettonia lidgettonioides*	1	0.01
39	C-short shoot	1	0.01
40	*Schizoneura africana*	1	0.01
	TOTALS:	9772	100.00

Table 3. Comparison of the Clouston Farm Flora to other floras of the Normandien Formation

Taxon	Mooi River: National Road	Loskop: quarry	Mooi River: Far End quarry	Estcourt: Sheba's Breasts	Inhluzani: Glandisrock	Inhluzani	Lidgetton	Mooi River: Rosetta	Bergville	Bulwer	Mt. West	Kiesbeen	Estcourt: Indian School	Kilburn: dam floor	Kilburn: dam south edge	Mooi River: Far End west	Estcourt: Rondedraai	Inhluzani: Boschoek	Oliviershoek	Loskop: donga	Estcourt: Lowlands	Kilburn: south site	Number of host localities
C1a	*																						**1**
C1b	*																						**1**
C2a	*	*	*		*	*	*	*		*	*	*		*		*				*	*		**14**
C2b	*	*	*	*	*			*	*	*	*	*	*	*	*	*		*	*		*	*	**18**
C2c	*	*							*	*													**4**
C3	*			*	*				*			*											**5**
C4		*	*																				**2**
C5		*																					**1**
C6a	*			*		*	*	*					*										**6**
C6b	*																						**1**
C7																							**0**
Phyllotheca australis	*	*	*	*	*	*	*	*	*	*	*		*					*	*	*			**15**
Schizoneura gondwanensis	*			*	*	*		*			*		*	*									**7**
Sphenopteris alata	*	*	*	*	*		*	*	*				*	*									**10**
Eretmonia natalensis	*	*	*	*	*	*	*		*	*		*					*						**11**
Lidgettonia africana	*	*	*			*	*				*				*		*						**8**
?Lycopod axis	*																						**1**
Samaropsoid seeds	*	*	*			*	*			*	*	*			*	*	*						**11**
Number of leaf morphotypes in common with Clouston Farm	8	5	3	3	3	2	2	3	3	3	2	3	2	2	1	2	0	1	1	1	2	1	
Number of other elements in common with Clouston Farm	7	5	5	4	4	5	5	3	3	3	4	2	3	2	3	1	3	1	1	1	0	0	
Total elements in common	15	10	8	7	7	7	7	6	6	6	6	5	5	4	4	3	3	2	2	2	2	1	

Identifiable vegetative specimens (Anderson & Anderson, 1985)	**7500**	**3000**	**700**	**3000**	**500**	**3000**	**5000**	**500**	**3000**	**6000**	**200**	**3000**	**75**	**50**	**50**	**200**	**1000**	**200**	**500**	**250**	**10**	**30**

Table 4. Descriptiona of glossopterid morphotypes occurring at the Clouston Farm locality.

MORPHO-TYPE	**TYPE SPECIMEN**	**LEAF SHAPE**	**APEX**	**BASE**	**LENGTH (mm)**	**WIDTH (mm)**	**LENGTH: WIDTH**	**LEAF SIZE CLASS**	**MIDRIB**	**MIDRIB: BASAL WIDTH (mm)**	**MIDRIB: MEDIAL WIDTH (mm)**
C1a	BP/2/29719	narrowly obovate to oblong	slightly tapering apex with bluntly rounded, obtuse tip	long, tapering, cuneate, with short petiole	33 (41) 56 (n=5; SD:9.1)	8 (10) 11 (n=7; SD:1.7)	4 (n=5)	microphyll	narrow and persistent; slightly raised; a few well-defined veins visible	1.3 (n=2)	0.7 (0.9) 1 (n=6; SD 0.1)
C1b	BP/2/29838	narrowly elliptical	moderately acute, tapering slightly to rounded tip	unknown	c. 40-50 (n=2)	16 (18) 20 (n=2)	c. 2.5 (n=2)	microphyll	gracile, narrow, persistent; individual veins visible	unknown	1.4 (1.2) 0.8 (n=2)
C2a	BP/2/29808b	narrowly elliptical to ligulate	acute, tapering to a pointed or bluntly rounded tip	long and cuneate	c. 55 - 90 (n=7)	8 (11) 14 (n=10; SD 1.7)	c. 6 - 8 (n=5)	microphyll	narrow, fairly weakly defined, but persistent; individual veins visible; raised in lower part of leaf	0.9 (1.2) 1.4 (n=4; SD 0.2)	0.5 (0.9) 1.1 (n=10; SD 0.2)
C2b	BP/2/29685	narrowly elliptical to ligulate	tapered, acute with a rounded tip	long, tapering and cuneate	c. 90 to >100	13 (17) 20 (n=5; SD 3)	c. 5-6	microphyll	moderately prominent, persistent, individual veins may be visible	2 (2.2) 2.4 (n=3; SD 0.2)	0.8 (1.1) 1.2 (n=5; SD 0.2)
C2c	BP/2/29780	narrowly elliptical to oblanceolate	slightly tapered, with bluntly rounded, obtuse tip	cuneate	c. 55-75 (n=6)	12 (13) 17 (n=6; SD 1.8)	4 (4.7) 5.7 (n=6; SD 0.6)	microphyll	narrow, persistent, well-defined; individual veins visible; raised in basal half	1.1 (1.3) 1.8 (n=5; SD 0.3)	0.7 (0.8) 0.9 (n=6; SD 0.1)
C3	BP/2/29644b	linear to narrowly elliptical; may be lingulate;	long, tapering, with pointed tip	long, tapering and cuneate	c. 40-70 (n=6)	6 (9) 11 (n=6; SD 1.9)	c. 7 (n=6)	microphyll	very prominent with high relief; very broad relative to leaf width, persistent; individual veins visible	0.8 (1) 1.1 (n=2; SD 0.2)	0.4 (0.7) 1 (n=6; SD 0.2)
C4	BP/2/29710	narrowly oblanceolate	?	long, tapering and cuneate	c. 30-80 (n=3)	c. 8 (13) 17 (n=5)	c. 4-5 (n=3)	microphyll	narrow, but well-defined and persistent; individual veins clearly visible	1.1 (2) 3 (n=4; SD 0.83)	0.4 (0.9) 1.3 (n=5; SD 0.33)
C5	BP/2/30051	?	?	?	?	c. 30	?	?microphyll	narrow, persistent, raised; some individual veins visible	?	c. 1

Table 4. Descriptiona of glossopterid morphotypes occurring at the Clouston Farm locality.

C6a	BP/2/30012	narrowly elliptical to oblong	acute, pointed	long, cuneate	c. 70-160 (n=8)	17 (28) 32 (n=8; SD 5.5)	c. 4-5 (n=5)	microphyll to notophyll	prominent, broad in base, narrow but persistent in apex; particularly robust and raised towards base; some individual veins may be visible	c. 1.5-2 (n=3)	0.7 (1.3) 1.5 (n=8; SD 0.3)
C6b	BP/2/29645b	?elongate elliptical to oblong	tapers to a blunt, obtuse point	?	c. 100 - >140 (n=2)	c. 20-50 (n=2)	c. 3 (n=2)	microphyll to notophyll	broad, prominent, well-defined but narrow for leaf size; raised, persistent; component veins clearly visible	?	0.8 (1.3) 1.8 (n=2)
C7	BP/2/29715	oblanceolate	broadly rounded, obtuse, with distinctive retuse tip	long, cuneate	c. 60-70 (n=3)	18 (28) 46 (n=5; SD 12)	c. 3 (n=3)	microphyll to notophyll	well-defined and fairly broad in base, tapering to apex; persistent; individual veins visible	1.2 (1.4) 1.7 (n=3; SD 0.26)	0.7 (1.1) 1.8 (n=5; SD 0.4)

Table 4. Descriptiona of glossopterid morphotypes occurring at the Clouston Farm locality.

Table 4. Descriptions of glossopterid morphotypes occurring at the Clouston Farm locality

MIDRIB: APICAL WIDTH (mm)	VEIN COURSE	PROXIMAL VEIN ANGLE (degrees)	MIDLAMINAR VEIN ANGLE (degrees)	MARGINAL VEIN ANGLE (degrees)	MARGINAL VEIN DENSITY (veins per 10 mm)	ANASTO-MOSES	MESH SHAPE	PROXIMAL MESH WIDTH (mm)	MID-LAMINAR MESH WIDTH (mm)
0.2 (0.4) 0.5 (n=3; SD 0.2)	veins depart from midrib at steep angle, curve gently to margin at steep angle	9 (14.5) 29 (n=26; SD 4.6)	25 (36) 50 (n=28; SD 4.5)	34 (47) 54 (n=27; SD 5.3)	10 (14) 16 (n=7; SD 2.1)	1-2	trullate, falcate, polygonal adjacent to pseudo-midrib; linear polygonal in mid-laminar and marginal regions; of fairly consistent width across lamina, although first meshes may be slightly broader	0.6 (0.8) 1.1 (n=27; SD 0.15)	0.4 (0.8) 1.2 (n=29; SD 0.17)
0.3 (0.6) 0.8 (n=2)	veins depart from midrib at steep angle and arch gently across the lamina at a moderate angle	19 (24) 30 (n=7; SD 4.1)	40 (48) 56 (n=8; SD 4.7)	57 (61) 65 (n=7; SD 3.9)	16 (20) 22 (n=2)	1-2	falcate, elliptical, elongate polygonal; of fairly even width across lamina, becoming slightly narrower and more linear towards margin	0.6 (0.8) 1 (n=9; SD 0.13)	0.6 (0.7) 0.8 (n=9; SD 0.09)
0.2 (0.3) 0.4 (n=9; SD 0.1)	veins diverge from the midrib at a steep angle and arch gently and steeply to margin	5 (12) 22 (n=47; SD 3.9)	22 (33) 47 (n=38; SD 6.5)	29 (44) 56 (n=41; SD 6.9)	18 (24) 28 (n=23; SD 3.7)	2-4	narrowly falcate, polygonal to trullate near midrib; elongate elliptical to linear across lamina; similar width across lamina, although may be slightly broader near midrib	0.3 (0.4) 0.6 (n=37; SD 0.08)	0.2 (0.3) 0.5 (n=40 ;SD 0.09)
0.2 (0.4) 0.6 (n=3; SD 0.2)	veins arise at steep angle, then very gently arch (or follow an almost straight path) to margin at moderate angle	9 (15) 24 (n=23; SD 4.9)	40 (49) 59 (n=19; SD 6.5)	49 (57.8) 63 (n=20; SD 3.9)	26 (30) 36 (n=10; SD 3.5)	2-4	elongate elliptical to linear meshes across lamina; meshes adjacent to midrib are slightly broader, and are narrowly falcate, polygonal, trullate to elliptical	0.3 (0.4) 0.6 (n=21; SD 0.1)	0.2 (0.3) 0.6 (n=19; SD 0.1)
0.4 (0.5) 0.7 (n=6; SD 0.1)	veins depart from the midrib at a steep angle and arch gently to the margin at increasingly moderate angle	11 (21) 33 (n=26; SD 5)	35 (46) 54 (n=26; SD 5.1)	48 (58) 65 (n=25' SD 4.3)	14 (21) 24 (n=20; SD 2.5)	2-3	elongate elliptical to linear; falcate near midrib; of even width across lamina	0.4 (0.5) 0.7 (n=24; SD 0.12)	0.3 (0.4) 0.7 (n=27; SD 0.09)
0.3 (0.4) 0.5 (n=5; SD 0.1)	arise at steep angle to midrib, follow a fairly straight course to margin at a moderate angle	11 (21) 37 (n=36; SD 6.9)	51 (62) 73 (n=30; SD 5.4)	63 (69) 75 (n=29; SD 3.4)	30 (40) 58 (n=20; SD 8)	0-2	single row of falcate, trullate to rhombic meshes next to midrib; elongate elliptical to linear across lamina	0.2 (0.4) 0.7 (n=28; SD 0.14)	0.2 (0.3) 0.4 (n=24; SD 0.07)
c. 0.2 (n=1)	arise at steep angle to midrib, follow a straight path to margin at a moderately acute angle	10 (15) 23 (n=23; SD 4.4)	22 (31) 42 (n=19; SD 7.6)	29 (38) 48 (n=20; SD 6.6)	10 (15) 22 (n=12; SD 3.8)	0-2	strikingly regular, long meshes; few elongate polygonal immediately adjacent to midrib; elongate elliptical to linear across lamina; of fairly consistent width across the lamina	0.3 (0.6) 0.9 (n=22; SD 0.16)	0.2 (0.5) 0.8 (n=20; SD 0.16)
?	veins depart from midrib at a moderate angle, follow a straight path across the lamina	36 (54) 66 (n=5; SD 13)	54 (64) 73 (n=4; SD 8)	61 (65) 69 (n=4; SD 4.1)	16 (n=2)	5-6	trullate to polygonal immediately adjacent to midrib; elliptical and polygonal, across lamina, becoming markedly shorter and narrower towards margin	0.7 (0.9) 1 (n=5; SD 0.11)	0.4 (0.5) 0.7 (n=6; SD 0.1)

Table 4. Descriptiona of glossopterid morphotypes occurring at the Clouston Farm locality.

0.2 (0.4) 0.6 (n=7; SD 0.12)	veins depart from midrib at a steep angle, immediately bifurcate, and then follow a straight path across the lamina to the margin at a moderate angle	12 (23) 35 (n=36; SD 5.9)	56 (66) 84 (n=35; SD 6.9)	64 (71) 84 (n=32; SD 5)	22 (28) 36 (n=21; SD 4.4)	1-3	first row of meshes larger, elongate falcate to elongate polygonal; parallel-linear in medial and marginal sectors and of consistent width across lamina	0.4 (0.7) 1 (n=34; SD 0.17)	0.3 (0.4) 0.7 (n=35; SD 0.11)
0.5 (n=2)	veins depart from midrib at a fairly steep angle; some bifurcate soon after leaving midrib, but not as consistently as in 6a; veins then follow a very gently curved to straight path across the lamina	12 (22) 31 (n=7; SD 8)	45 (56) 67 (n=7; SD 10)	51 (61) 70 (n=7; SD 7.4)	22 (28) 32 (n=6; SD 5.2)	2-4	very fine, dense venation; parallel, linear, fairly consistent width across lamina, although first row of meshes may be slightly broader	0.4 (0.5) 0.5 (n=8; SD 0.05)	0.3 (0.4) 0.5 (n=10; SD 0.07)
0.4-0.5 (n=2)	alterative vein course: veins depart from midrib at a steep angle, follow a gently curved path across the lamina; in marginal third of lamina, veins recurve slightly to the margin; recurving of the veins becomes progressively more pronounced from the base to the apex (it is more difficult to detect in the basal region)	11 (18) 26 (n=19; SD 5.3)	43 (58) 74 (n=22; SD 9.8)	29 (56) 68 (n=17; SD 12.2)	14 (21) 28 (n=12; SD 5.2)	1-3	elongate falcate to linear, elongate polygonal; rarely elongate elliptical; narrower and more linear in marginal region	0.5 (0.8) 1 (n=22; SD 0.2)	0.5 (0.6) 0.8 (n=26; SD 0.1)

Table 4. Descriptiona of glossopterid morphotypes occurring at the Clouston Farm locality.

MARGINAL MESH WIDTH (mm)
0.3 (0.6) 1.1 (n=29; SD 0.21)
0.4 (0.4) 0.5 (n=9; SD 0.05)
0.1 (0.3) 0.5 (n=39; SD 0.1)
0.2 (0.3) 0.3 (n=21; SD 0.05)
0.3 (0.4) 0.6 (n=21; SD 0.09)
0.1 (0.2) 0.3 (n=28; SD 0.07)
0.2 (0.4) 0.7 (n=20; SD 0.14)
0.2 (n=5)

Table 4. Descriptiona of glossopterid morphotypes occurring at the Clouston Farm locality.

0.2 (0.3) 0.6 (n=32; SD 0.09)
0.2 (0.4) 0.4 (n=8; SD 0.08)
0.2 (0.4) 0.7 (n=23; SD 0.1)

Table 5. Semiquantitative abundance of pollen and spore taxa. Spore and pollen taxa are identified at the generic or species level, and originate from the Clouston Farm locality of the Estcourt Formation. Relative frequencies are: R rare < 1%, C common 1-5%, F frequent 5-10%, A abundant 10-25, D dominant 25-100.

Taxon	Frequency
Calamospora plicata (Luber and Waltz) Hart 1965	R
cf. *Cyclogranisporites gondwanensis* Bharadwaj and Salujha 1964	R
Granulatisporites papillosus Hart 1965	C
Lophotriletes novicus Singh 1964	C
cf. *Apiculatisporis cornutus* (Balme and Hennely) Høeg and Bose 1960	R
Horriditriletes ramosus (Balme and Hennely) Bharadwaj and Salujha 1964	R
Acanthotriletes tereteangulatus Balme and Hennely 1956	C
cf. *Alisporites ovatus* (Balme and Hennely)	R
Falcisporites sp. (Leschik) Klaus 1963	R
Weylandites lucifer (Bharadwaj and Saluhja) Foster 1975	R
Chordasporites waterbergensis. MacRae 1988	R
Lunatisporites spp. (Leschik) Maedler 1964	F
Protohaploxypinus spp. (Samoilovich) Morbey 1975	F
Protohaploxypinus limpidus (Balme and Hennely) Balme and Playford 1967	R
Striatopodocarpites spp.	F
Striatopodocarpites cancellatus (Balme and Hennely) Hart 1965	R
Striatopodocarpites fusus (Balme and Hennely) Potonié 1958	R
Striatoabieites multistriatus (Balme and Hennely) Hart 1964	C

Table 6. Distribution of Insect Damage Types at Clouston Farm

			C-plant hosts																					
Functional feed. group	*Damage type*	*Brief description*	*C1*	*C1a*	*C1b*	*C2*	*C2a*	*C2b*	*C2c*	*C3*	*C4*	*C5*	*C6*	*C6a*	*C6b*	*C7*	*scale leaf*	*gloss eunid*	*lyco axis*	*sphen roots*	*sphen axis*	*nongl unid*	*unid axis*	*#*	*%*
EXTERNAL FOLIAGE FEEDING																									
Hole feeding	DT01	Hole feeding; circular (<1 mm diameter)			1															1			1	3	*2.2*
“	DT02	Hole feeding; circular (1 to 5 mm diameter)												1		1		4						6	*4.4*
“	DT03	Hole feeding; polylobate (1 to 5 mm diameter)				1	2										1							4	*2.9*
“	DT07	Hole feeding; linear to curvilinear				3	1	1	1	1							1							8	*5.8*
Margin feeding	DT12	Margin feeding; cuspate excisions on leaf edge		1		6	8	1		1			1	1			1	3	1	1				25	*18.2*
“	DT13	Margin feeding at leaf apex				1												1						2	*1.5*
“	DT14	Margin feeding to primary vein				1	1																	2	*1.5*
“	DT15	Margin feeding; trenched into lamina				2	1																	3	*2.2*
Skeletonization	DT16	General skeletonization; weak reaction rim					1																	1	*0.7*
“	DT17	General skeletonization; distinct callus rim					1																	1	*0.7*
Surface feeding	DT29	General window feeding; indistinct callus rim	1	1				1		1				1				1						6	*4.4*
“	DT30	Polylobate window feeding; distinct callus				2	1	1					1				1	3				1		10	*7.3*
“	DT31	Subrounded window feeding; robust callus				1	4											1						6	*4.4*

“	DT75	V-shaped necroses with callus at vein border				2	2							1			1							6	*4.4*
“	DT103	Elongate, slot-like window feeding																1						1	*0.7*
“	DT106	Epidermal patches with pockmarked pattern																1						1	*0.7*
GALLING	DT33	Gall on a primary or other major vein				1	1																	2	*1.5*
PIERCING-&-SUCKING	DT46	Circular depressions; concave, <2 mm																1						1	*0.7*
“	DT48	Elliptical depressions; concave, <4 mm				1																		1	*0.7*
OVIPOSITION	DT76	On midrib or other major vein	1			$\boxed{5}$	$\boxed{11}$		1	2			2				2	3					1	28	*20.4*
“	DT101	On leaf; scars randomly distributed					1		1	2								2			1			7	*5.1*
“	DT102	Near leaf margin, parallel to venation				1	$\boxed{7}$	1										4						13	*9.5*
																								137	***99.8***
		Occurrences (#)	1	3	1	27	42	5	3	7	0	0	4	4	0	1	7	25	1	2	1	1	2	**137**	
		Frequency (%)	*0.7*	*2.2*	*0.7*	*19.7*	*30.7*	3.7	2.2	5.1	—	—	2.9	2.9	—	0.7	5.1	18.2	0.7	1.5	0.7	0.7	1.5	***99.9***	

Fig 1

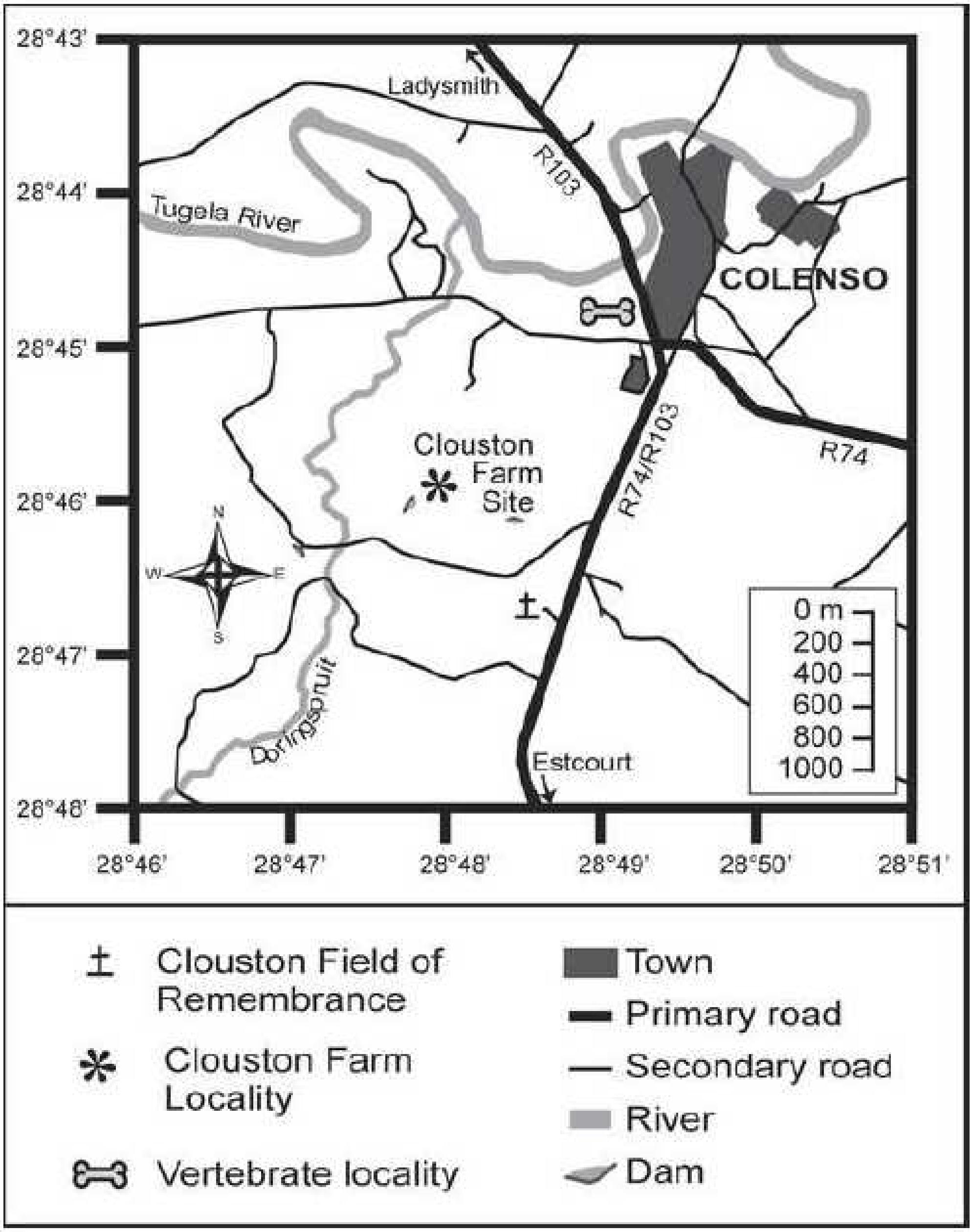

28°43'
28°44'
28°45'
28°46'
28°47'
28°48'
28°46'
28°47'
28°48'
28°49'
28°50'
28°51'
Ladysmith
R103
Tugela River
COLENSO
Clouston Farm Site
R74/R103
R74
N
W
E
S
Doringspruit
Estcourt
0 m
200
400
600
800
1000
Clouston Field of Remembrance
Clouston Farm Locality
Vertebrate locality
Town
Primary road
Secondary road
River
Dam

Fig 2

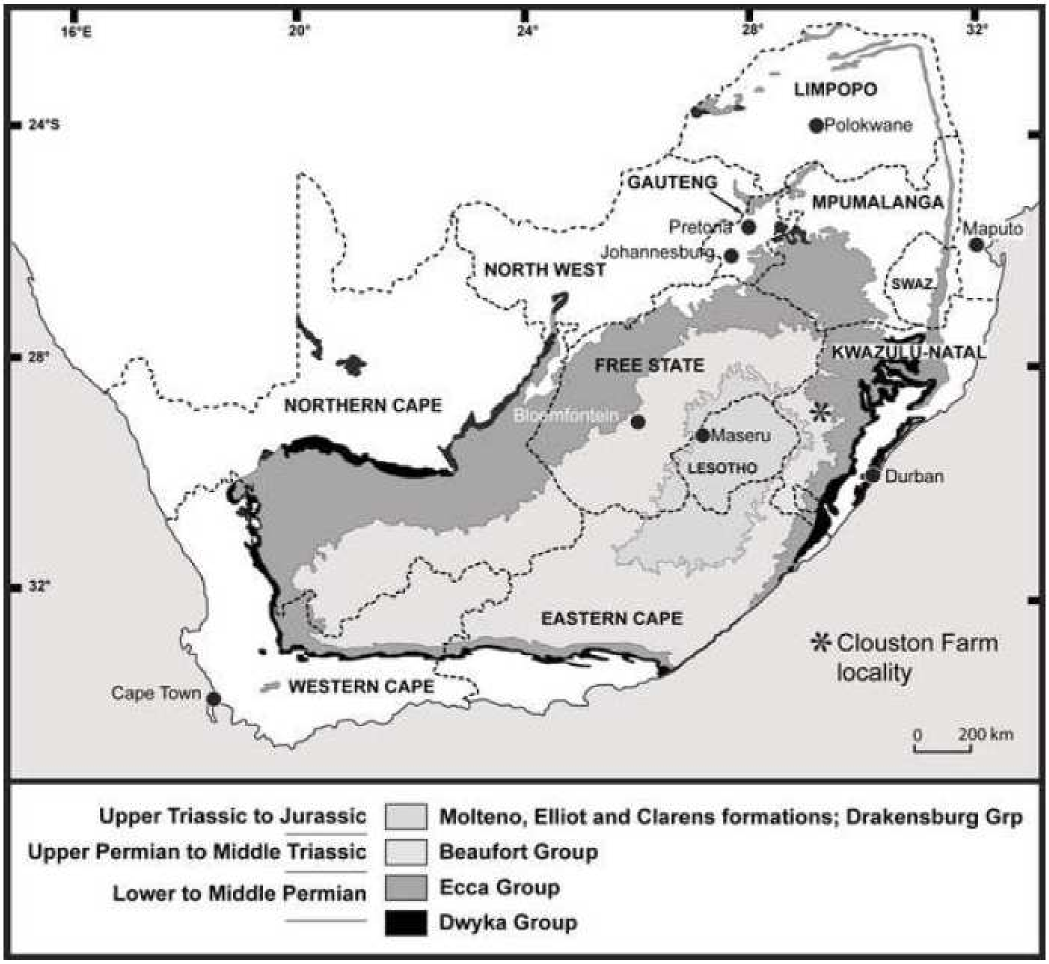
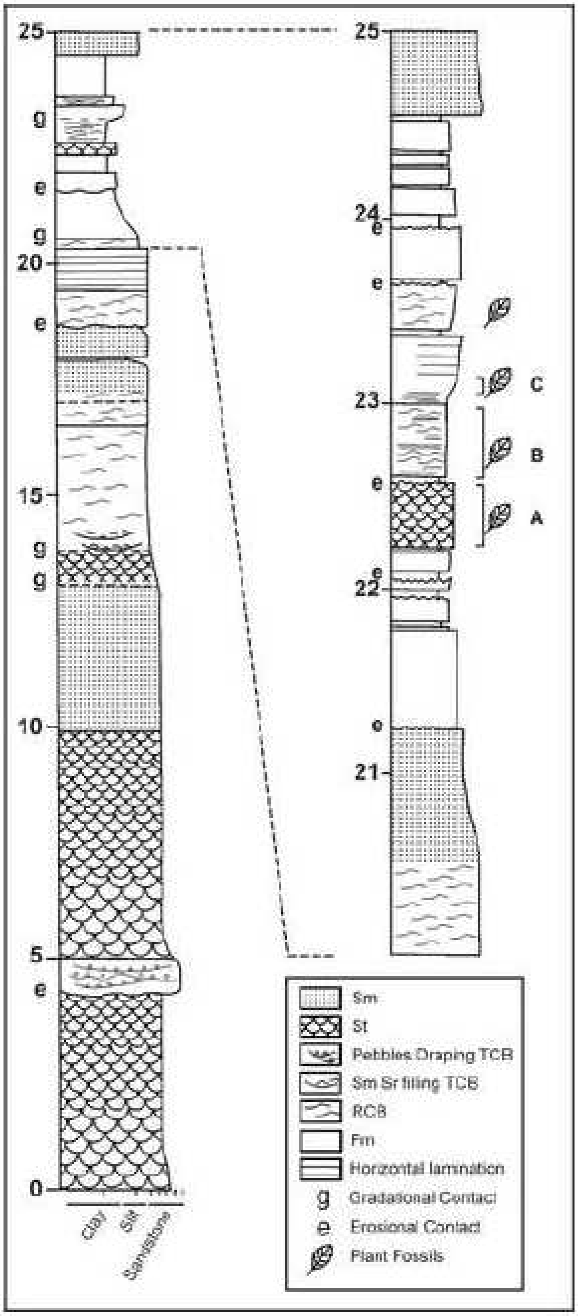

16°E
20°
24°
28°
32°
24°S
28°
32°
LIMPOPO
Polokwane
GAUTENG
MPUMALANGA
Pretoria
Johannesburg
Maputo
NORTH WEST
SWAZ.
FREE STATE
KWAZULU-NATAL
NORTHERN CAPE
Bloemfontein
Maseru
LESOTHO
Durban
EASTERN CAPE
* Clouston Farm locality
Cape Town
WESTERN CAPE
0
200 km
Upper Triassic to Jurassic
Upper Permian to Middle Triassic
Lower to Middle Permian
Molteno, Elliot and Clarens formations; Drakensburg Grp
Beaufort Group
Ecca Group
Dwyka Group

Fig 3

Fig 4


25
g
e
g
20
e
15
g
g
10
5
e
0
Clay
Silt
Sandstone
25
24
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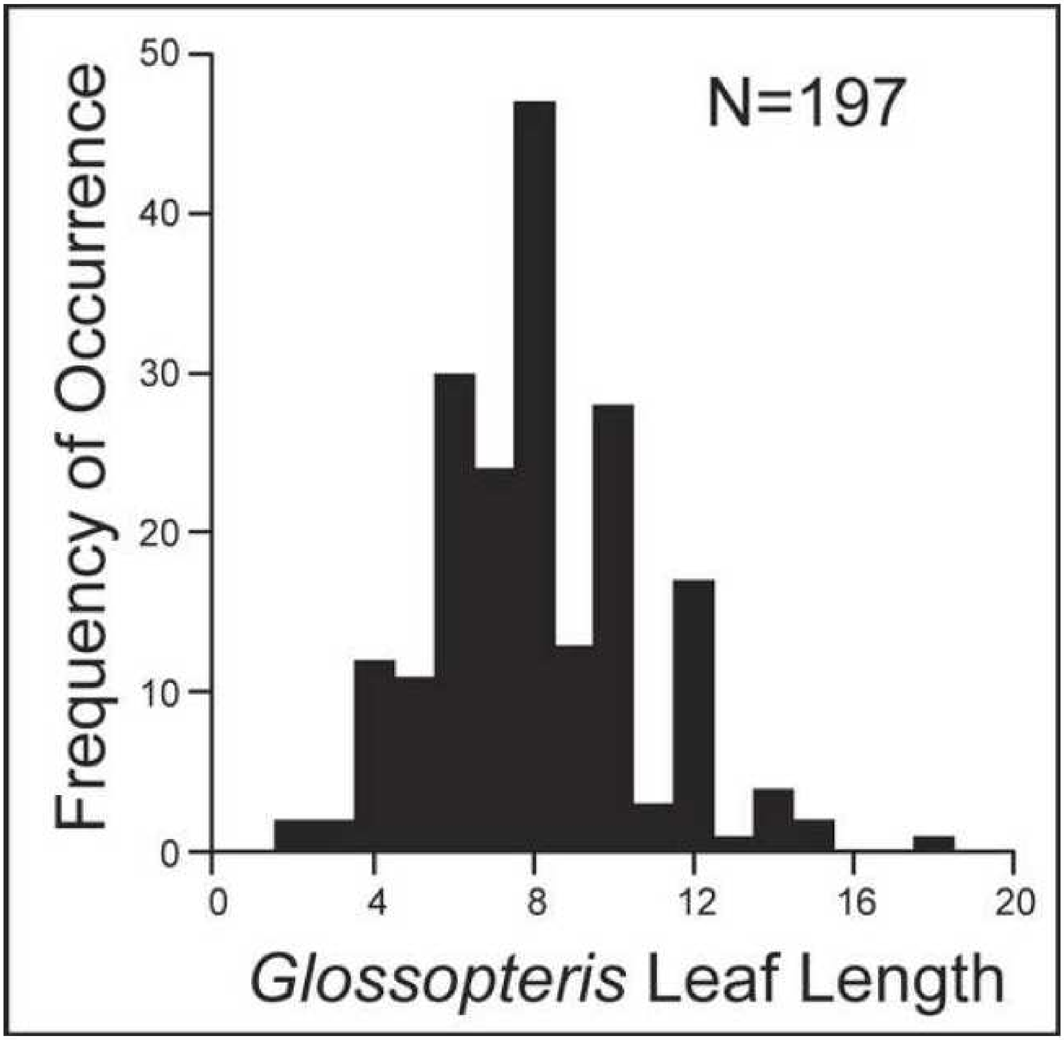
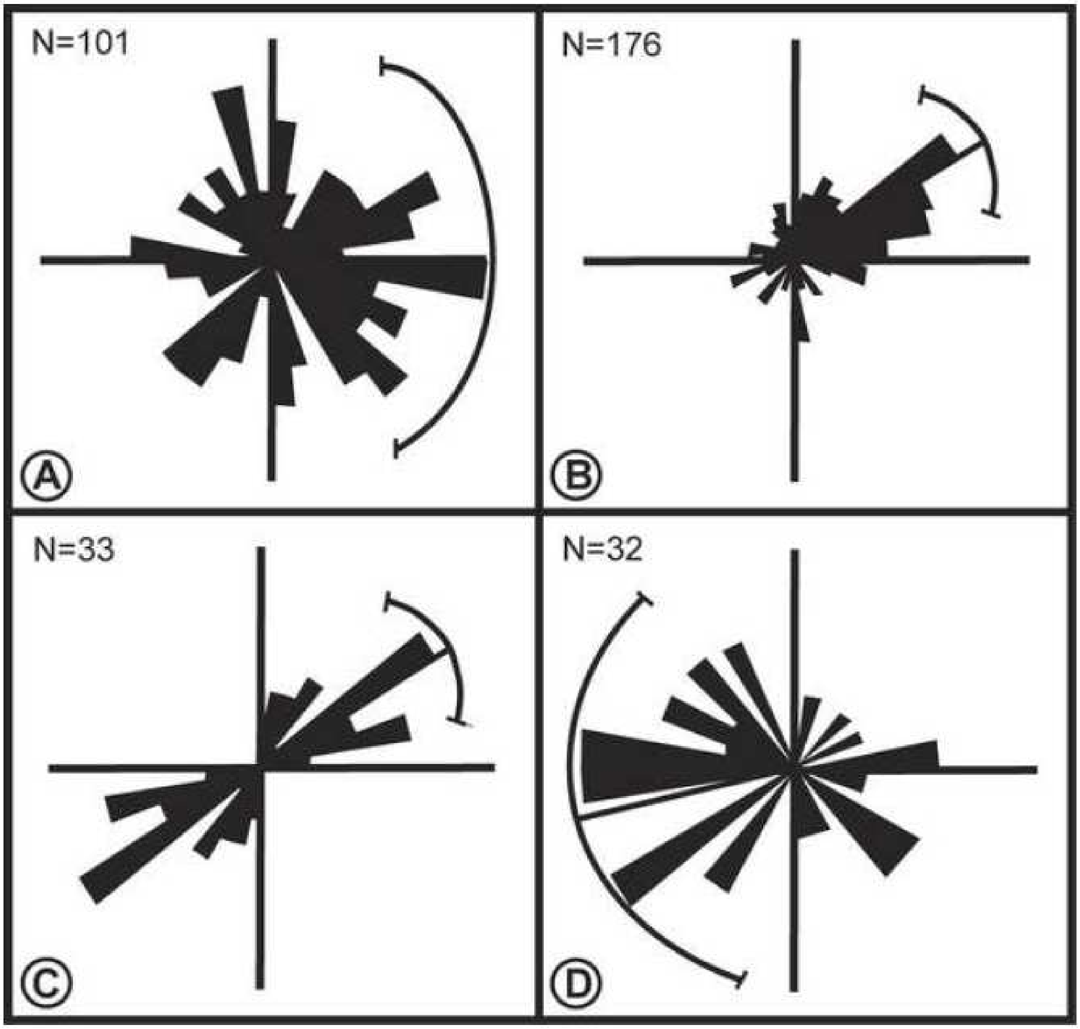
e
C
23
B
e
A
e
22
e
21
Sm
St
Pebbles Draping TCB
Sm Sr filling TCB
RCB
Fm
Horizontal lamination
g Gradational Contact
e Erosional Contact
Plant Fossils

Fig 5

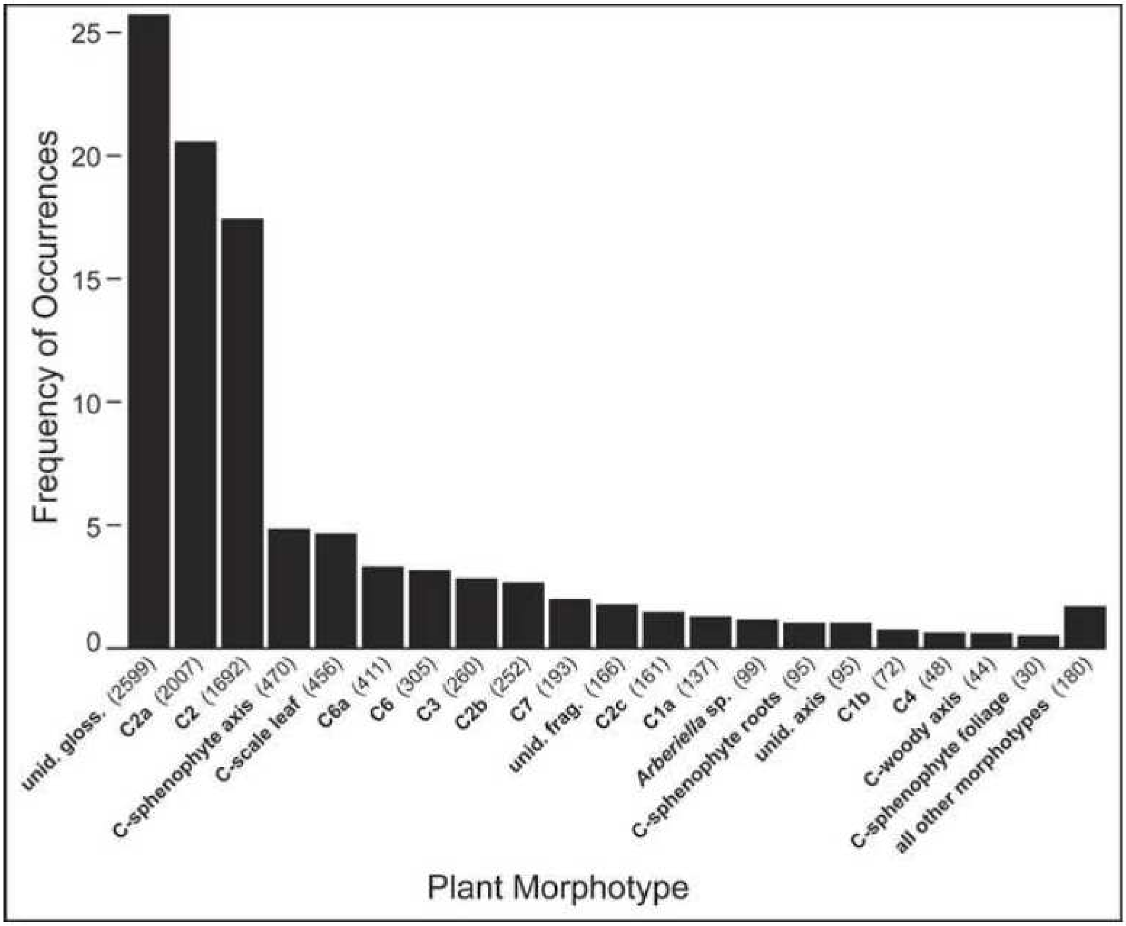

N=197
Frequency of Occurrence
0
10
20
30
40
50
0
4
8
12
16
20
Glossopteris Leaf Length

2374 ***Fig 6***



2375

Fig 7


Frequency of Occurrences
25
20
15
10
5
0
unid. gloss. (2599)
C2a (2007)
C2 (1692)
C-sphenophyte axis (470)
C-scale leaf (456)
C6a (411)
C6 (305)
C3 (260)
C2b (252)
C7 (193)
unid. frag. (166)
C2c (161)
C1a (137)
Arberiella sp. (99)
C-sphenophyte roots (95)
unid. axis (95)
C1b (72)
C4 (48)
C-woody axis (44)
C-sphenophyte foliage (30)
all other morphotypes (180)
Plant Morphotype

Plates 1

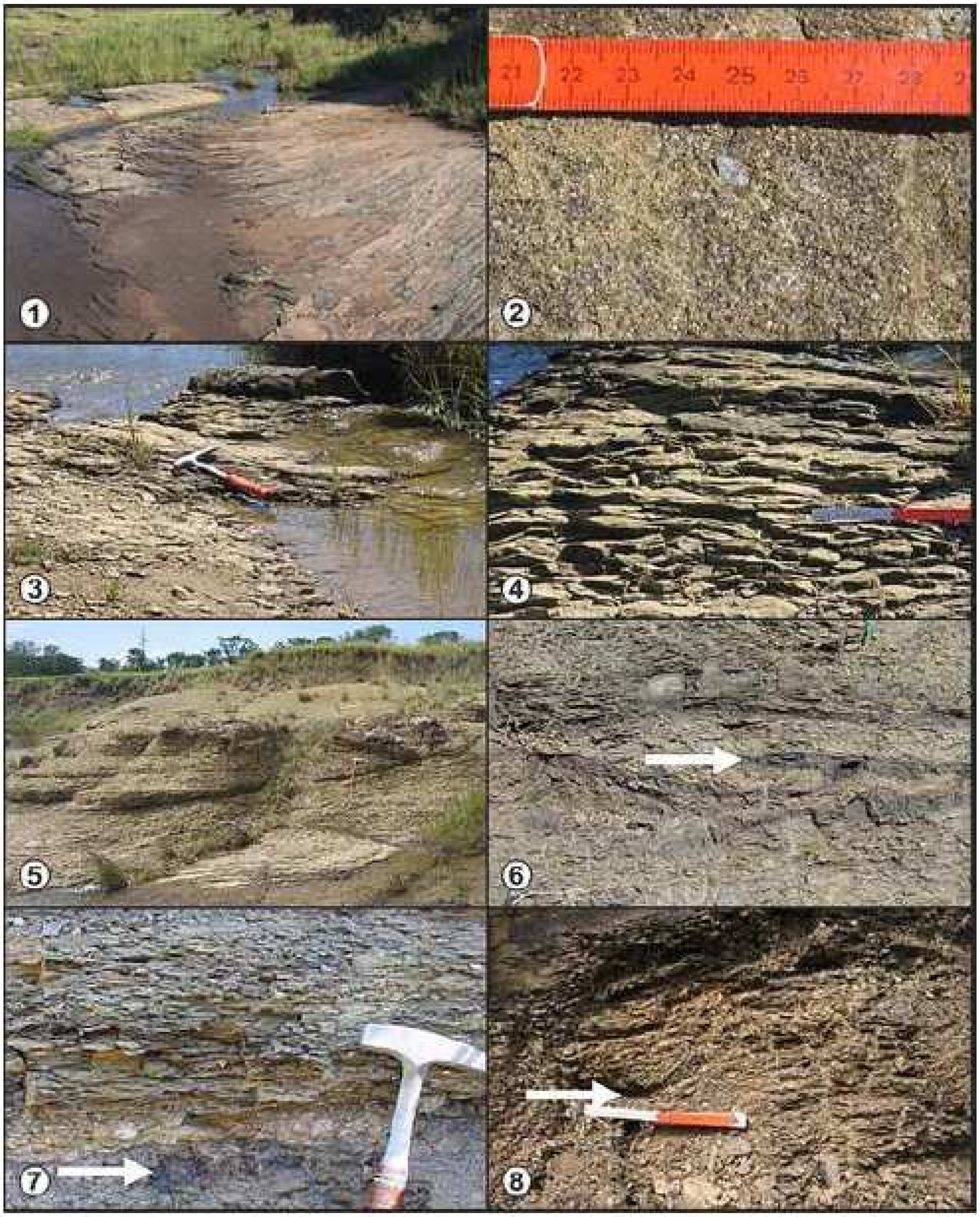


Plate 2

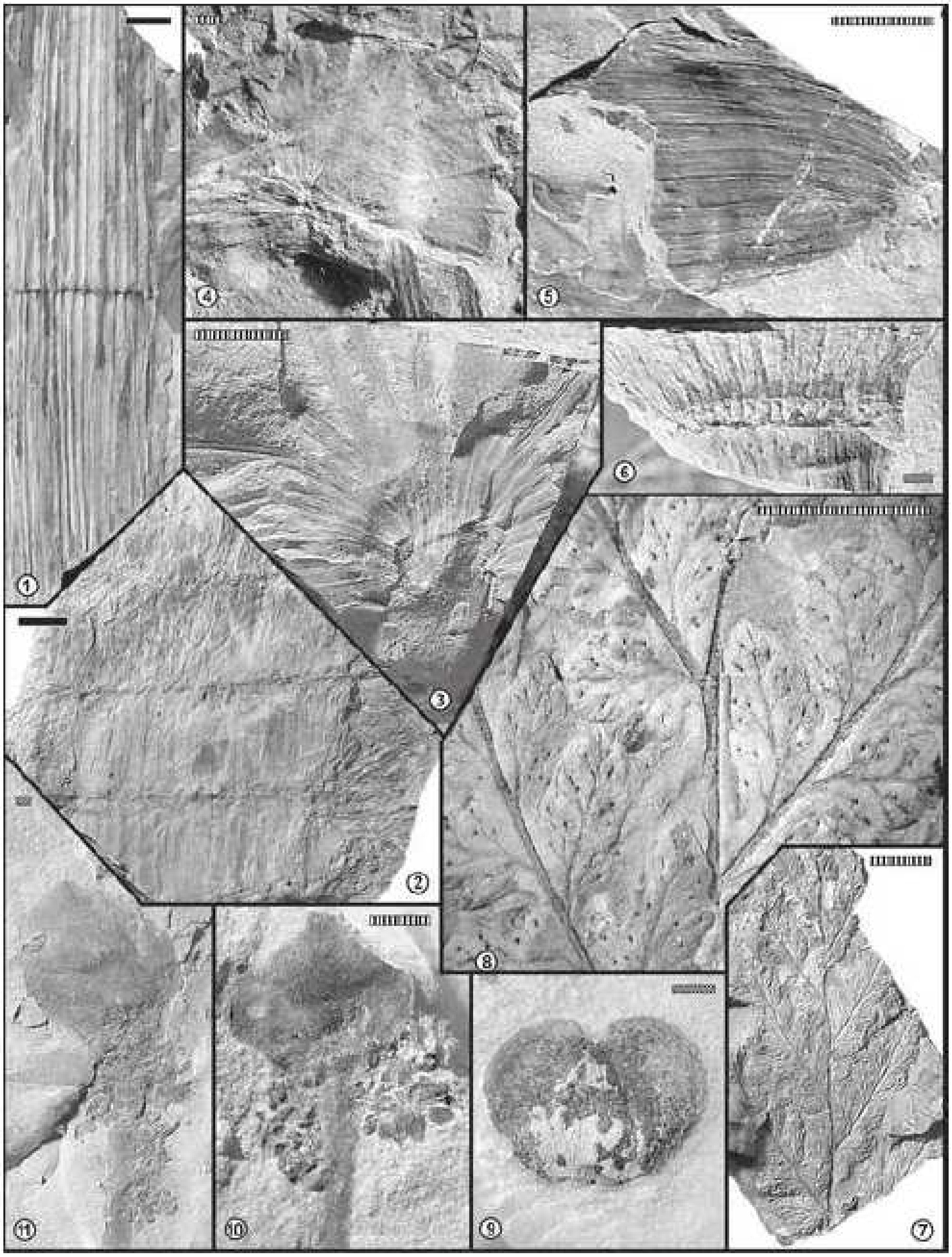


Plate 3

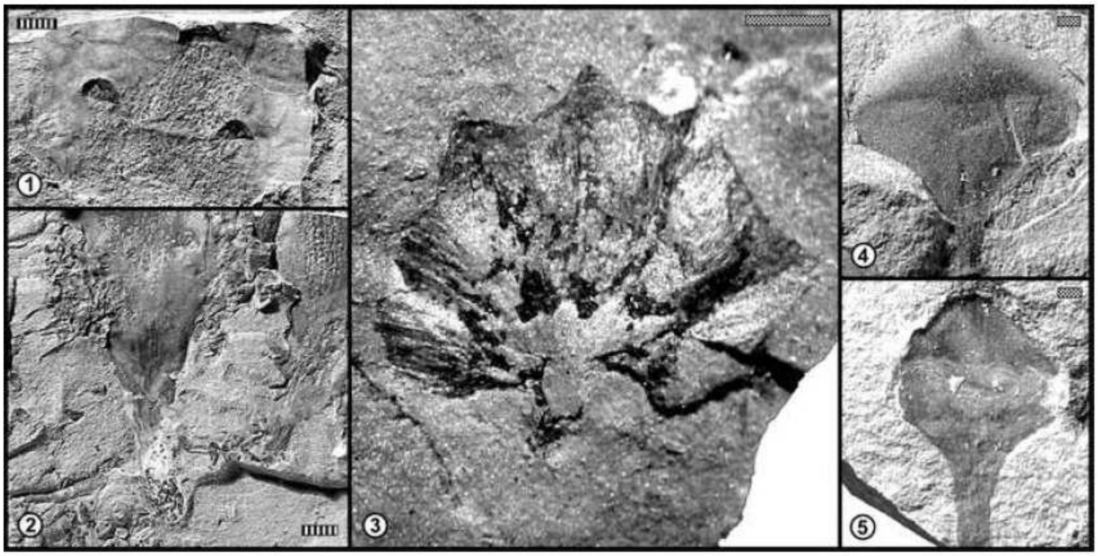


Plate 4

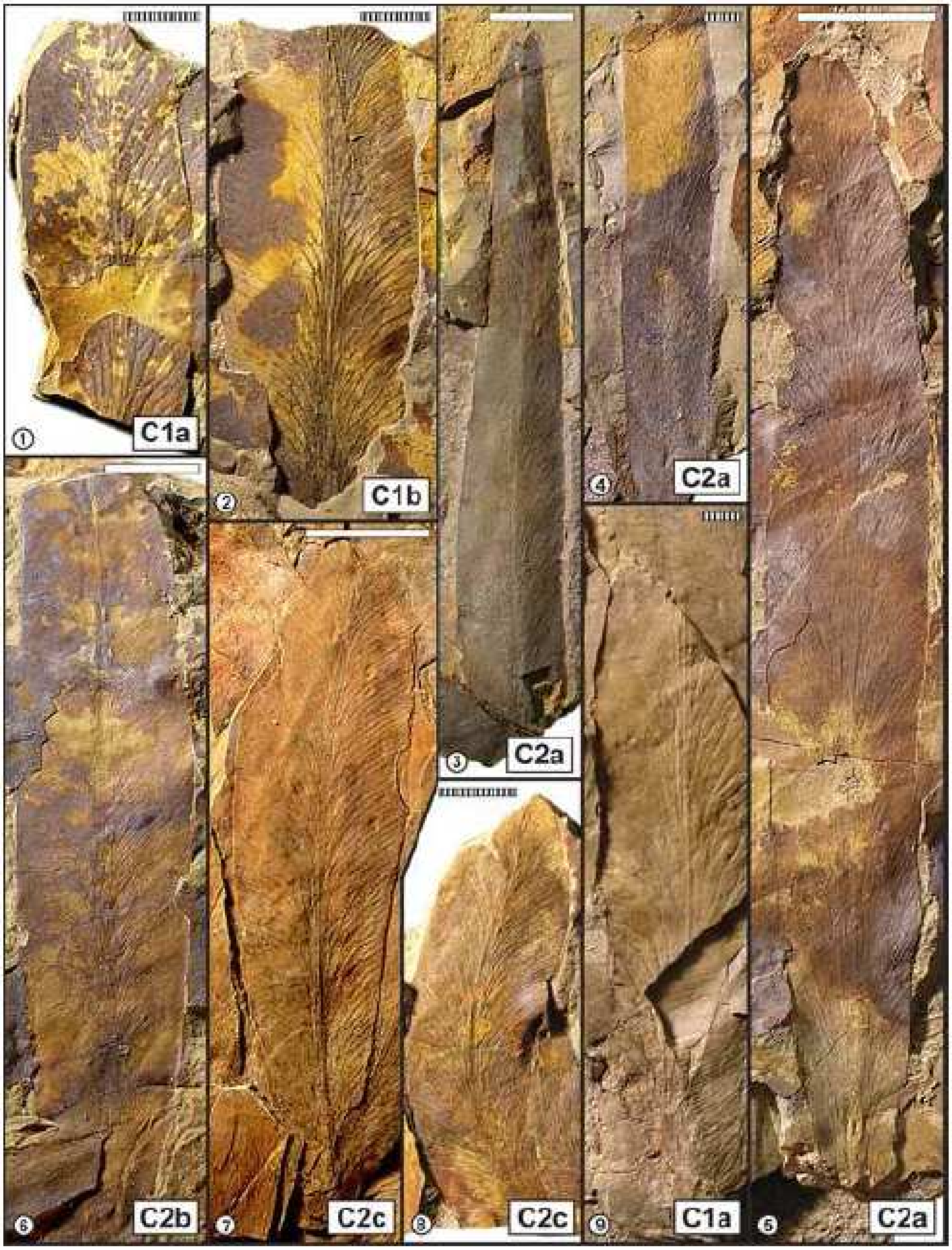


Plate 5

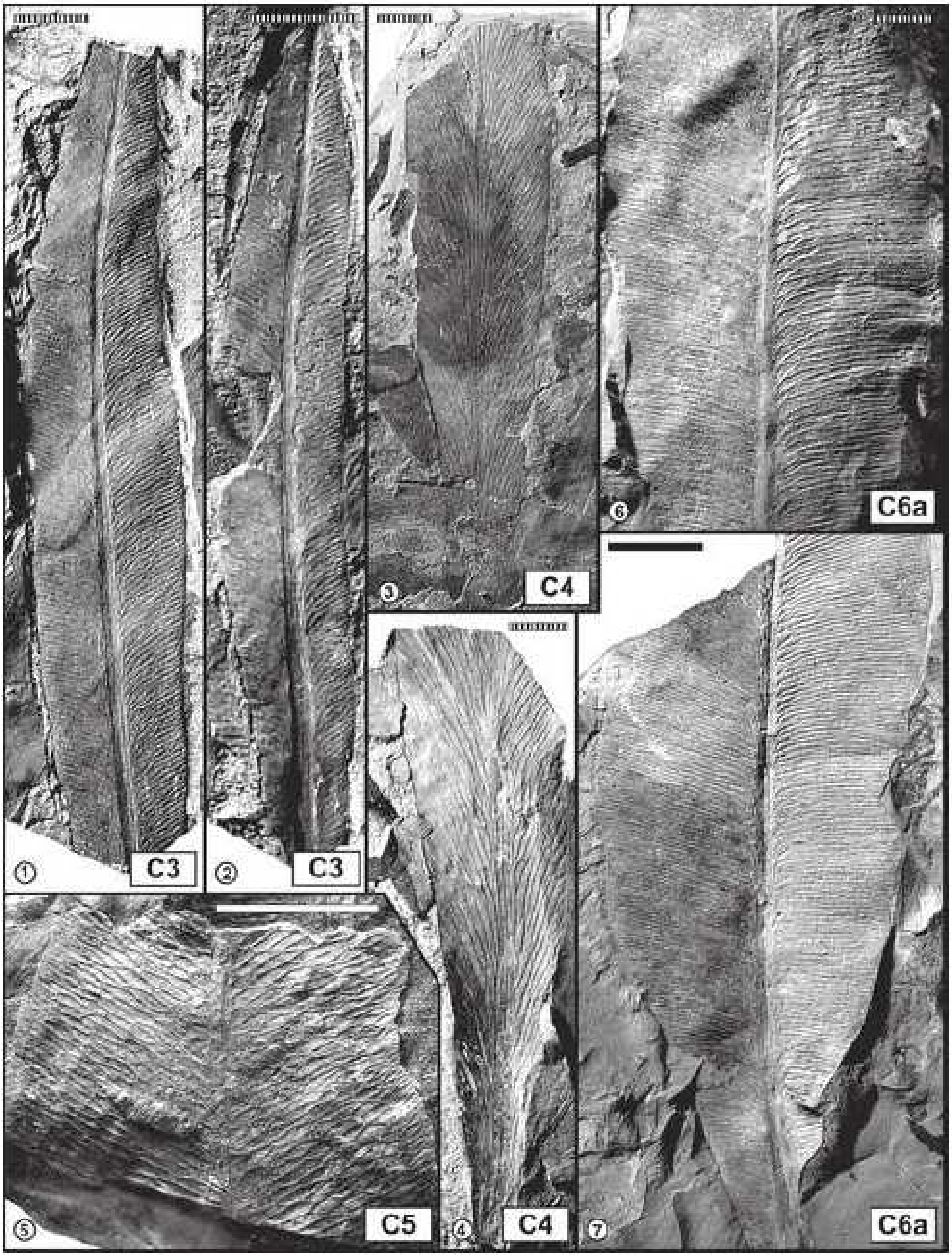


Plate 6

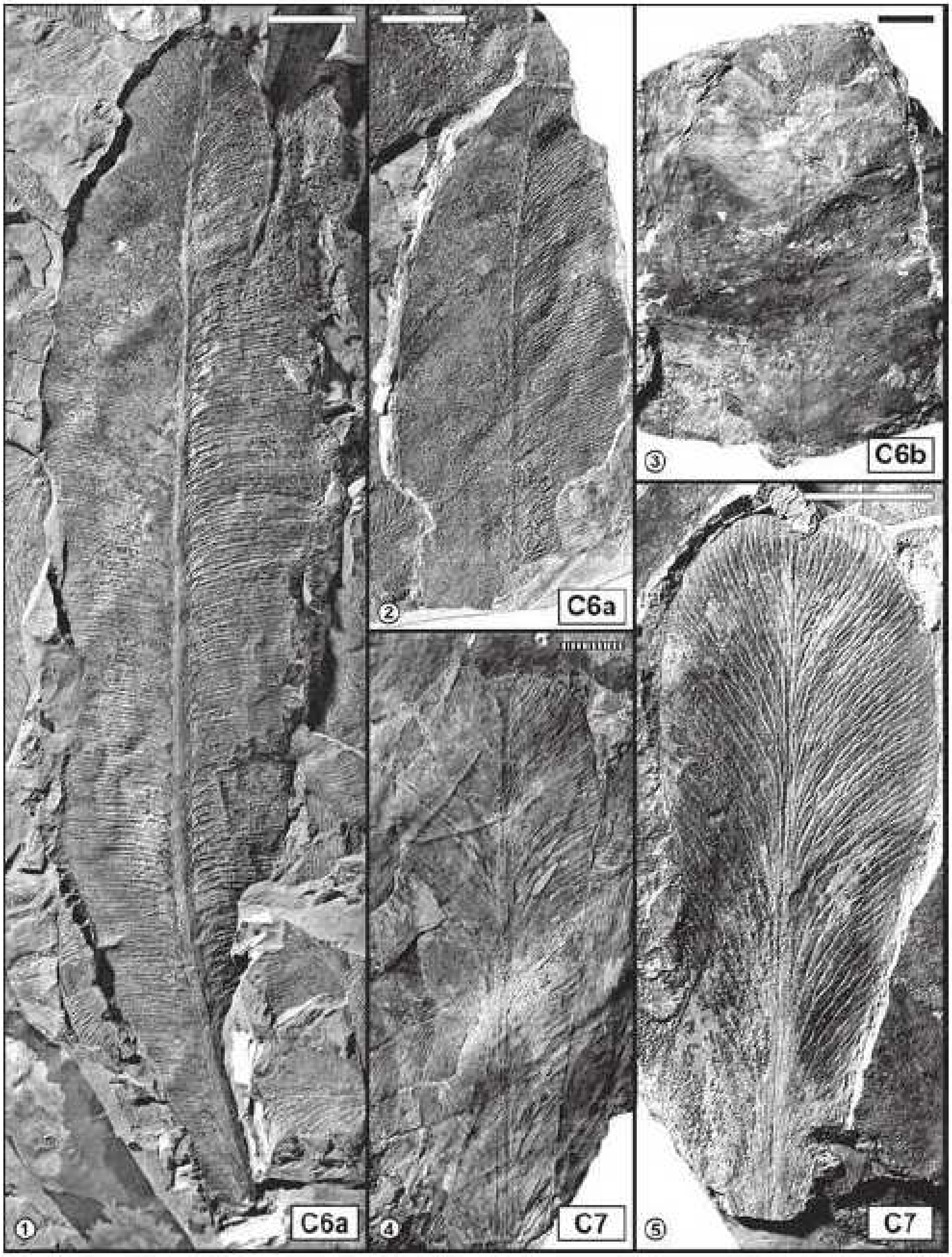
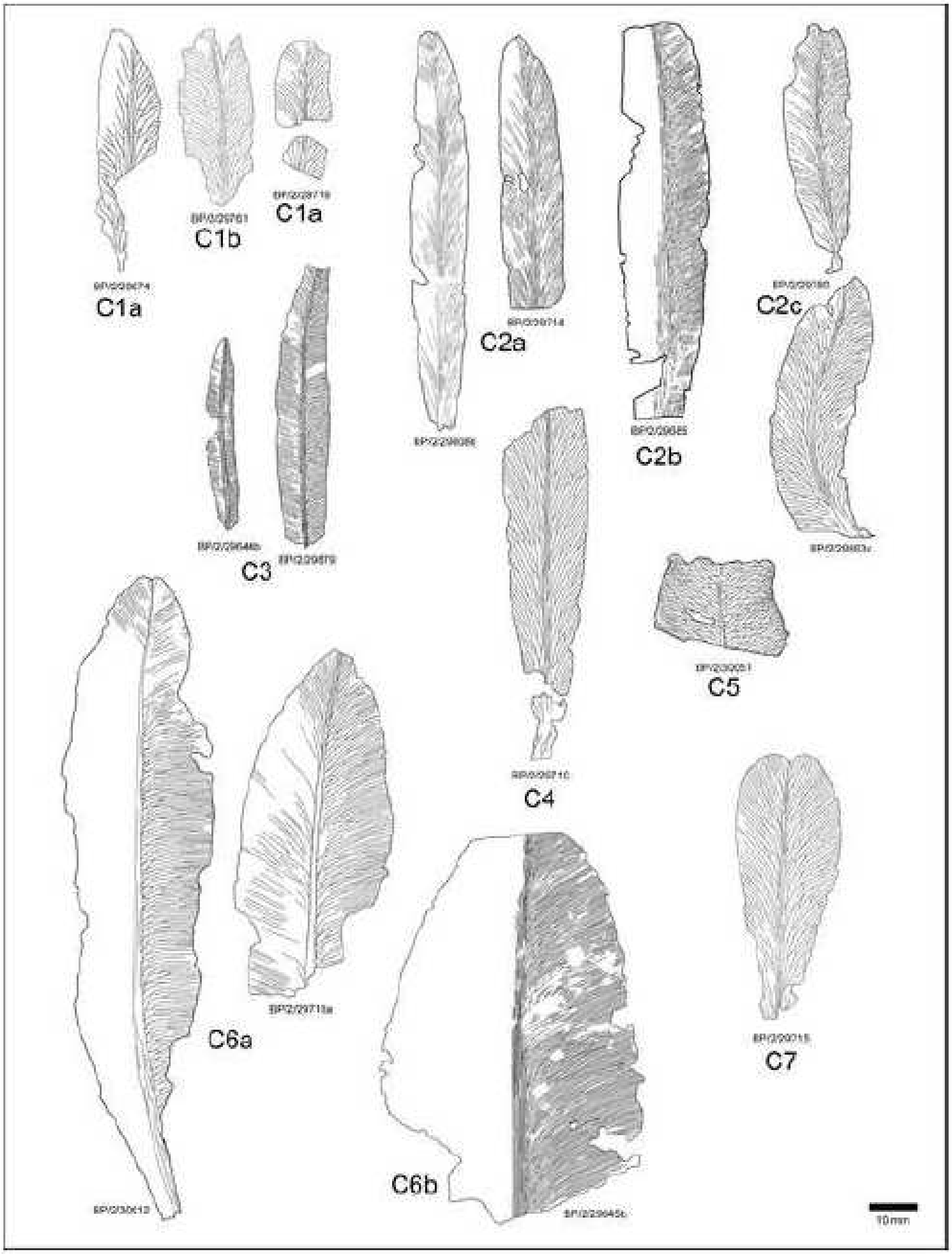


Plate 7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C1a
BP/2/29761
C1b
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C1a
BP/2/29686
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C2b
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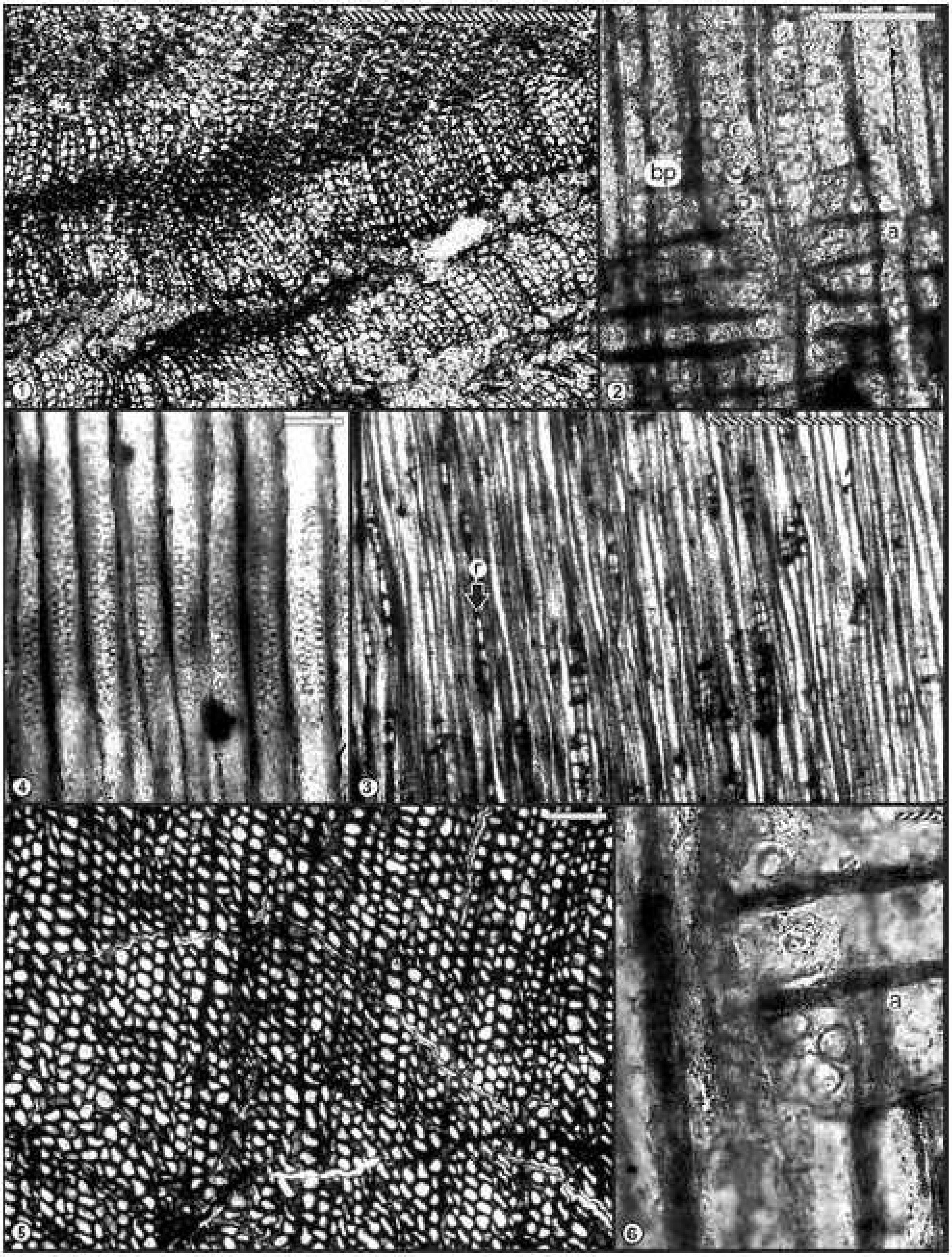
C2c
BP/2/29683c
BP/2/29648b
BP/2/29679
C3
BP/2/29710
C4
BP/2/30051
C5
BP/2/29711a
C6a
BP/2/30012
C6b
BP/2/29645b
BP/2/29715
C7
10mm

2392 ***Plate 8***



2393

Plate 9

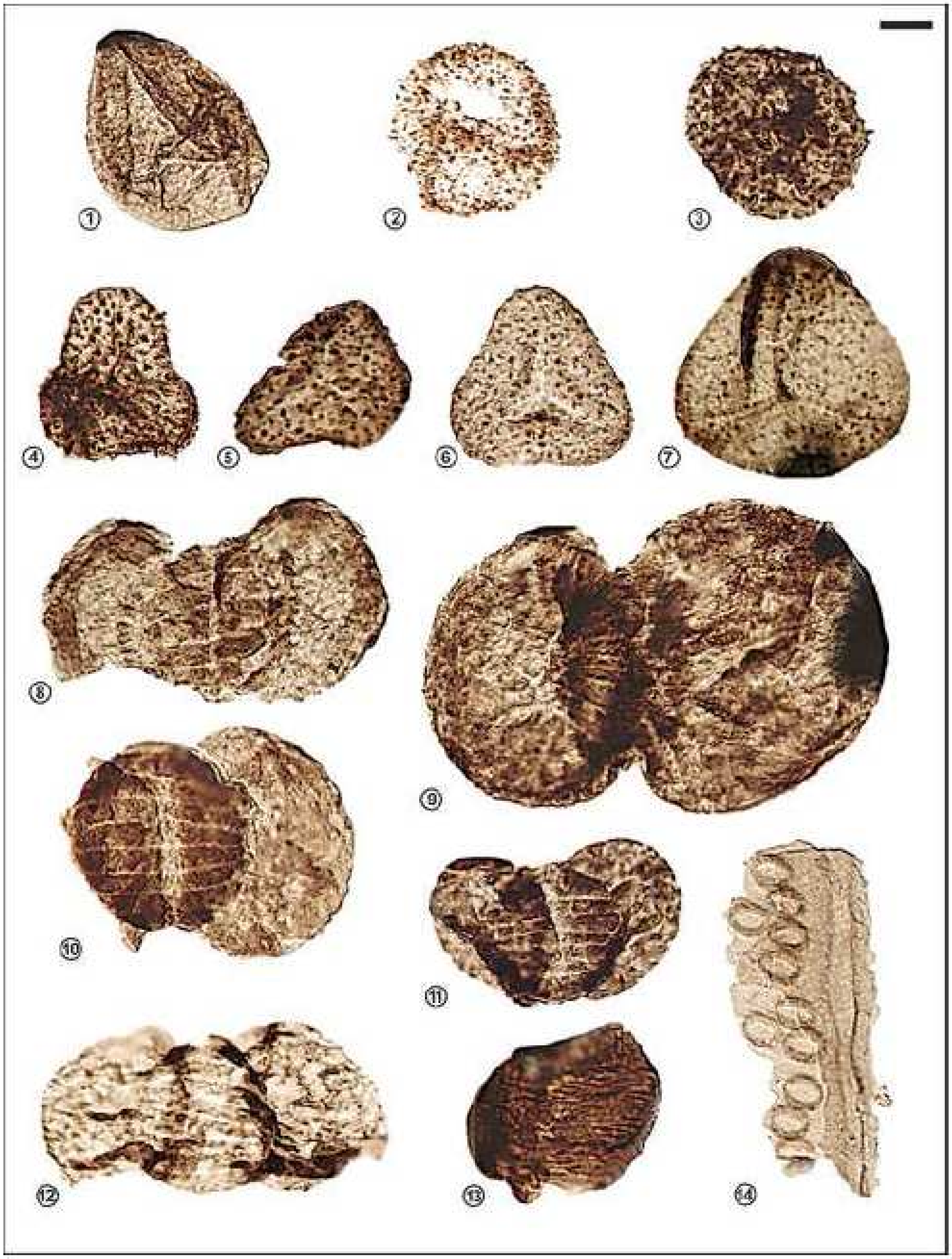


Plate 10

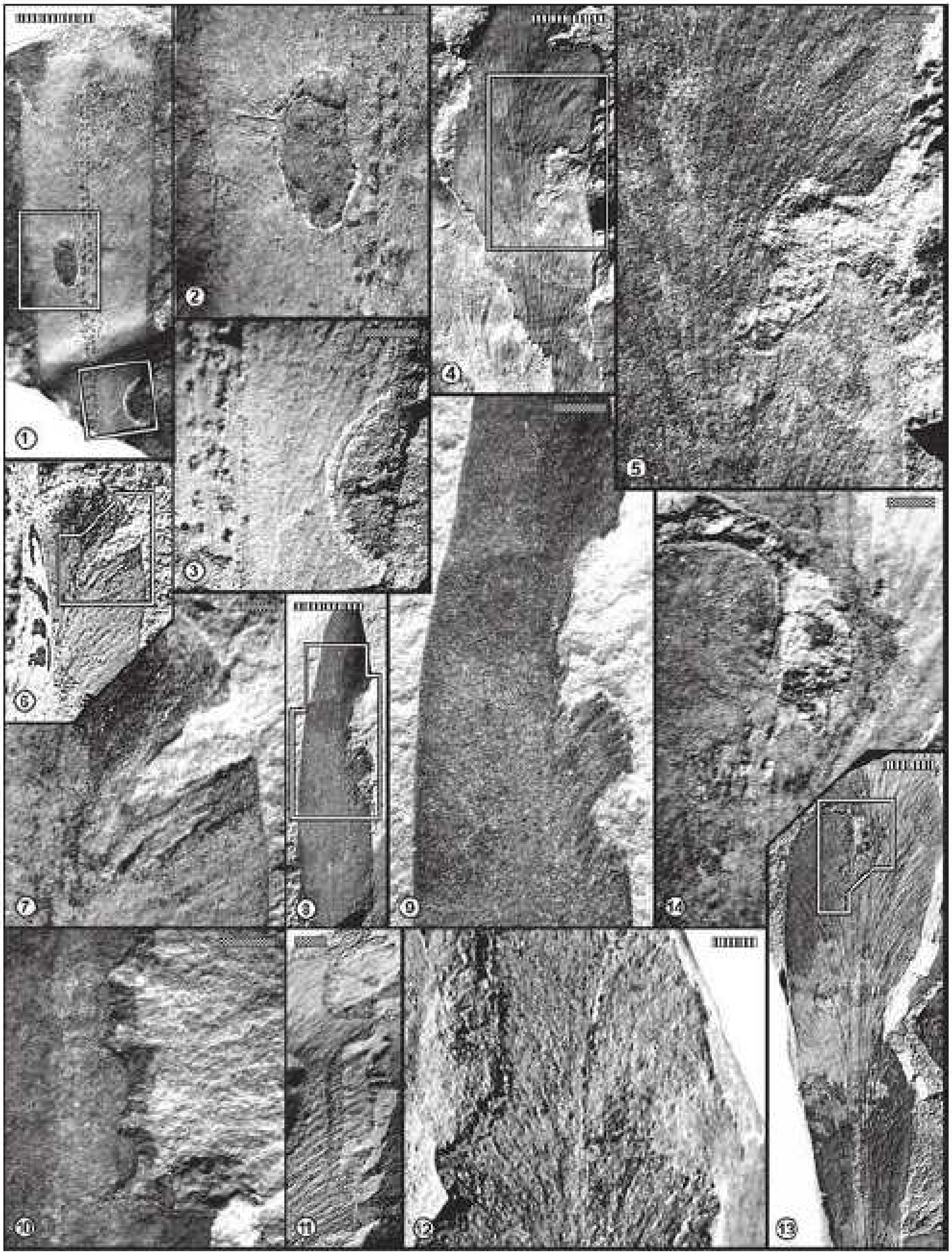


Plate 11

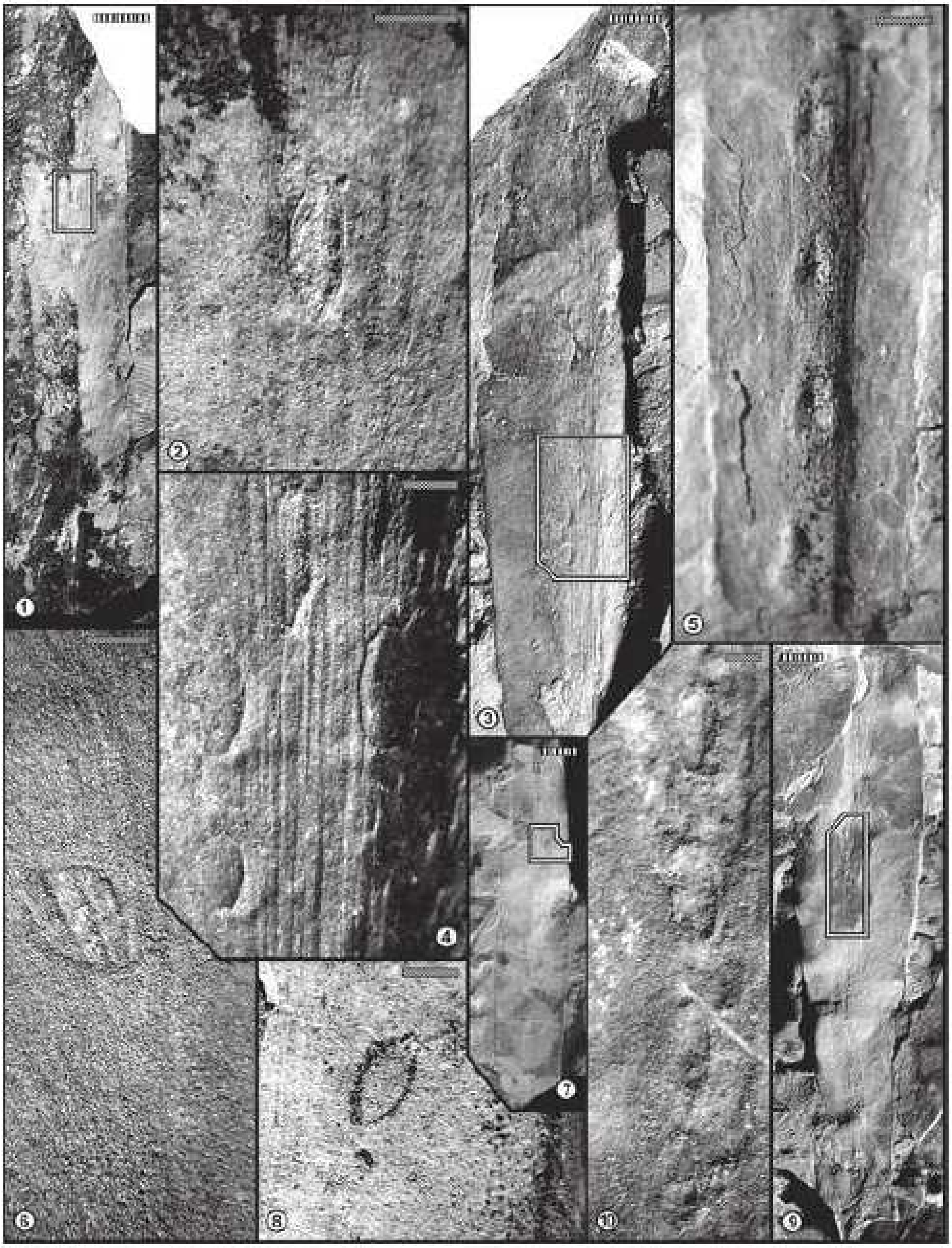


Plate 12

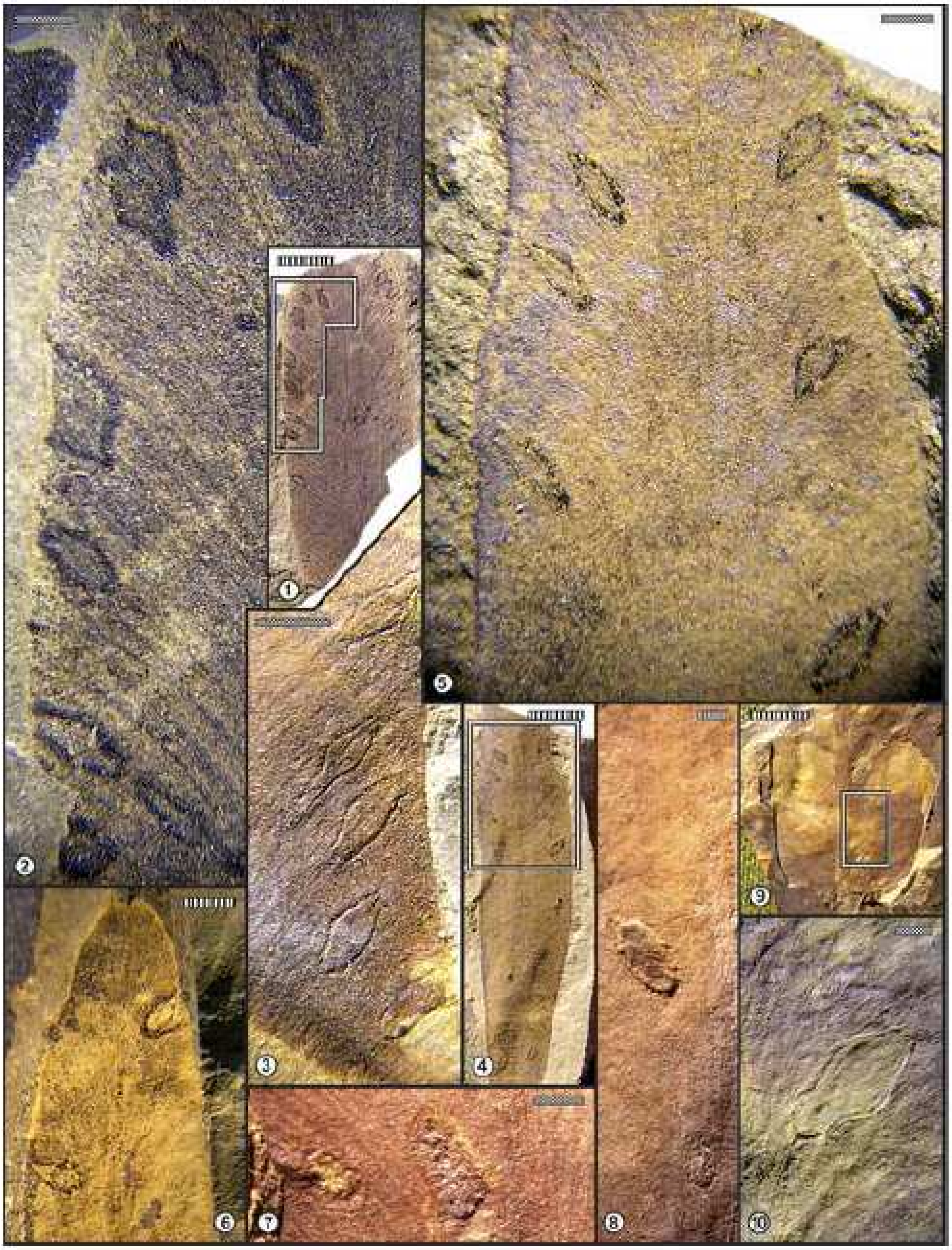


Plate 13

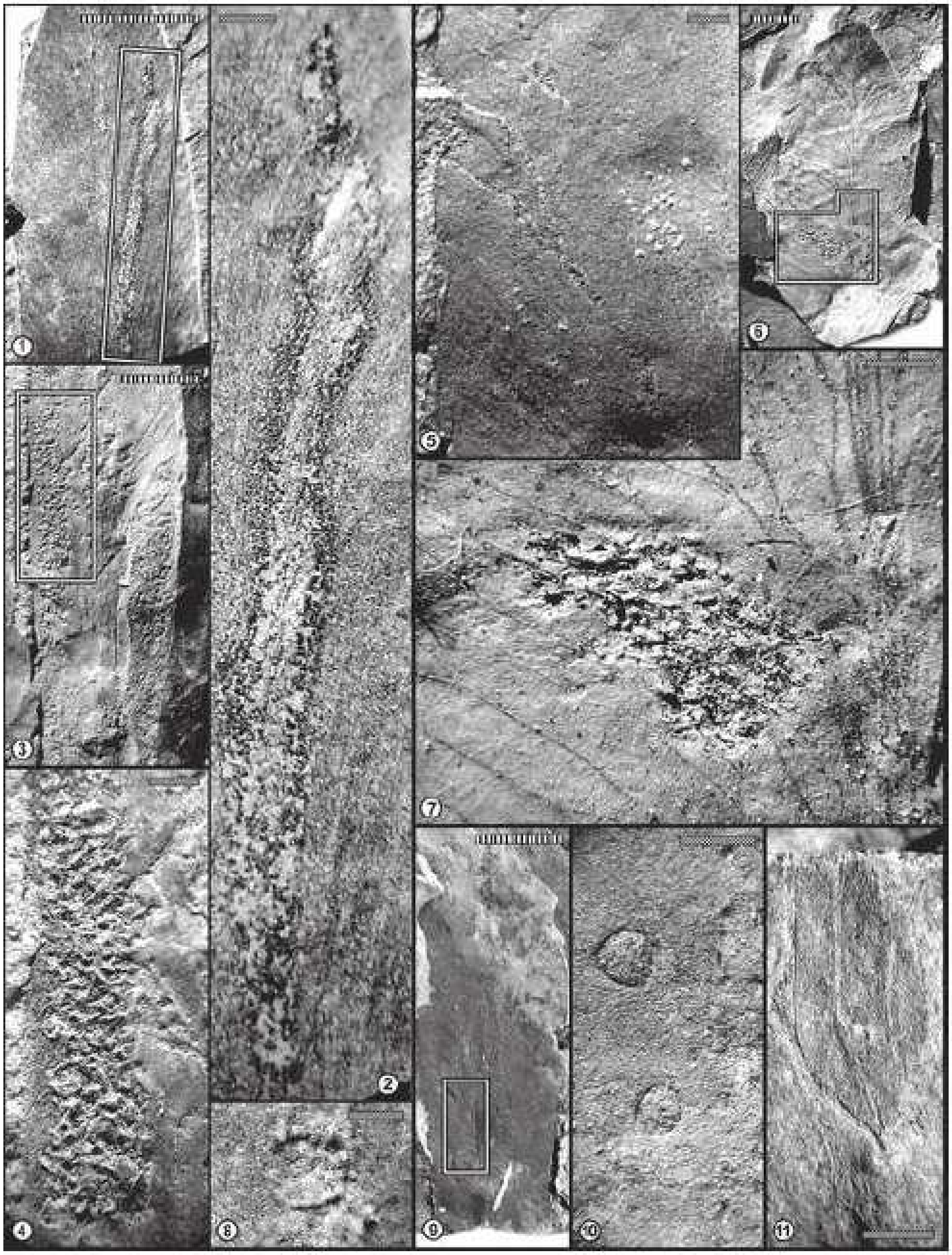


Plate 14