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PERMO-TRIASSIC FOSSIL WOODS FROM THE SOUTH AFRICAN KAROO BASIN

by

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ABSTRACT

The Karoo Basin extends over more than half of the South African land surface and incorporates sediments deposited over a period of more than 100 million years, from the Upper Carboniferous to the Lower Jurassic. Biozones have been established on the basis of the abundant vertebrate fauna. Fossil plant deposits are numerous but best represented by the Lower Permian *Glossopteris* floras and Middle to Upper Triassic *Dicroidium* floras. Fossil woods occur throughout the sequence. In this paper previously described woods are discussed, newly collected woods are described and an attempt is made to correlate the woods with the Formations and vertebrate biozones. *Prototaxoxylon africanum* (Walton) Krausel and Dolianiti is common but restricted to the Permian (Ecca and Lower Beaufort Groups). *Prototaxoxylon uniseriale* Prasad has the same distribution but is rare. *Australoxylon teixeirae* Marguerier extends from the Ecca to the middle Beaufort. *Araucarioxylon* occurs throughout the Karoo but there are several species that have different ranges. *Araucarioxylon africanum* Bamford sp. nov. occurs throughout the Beaufort and into younger deposits. *Araucarioxylon karooensis* Bamford sp. nov. occurs in the Normandien Formation of the Beaufort Group. Woods with podocarpacean affinities, recognized as *Mesembrioxylon*, first occur in the uppermost Beaufort and extend into the Cretaceous. The woods can, therefore, be used as broadscale biostratigraphic indicators but further data need to be collected.

KEYWORDS: gymnosperm woods, *Araucarioxylon, Australoxylon, Mesembrioxylon Prototaxoxylon,* biostratigraphy.

INTRODUCTION

The first good description of Karoo fossil woods was by Warren (1912) on collections in the Natal Museum but woods had been recorded earlier than that. Atherstone (1857) described the "wood beds" of the Uitenhage area (now Kirkwood Formation, Lower Cretaceous) and Mellor & Leslie (1906) described fossil root casts of *Stigmaria* in the Vaal River near Vereeniging which is in the Ecca Group. Bancroft (1913) described the unusual wood *Rhexoxylon africanum* from the Molteno Formation. The locality and whereabouts of the holotype are unknown but several *Rhexoxylon* species have been described from other Gondwana Triassic deposits. A taxonomic revision of the genus is needed as well as a more feasible interpretation of the growth form of the plant. Walton (1923, 1925, 1956), Rodin (1956), Marguerier (1973) and Erasmus (1976) have also described fossil woods from the Karoo. These woods are summarised in Table 1 together with this author's interpretation and updating of nomenclature.

Dadoxylon is the most common genus in Palaeozoic deposits but this is a most unsatisfactory taxon because there are several interpretations of its diagnostic features and no consensus. Endlicher erected this genus in 1847 and included specimens described by Lindley & Hutton (1831) and Witham (1833). The type species is usually considered to be *D. withamii* which has a homogeneous pith, but this feature was not noted in the original description. There is considerable nomenclatural confusion and Philippe (1993) also showed that the genus is invalid according to the Botanical Code of Nomenclature because Endlicher (1847) included all the syntypes of *Pinites* Witham 1833. *Dadoxylon* is, therefore, a synonym of *Pinites* but *Pinites* is not a homoxylous wood. Furthermore the diagnostic features are in contention; species have been described with or without pith and primary xylem, and with or without multiseriate rays. Revisions of *Dadoxylon* tend to be lengthy because the original diagnosis is too general. *Araucarioxylon* Kraus is another genus with which there is much confusion and some authors synonymise *Araucarioxylon* and *Dadoxylon* or use the names together with one or other genus in parentheses (see Giraud 1991).

The present author prefers the use of "*Dadoxylon*" as a catch-all for woods with araucarian tracheid pitting and pith, which do not fit into the described woods with characteristic or distinctive pith types. With so much new data and more narrowly defined taxa, *Dadoxylon* is of limited biostratigraphic or phylogenetic application as a genus. Perhaps Lepekhina's (1972) group Dadoxyleae has greater use because she made a clear distinction between woods with secondary xylem only and woods with secondary xylem and associated pith. *Araucarioxylon* and *Agathoxylon* Hartig (1848) are useful designations for woods which have secondary xylem with araucarian tracheid pitting and

TABLE 1

Previously described Karoo woods from South Africa. The right hand column shows the most recent taxonomic status. * specimen is redescribed in this paper.

STRATIGRAPHY	NUMBER	LOCALITY	AUTHOR	WOOD	COMMENT
MOLTENO Formation	AM619	Modderpoort	Walton 1925	*Dadoxylon sclerosum*	pith
	SAM 2954	Kromme Spruit	Walton 1925	cf *Dadoxylon sclerosum*	
	--	Dordrecht	Walton 1925	*Rhexoxylon priestleyi*	
BEAUFORT Group	--	Empangeni	Erasmus 1976	*Dadoxylon arberi*	*Australoxylon teixeirae*
	SAM 1089	Klipgat	Walton 1925	*Dadoxylon arberi*	*Australoxylon teixeirae*
	AM 508	Van Wyk's Vlei	Walton 1925	*Dadoxylon arberi*	*Australoxylon teixeirae*
	NM 219	Umkomaas	Walton 1925	*Dadoxylon arberi*	*Australoxylon teixeirae*
	NM 11	Umkomaas	Walton 1925	*Dadoxylon arberi*	*Australoxylon teixeirae*
	SAM 4354	Weltevreden	Walton 1925	*?Dadoxylon arberi*	*?Australoxylon teixeirae*
	*SAM 2945	Hamsfontein	Walton 1925	*Spiroxylon africanum*	
	NM 160	Natal	Warren 1912	*Dadoxylon* sp.2	*Protophyllocladoxylon?*
ECCA Group	AM 2296	Van Wyk's Vlei	Walton 1925	*Dadoxylon arberi*	
	--	Tete	Marguerier 1973	*Australoxylon teixeirae*	
	--	Natal	Marguerier 1973	*Australoxylon natalense*	
	SAM 2946	Noro Kei Pan	Walton 1925	*Dadoxylon* sp.	
	SAM 2947	Van Wyk's Vlei	Walton 1925	*Dadoxylon arberi*	*Australoxylon teixeirae*
	NM (23 specimens)	Natal Coal Measures	Warren 1912	*Dadoxylon* sp.1	*Australoxylon teixeirae* *Australoxylon natalense* *Araucarioxylon spp.*

no additional distinguishing characteristics, such as the ray border cells of *Dammaroxylon* (Schultze-Motel 1966), clustered pits of *Australoxylon* (Marguerier 1973) or traumatic resin canals of *Brachyoxylon* (Hollick & Jeffrey 1909). Philippe (1993) said that *Araucarioxylon* (also a synonym of *Pinites*) was invalid and *Agathoxylon* or *Brachyoxylon* should be used. This author (and many others) consider that *Brachyoxylon* should be restricted to taxa with traumatic resin canals. *Agathoxylon* is rarely used but has abundant axial parenchyma and so could be used for woods with parenchyma which is not confused with resin-filled tracheids. This could mean that *Araucarioxylon* could be emended for woods with secondary xylem only and little to no axial parenchyma. Pant & Singh (1987) have also reviewed this group of woods but came to no conclusion about their affinities.

MATERIALS AND METHODS

Fossil woods have been collected from all over South Africa but only those from known biozones will be considered here. The specimens, localities and stratigraphy are summarised in Tables 2 and 3 in the Discussion.

Polished thin sections have been made of all the samples using the standard method for the transverse, radial longitudinal and tangential longitudinal sections: the polished surface of a small block was mounted on a petrographic glass slide and the rest of the block was cut using a discoplan. The newly cut surface was then ground and polished to the required thickness, usually 25-80 µm, depending on the cell size and crystal size, and studied under a transmitted light microscope. Most woods are silicified but some are calcified.

TABLE 2

Fossil woods studied by the author and used for the biostratigraphy. All specimens are housed in the Bernard Price Institute.

Group FORMATION Member	LOCALITY	SPECIMEN NUMBERS BP/16/ –	COLLECTOR	FOSSIL WOOD
CLARENS	Rhebokhoek	351-363	M. Bamford	*Mesembrioxylon sp. (?)*
MOLTENO	Kannaskop Boesmanshoek Sterkstroom	728-729 727 392	H. Anderson P. J. Hancox	*Araucarioxylon sp.* *Araucarioxylon sp.* *Araucarioxylon sp.*
Beaufort BURGERSDORP	Sterkstroom	490 395		*Mesembrioxylon cf rajmahalense* *Mesembrioxylon sp.*
NORMANDIEN	Thukela, Natal Harrismith McFie's donga	550 551, 552 311, 312 313-315 316 302	C. Gow C. MacKnight T. Mason	*Araucarioxylon karooensis* *Araucarioxylon africanum* *Araucarioxylon africanum* *Australoxylon teixeirae* *Araucarioxylon africanum*
BALFOUR	Aberdeen	721	P. Karpeta	*Australoxylon teixeirae*
TEEKLOOF Poortjie Member	Stellenboschvlei	303-308	J. Loock	*Australoxylon teixeirae*
ABRAHAMSKRAAL Koornplaats Member	Wildheuvel Swaerskraal	281, 282a, 283d 284a 298, 299 300	B. Rubidge R. Heard	*Prototaxoxylon africanum* *Prototaxoxylon uniseriale* *Australoxylon teixeirae* *Prototaxoxylon uniseriale*
Ecca WATERFORD FORT BROWN	Laingsburg	387	B. Rubidge	*Prototaxoxylon africanum*
KOOKFONTEIN	Paardekraal	285, 286f	B. Rubidge	*Prototaxoxylon africanum*
COLLINGHAM	Ecca Pass	469	M. Bamford	*Australoxylon teixeirae*

The thin sections were studied under a Zeiss Axiophot microscope, measured and photographed. Descriptions of the taxa are given below. All specimens and slides are catalogued and housed in the Bernard Price Institute, Johannesburg.

DESCRIPTION OF FOSSIL WOODS

Prototaxoxylon africanum (Walton) Kräusel & Dolianiti 1958

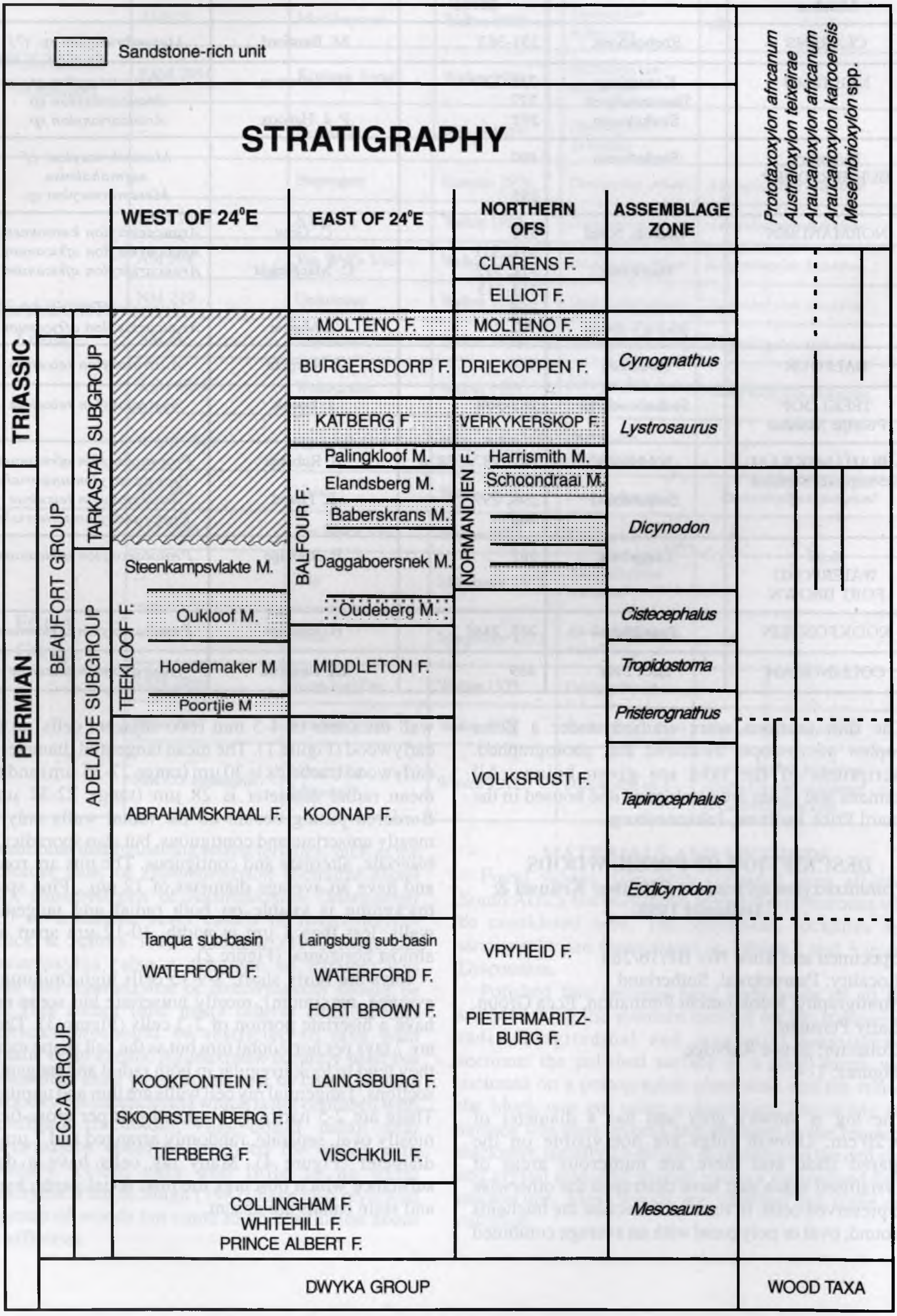
Specimen and Slide No: BP/16/285
Locality: Paardekraal, Sutherland
Stratigraphy: Kookfontein Formation, Ecca Group, Early Permian
Collector: Bruce Rubidge
Figures: 1- 4

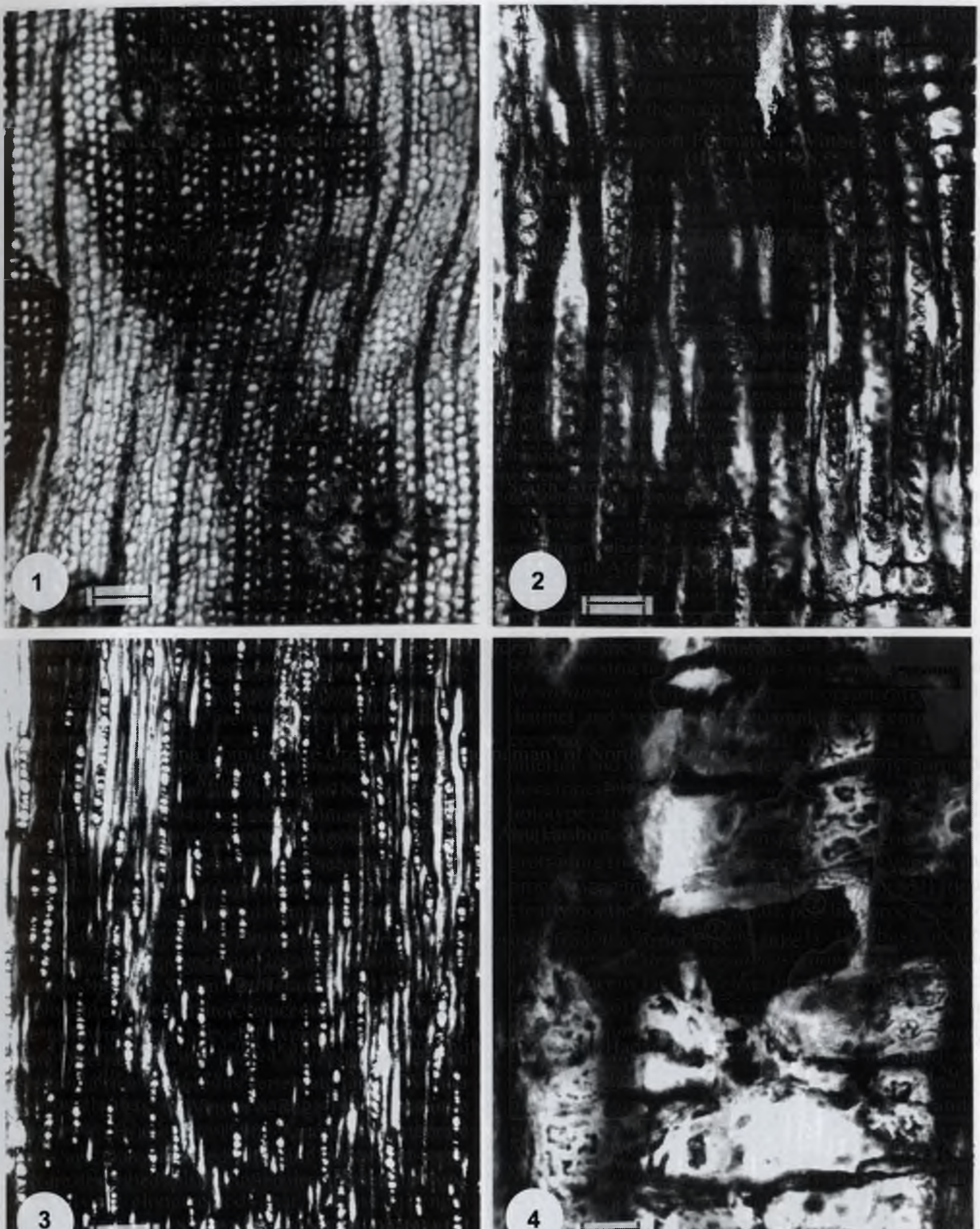
The log is streaky grey and has a diameter of 25 x 20 cm. Growth rings are not visible on the prepared slide and there are numerous areas of recrystallised silica that have destroyed the otherwise well preserved cells. In transverse section the tracheids are round, oval or polygonal with an average combined wall thickness of 4-5 mm (two adjacent cells) in the earlywood (Figure 1). The mean tangential diameter of earlywood tracheids is 30 µm (range 27-35 µm) and the mean radial diameter is 28 µm (range 22-32 µm). Bordered pitting occurs on the radial walls only, is mostly uniseriate and contiguous, but also sporadically biseriate, alternate and contiguous. The pits are round and have an average diameter of 12 µm . Fine spiral thickening is visible on both radial and tangential walls, less than 1 µm in width, 10-12 µm apart and almost horizontal (Figure 2).

Rays are fairly short, 2-9-15 cells high (minimum, average, maximum), mostly uniseriate but some rays have a biseriate portion of 2-3 cells (Figure 3). There are 7 rays per horizontal mm but as the cell shape varies they tend to look irregular in both radial and tangential sections. Tangential ray cell walls are thin and unpitted. There are 2-5 narrowly bordered pits per cross-field, mostly oval, separate, randomly arranged and 7 µm in diameter (Figure 4). Many ray cells have a dark substance which obscures the pits. Axial parenchyma and resin canals are absent.

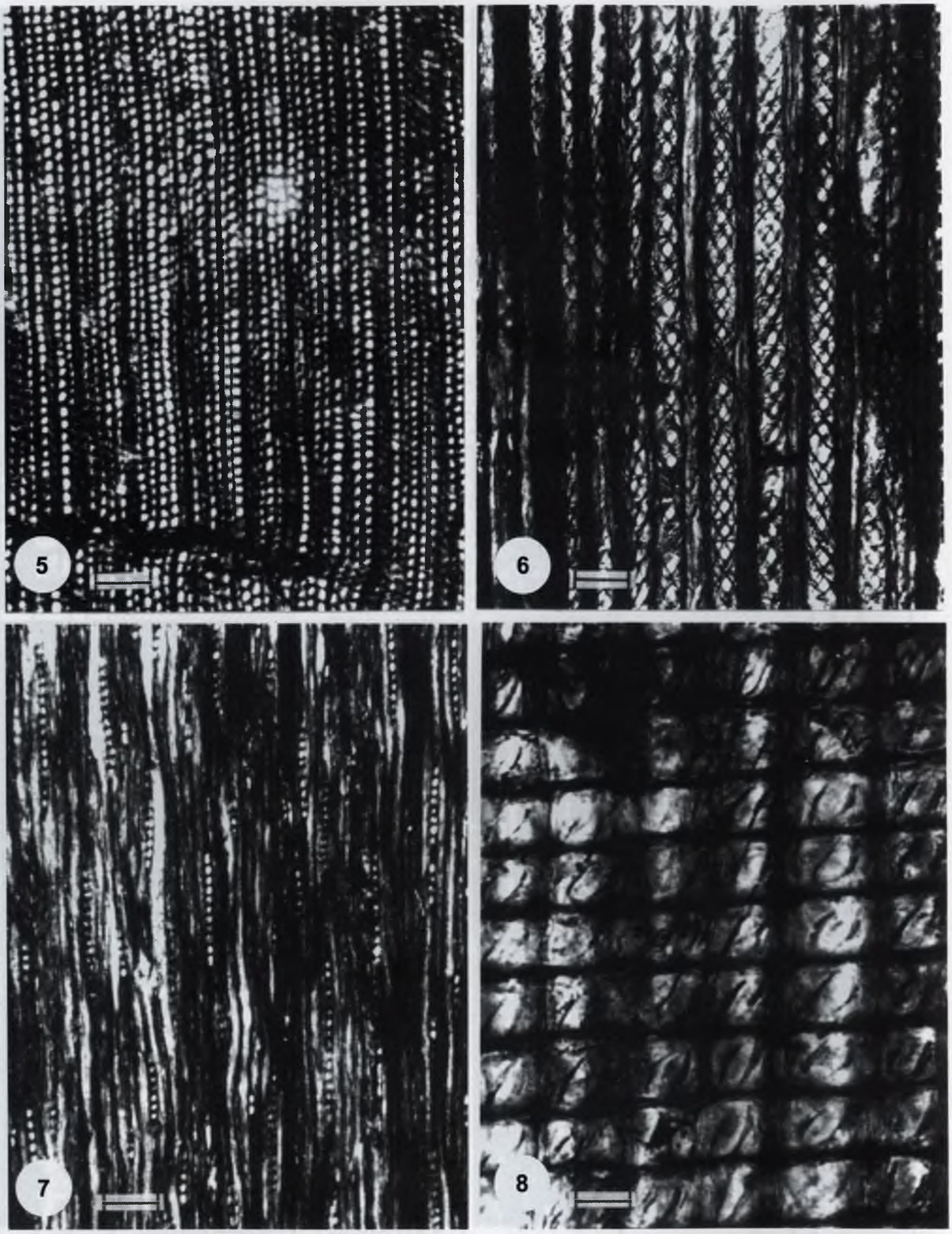
TABLE 3

Stratigraphy of the Permian and Triassic Karoo Basin. Ecca stratigraphy from Wickens (1994). Beaufort stratigraphy from Rubidge *et al.* (1995) and SACS (1980). Ranges of fossil wood taxa from this study.





FIGURES 1-4. *Prototaxoxylon africanum* BP/16/285. **1:** TS (transverse section) showing regular tracheids and no growth rings. The dark patches are a preservational artefact. Scale bar = 150 μm. **2:** RLS (radial longitudinal section) showing the uniseriate and biseriate alternate bordered pits and fine spiral thickenings on the radial walls of the tracheids. Scale bar = 30 μm. **3:** TLS (tangential longitudinal section) showing uniseriate rays and fine spiral thickenings on the tracheid walls. Dark deposits in the cells are probably resiniferous. Scale bar = 200 μm. **4:** RLS showing narrowly bordered pits in the cross-field. Scale bar = 15 μm.



Figures 5-9. *Prototaxoxylon uniseriale* BP/16/300. **5:** TS showing a partial (false) growth ring. Scale bar = 130 μm. **6:** RLS with heavy spiral thickening criss-crossing on the tracheid walls, and uniseriate bordered pits. Scale bar = 50 μm. **7:** TLS uniseriate rays. Scale bar = 130 μm. **8:** RLS with single, oblique cross-field pits partially obscured by the spiral thickening. Scale bar = 15 μm.

Prototaxoxylon uniseriale Prasad 1982

Specimen No: BP/16/300
Locality: Swaerskraal, Laingsburg
Stratigraphy: Koornplaats Member, Abrahamskraal Formation, Beaufort Group, Late Permian
Collector: Rob Heard
Figures: 5 - 8

The log is 9 x 6 cm in diameter and 4 cm in length, beige and browns in colour. Growth rings are distinct but the earliest earlywood is distorted and crushed, compacted into the latewood, so growth rings are difficult to measure; they range from 1-3 mm. In transverse section (Figure 5) the tracheids have roundish lumina and square to polygonal outlines (but the corners are not thickened). Wall thickness is 3-5 µm. The earlywood tracheid mean tangential diameter is 26 µm(range 17-35µ m) and mean radial diameter is 26 µm (range 20-35 µm). Bordered pits occur on the radial walls only, are uniseriate, contiguous and not compressed, with a diameter of 20 µm. Spiral thickening is biseriate, criss-crossing over the pits, 3-5 µm thick and 7-10 µm apart (Figure 6). The spirals are about 45° to the horizontal.

These are definitely spirals; wall degradation was seen in some specimens and the markings are at a steeper angle and appear more broken up and erratic.

Rays are uniseriate, homogeneous, 7-10-20 cells high and there are 10 rays per horizontal mm (Figure 7). Cross-field pits are mostly single, bordered and oblique and also covered by the spiral thickening (Figure 8). Very rarely there are two pits per field. The pits are 7 x 17 mm. There are no resin canals or axial parenchyma.

Discussion

This genus, *Prototaxoxylon,* was first described as *Spiroxylon africanum* by Walton from Harmsfontein, Cape (1925, unknown age) but, as the generic name had already been used, Kräusel and Dolianiti (1958) transferred it to their new genus *Prototaxoxylon.* Although Walton's slides cannot be traced, the type specimen, SAM 2945, was borrowed from the South African Museum and new thin sections made. There is no doubt that the Paardekraal and other specimens (Table 2) belong to the same taxon.

Prototaxoxylon africanum - description of holotype SAM 2945

Figures: 9-12

The specimen is black, smooth and measured 8 x 4 x 3 cm but had already been sectioned. In transverse section the tracheids are square to polygonal with fairly thick walls, 7-10 µm. Growth rings are 4-7 mm wide, indistinct, with very little latewood, and the earlywood tracheid mean tangential and radial diameters are 41 and 40 µm respectively (Figure 9). Bordered pits occur on the radial walls, 1-2 seriate, contiguous, alternate and with a diameter of 12-14 µm (Figure 10). The same pitting occurs on the tangential walls but much less frequently. Rays are uniseriate with occasional biseriate portions of 1-3 cells, 2-9-14 cells high (Figure 11). Cross-field pits are round to oval with a thick, poorly preserved border. The aperture is 5-7 µm and the border 1-2 µm (total diameter 6-8 µm). There are 2-8 of these pits, which are between cupressoid and dacrydioid, per field (Figure 12). Walton described them as "There are two to eight small pits per field. No border can be seen to the pits, though it is possible that a border may have been present." (1925, p. 19). The spiral thickening is very delicate, less than 1 µm in thickness, 10-14 µm apart, almost at right angles to the vertical tracheid walls and passing between the tracheid pits (Figures 10-12).

Emended diagnosis:

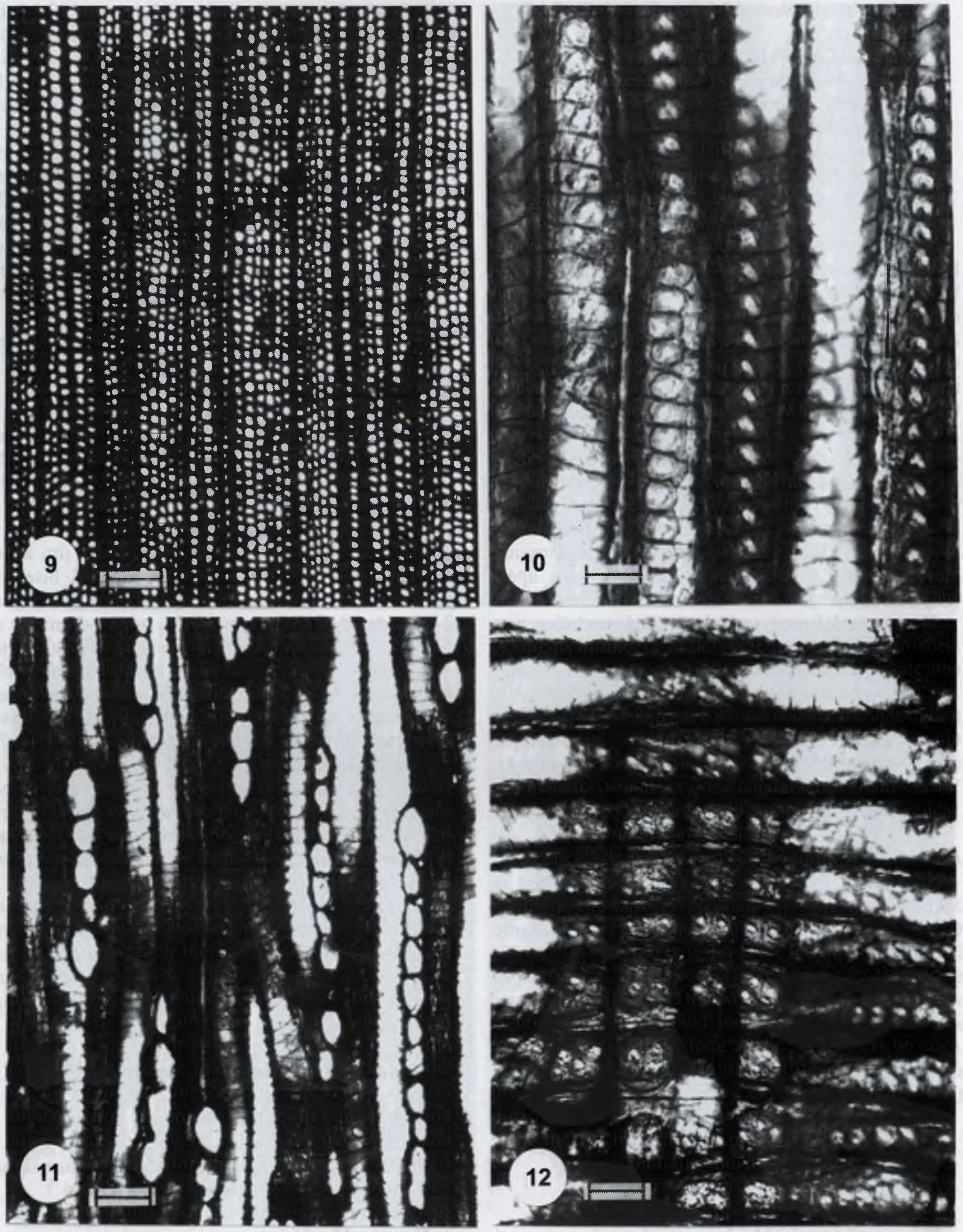
Secondary xylem wood with 1-2 seriate alternate bordered pitting on radial walls of the tracheids. The pits are 12-14 µm in diameter and also occur on the tangential walls but less frequently. Fine spiral thickening on the tracheids is almost at right angles to the walls, less than 1 µm thick and 10-14 µm apart. Rays are low, uniseriate with occasional biseriate portions and the walls are thin and unpitted. There are 2-8 bordered pits per cross-field, with a diameter of 6-8 µm. Axial parenchyma and resin canals are absent.

Prototaxoxylon africanum has been described only from South Africa. Several other species have been documented, mostly from India but also from Russia and Brazil (Prasad 1982). They range in age from the Carboniferous to "Mesozoic". *P. intertrappeum* (Prakash & Srivastava 1962) is of questionable Tertiary age. *Prototaxoxylon uniseriale* was first described from the Upper Permian of India (Prasad 1982) and is quite distinct from *P. africanum* as it has much heavier spiral thickening. *P. africanum* is common in the South African Karoo with occurrences in the Waterford, Fort Brown (Ecca) and Abrahamskraal Formations (Lower Beaufort) which are Lower Permian. In South Africa, *P. uniseriale* has to date only been recorded in the Abrahamskraal Formation.

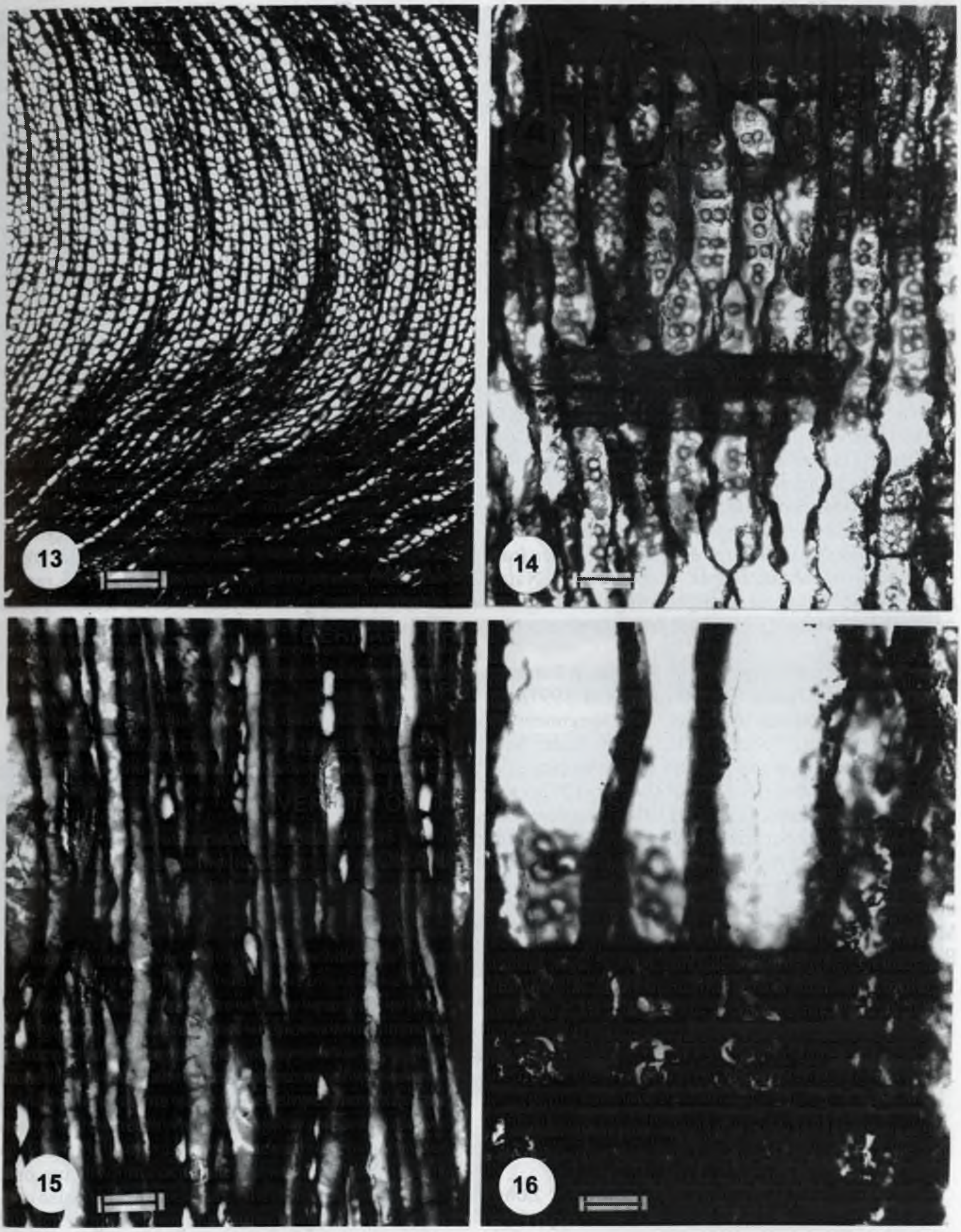
Australoxylon teixeirae Marguerier 1973

Specimen No: BP/16/298
Locality: Swaerskraal, Laingsburg
Stratigraphy: Koornplaats Member, Abrahamskraal Formation, Beaufort Group, Late Permian
Collector: Rob Heard
Figures: 13 - 16

The log measures 10 x 5 x 6 cm and is beige with orange streaks. Growth rings are distorted. Tracheids are square to rectangular in transverse section and the cell walls are 5-7.5 µm thick (Figure 13). The earlywood tracheid mean tangential diameter is 39 µm (range 35-55 µm) and the mean radial diameter is



Figures 9-12. *Prototaxoxylon africanum SAM 2945* (type specimen). **9:** TS with growth ring. Scale bar = 200 μm. **10:** RLS showing uni- and biseriate pitting and fine spiral thickening. Scale bar =30 μm. **11:** TLS with uniseriate rays, some with resin deposits, and fine spiral thickening. Scale bar = 60 μm. **12:** RLS showing narrowly bordered cross-field pits. Scale bar = 10 μm.



Figures 13-16. *Australoxylon teixeirae* BP/16/298. **13:** TS with distorted preservation. Scale bar = 200 μm. **14:** RLS with clusters or stellate groups of pits. Scale bar = 50 μm. **15:** TLS with uniseriate rays and occasional biseriate portions. Scale bar = 100 μm. **16:** RLS with narrowly bordered pits in the cross-field. Scale bar = 20 μm.

44 μm (range 25-60 μm). Bordered pits occur on the radial walls only, are mostly 1-2 seriate, very rarely 3-seriate, opposite or alternate, and mostly in distinct clusters (Figure 14). When contiguous, the pits are still round with no compression. The pits are 10 μm in diameter with an aperture of 5 μm.

Uniseriate rays predominate and occasionally there are biseriate portions of 1-4 cells. The rays are 3-8-21 cells high, homogeneous and there are 10 rays per horizontal mm (Figure 15). The cross-field pits have narrow borders, are round to oval, 7.5 μm in diameter, and there are 3-7 pits randomly arranged in the cross-field (Figure 16). There are no resin canals or axial parenchyma.

Discussion

This species occurs in the Permian of southern Africa. It is very common in the Abrahamskraal Formation and the lower part of the Teekloof Formation (Lower and Middle Beaufort Group). The youngest specimen is from the contact of the *Aulacephalodon* and *Cistecephalus* Assemblage Zones in the Aberdeen area. Marguerier (1973) described two species, *Australoxylon teixeirae* and *A. natalense* from the Karoo of Mozambique and Ecca of Natal, respectively. They are easily distinguished by the quadriseriate tracheid pitting and presence of crassulae in *A. natalense*.

Twenty one other species of *Australoxylon* have been described (Giraud 1991, Weaver et al. 1997) and all are from Permian deposits. The specimens of *Dadoxylon arberi* (Warren 1912) from Natal have definite clustering of the pits and should be placed in *Australoxylon teixeirae* (Marguerier 1973, and personal observation). Erasmus (1976) also described *Dadoxylon arberi* but from the Beaufort Series of the Empangeni district in Natal. His material also has the characteristic stellate groups or clusters of tracheid pits of *Australoxylon* but he overlooked the work of Marguerier. Thus, the restriction of this genus to Permian sediments in southern Africa is to be expected.

Araucarioxylon Kraus 1870

Type species: *Araucarioxylon carbonaceum* (Witham 1833) Kraus

Araucarioxylon africanum Bamford sp. nov.

Holotype: BP/16/311
Locality: Near Harrismith
Stratigraphy: *Dicynodon* Assemblage Zone, Normandien Formation, Beaufort Group, Late Permian
Collector: Chris MacKnight
Etymology: named for southern Africa
Figures: 17 - 20

The log is 13 x 10 x 14 cm and is a streaky beige colour. Growth rings are distinct with 8-9 rows of thick-walled radially compressed tracheids comprising the latewood. The average width of the growth rings is 2mm. In transverse section the tracheids are square (Figure 17). The earlywood tracheid mean tangential diameter is 37 μm (range 30-45 μm) and mean radial diameter is 41 μm (range 27-50 μm). The latewood tracheid mean tangential diameter is 36 μm (range 32-48 μm) and mean radial diameter is 13 μm (range 10-20 μm). Bordered pits occur on the radial walls only, are mostly biseriate and alternate, sporadically uniseriate, contiguous to compressed and hexagonal in shape, with a diameter of 12-15 mm and aperture of 5 μm (Figure 18).

Rays are uniseriate only, 2-8-18 cells high and there are 5 rays per horizontal mm (Figure 19). The cross-field pits are araucarioid with narrow borders, 2-4-7 per field and the pits are round to oval and 6-8 μm in diameter (Figure 20). There are no resin canals or axial parenchyma.

Diagnosis

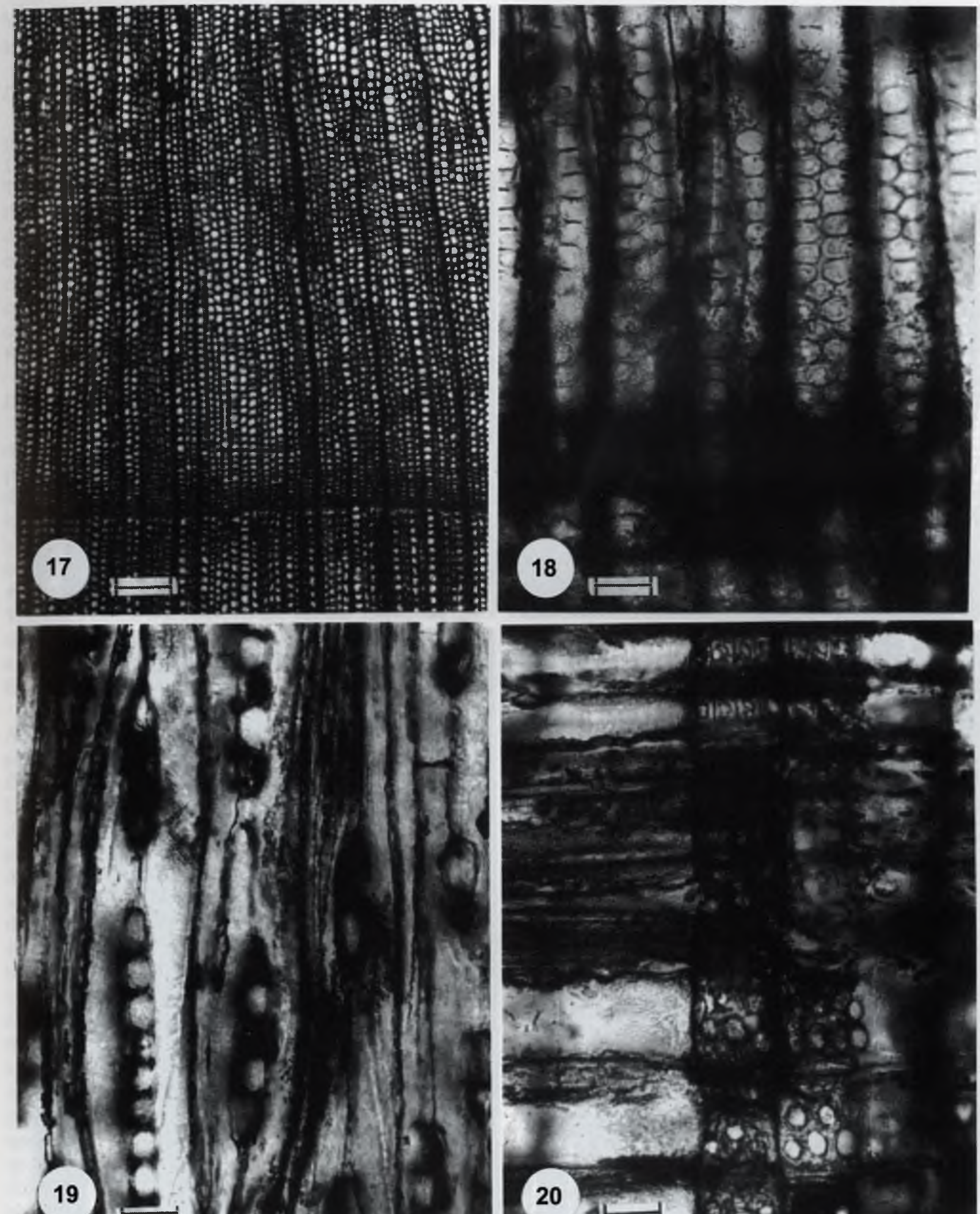
Secondary xylem wood with 1-2 seriate bordered pits on the radial walls of the tracheids, contiguous to slightly compressed, alternate, pit diameter 12-15 μm. Rays are uniseriate and have an average height of 15 cells. Cross-field pits are araucarioid (i.e. narrow border), oval shape, 6-8 μm and 2-4 per field, rarely up to 7. No axial parenchyma or resin canals. Resin in varying amounts in rays and/or tracheids.

Araucarioxylon karooensis Bamford sp. nov.

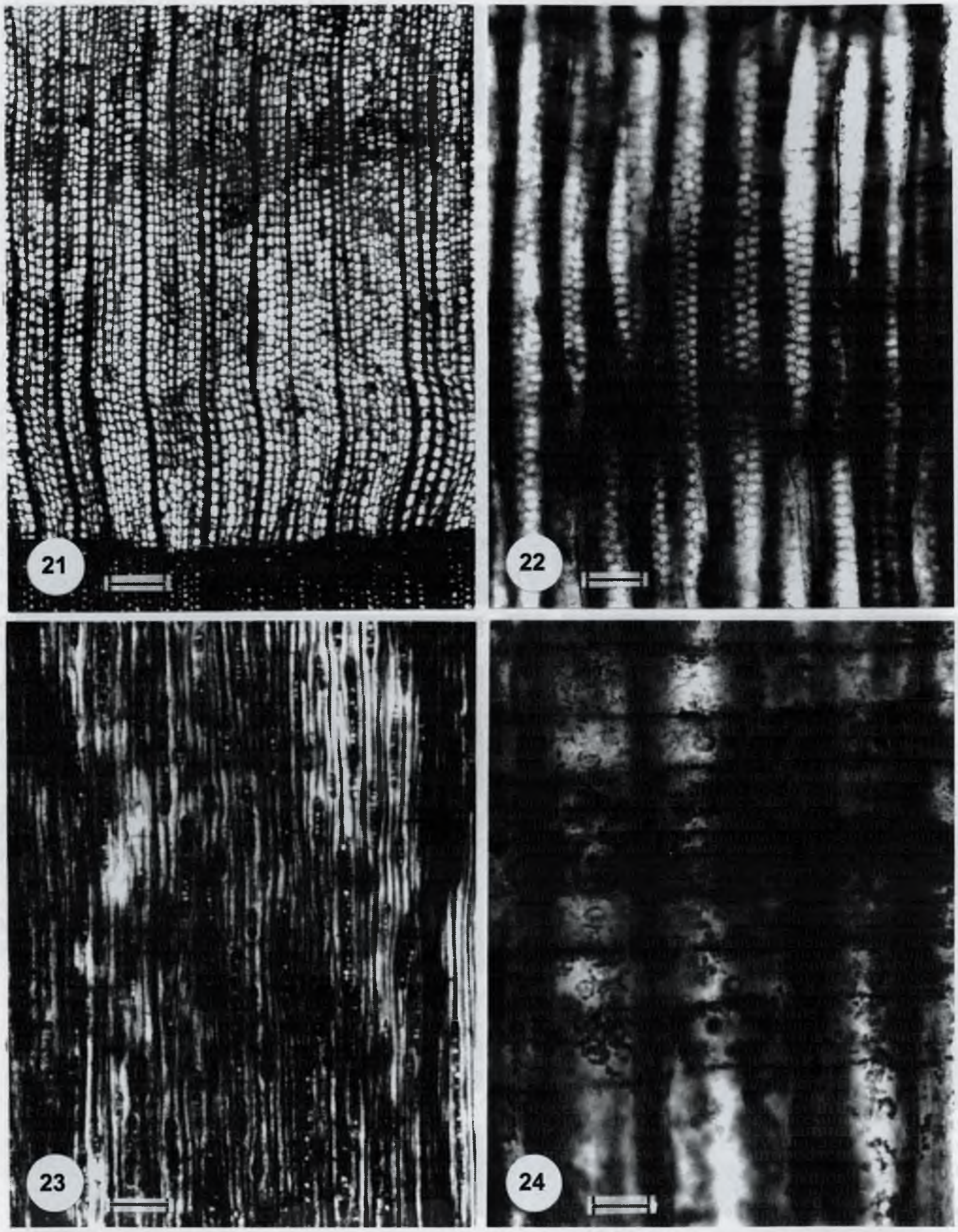
Holotype: BP/16/313
Locality: Near Harrismith
Stratigraphy: *Dicynodon* Assemblage Zone, Normandien Formation, Beaufort Group, Late Permian
Collector: Chris MacKnight
Etymology: named after the Karoo Basin and Karoo Supergroup
Figures: 21 -24

The specimen is 5 x 6.5 x 4 cm and beige with streaks. Growth rings are distinct, on average 6mm wide and terminated by 5-7 rows of latewood cells (Figure 21). In transverse section the tracheids are roundish and the earlywood tracheid mean tangential diameter is 37 μm (range 27-50 μm) and mean radial diameter is 39 μm (range 27-50 μm). The latewood tracheid mean tangential diameter is 30 μm (range 25-38 μm) and mean radial diameter is 17 μm (range 12-25 μm). Alternate bordered pitting occurs on the radial walls only and is mostly biseriate, but also uni- or triseriate, contiguous to hexagonal (Figure 22). The pits are 12-15 μm in diameter with an aperture of 5-7.5 μm.

The rays are uniseriate with sporadic biseriate portions of 1-2 cells, 3-15-25 cells high and there are 5 rays per horizontal mm (Figure 23). The cross-field pits are round to slightly oval with a very narrow border, and there are 2-4 pits per field, 7.5-10 μm in diameter (Figure 24). There are no resin canals or parenchyma.



Figures 17-20. *Araucarioxylon africanum* sp. nov. BP/16/311. **17:** TS with growth ring. Scale bar = 250 µm. **18:** RLS with biseriate, alternate and compressed bordered pitting (i.e. araucarian). Scale bar = 10 µm. **19:** TLS with uniseriate rays. Scale bar =30 µm. **20:** RLS cross-field pits with narrow borders. Scale bar = 15 µm.



Figures 21-24 *Araucarioxylon karooensis* sp. nov. BP/16/313. **21:** TS with growth ring. Scale bar = 200 µm. **22:** RLS showing triseriate araucarian pitting in the central part of the tracheid. Scale bar = 30 µm. **23:** TLS with uniseriate rays and occasional low biseriate portions. Scale bar = 200 µm. **24:** RLS with narrowly bordered cross-field pits. Scale bar = 30 µm.

The pit size varies in some specimens, but this may be an artefact of preservation.

Diagnosis

Secondary xylem wood with araucarian bordered pitting in the radial walls of the tracheids only. Pitting 1-3 seriate, contiguous, slightly compressed, alternate. Triseriate pitting must occur at least 5% of the time in the central part of the tracheid. Pits 12-15 μm in diameter. Rays predominantly uniseriate with occasional low, biseriate portions, average height 15 cells, maximum around 30 cells. 2- 4 cross-field pits, oval with a narrow border (araucarioid), and a diameter of 7.5-10 μm. No axial parenchyma or resin canals. Resin sometimes present in rays and tracheids.

Discussion

The two new species are very similar but *Araucarioxylon africanum* does not have any triseriate pitting whereas *Araucarioxylon karooensis* does have this feature. The rays in both species are similar in height but they are exclusively uniseriate in *A. africanum* whereas in *A. karooensis* there are occasional biseriate portions. Ray features, however, are not usually considered to be as important as pitting. The sizes of the tracheid pits are similar and so are the sizes of the cross-field pits in both species. Their numbers differ: *A. africanum* tends to have more cross-field pits than *A. karooensis*.

New species have been erected because the South African woods show some differences from the previously described species. *A. africanum* is similar to *Dadoxylon (Araucarioxylon) dallonii* (Dupéron-Laudoueneix 1976) from the Cretaceous of Chad. *D. dallonii* has araucarian bordered pitting which is predominantly uniseriate, also biseriate, with diameters of 16-22 μm, the rays are mostly uniseriate with occasional biseriate portions, 1-29 cells high, and there are 1-2 half bordered pits per cross-field with a diameter of 9-10 μm. The differences are in the larger bordered pits of *D. dallonii* and the type and number of cross-field pits. *A. africanum* is also similar to *Dadoxylon (Araucarioxylon) kiliani* (Batton, 1965) from the Cretaceous of Morocco. *D. kiliani* has much larger bordered pits which are predominantly uniseriate and araucarian, but the rays and cross-field pits are the same as the South Africa woods. A third species which is similar to *A. africanum* is *Dadoxylon* sp. 1 (Lemoigne 1981) from the Permian of Saudi Arabia. The difference is again in the more uniseriate nature of the tracheid pitting. No pit sizes are given in the description. The differences described above are sufficient to warrant a new species designation for the South African wood.

Araucarioxylon karooensis is similar to several Indian woods. *A. agathioides* (Kräusel & Jain 1964, Jurassic) has 1-3 seriate araucarian pitting but the pits, 10-23 mm, are larger, and more variable in size than those of *A. karooensis*. The rays and cross-field pits of both species are virtually identical. *D. amraparense* (Sah & Jain 1963, Jurassic) and *D. kharkhariense* (Maithy 1965, Permian) are also very similar but the tracheid pitting is more randomly arranged, with some degree of opposite pitting, unlike the South African specimens. These differences justify the erection of a new species.

There are numerous other species of *Araucarioxylon* and *Dadoxylon* described from Palaeozoic and Mesozoic sediments all over the world, all with fairly minor differences. The taxonomy and affinities have yet to be sorted out, however, careful description is necessary for distinguishing useful biostratigraphic types. *A. africanum* occurs in the Normandien Formation and in younger rocks (unpublished internal reports). *A. karooensis* occurs in the Normandien Formation. The Dwyka woods observed or described in the literature tend to be small, have araucarian tracheid pitting but non-araucarioid cross-field pits, and pith. According to a survey on araucarian woods (Giraud 1991), woods with multiseriate tracheid pitting are older than the biseriate ones and by the end of the Triassic 5-seriate pitting no longer occurred, by the end of the Jurassic 4-seriate pitting no longer occurred, so during the Cretaceous only uniseriate and biseriate araucarian pitting is found. No specimens of *A. karooensis* have yet been found in the younger sediments of South Africa either, but further collecting will confirm or refute these results and the ranges shown in Table 3 will have to be modified.

Mesembrioxylon **cf.** ***M. rajmahalense*** Jain 1964

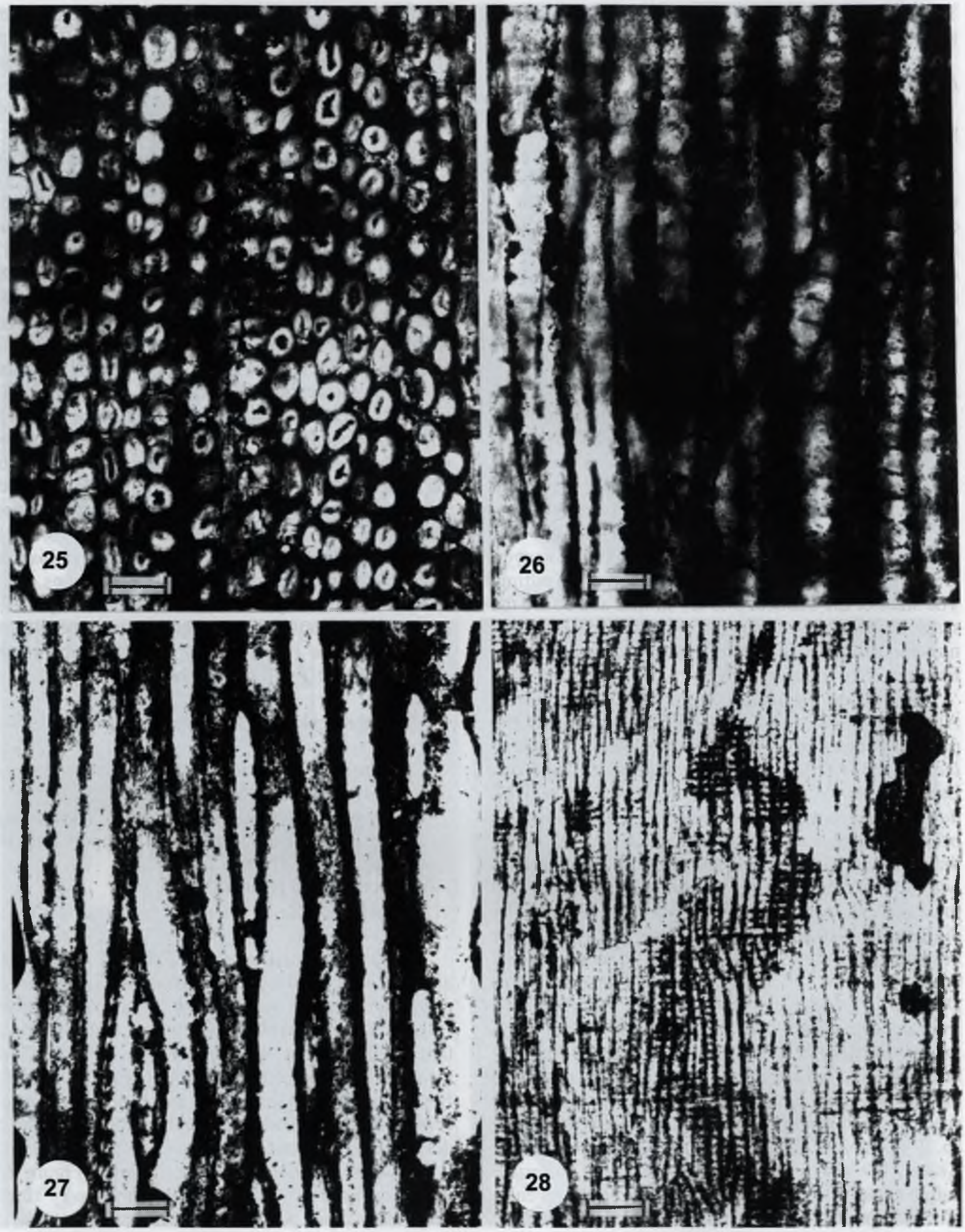
Specimen No: BP/16/470
Locality: Norwood, Sterkstroom.
Stratigraphy: Upper *Cynognathus* Assemblage Zone, Burgersdorp Formation, Upper Beaufort Group, Middle Triassic
Collector: John Hancox
Figures: 25 - 28

The piece of wood measured 5.5 x 5.5 x 3cm and is a milky beige. The tracheids are roundish in outline and neatly arranged in radial rows (Figure 25). Growth rings are not visible. Earlywood tracheid mean tangential diameter is 24 μm (range 20-32 μm) and mean radial diameter is 29 μm (range 22-37 μm). Bordered pitting is uniseriate and contiguous but not compressed, confined to radial walls, with the pit diameters 17-20 μm (Figure 26).

Rays are uniseriate, 1-8-13 cells high (Figure 27). The cross-field pits are round to oval, mostly single, very rarely 2 pits per field, and have a diameter of 12 mm (Figure 28). They are too poorly preserved to see if narrow borders are present. Other ray cell walls are thin and smooth. No resin canals or axial parenchyma occurs.

Discussion

Woods with abietinian pitting (uni- to biseriate, opposite, separate to contiguous but not compressed)



Figures 25-28. *Mesembrioxylon* cf. *rajmahalense* BP/16/470. **25:** TS with no growth rings. Scale bar = 50 μm. **26:** RLS with uniseriate, contiguous but not compressed bordered pits (abietinian). Scale bar = 20 μm. **27:** TLS uniseriate rays. Scale bar = 20 μm. **28:** RLS with single, large, simple cross-field pits. Scale bar = 120 μm.

first occurred in the Upper Triassic (Selmeier & Vogellehner 1968, Mueller-Stoll 1986) as did the Protopinaceae which have "mixed" pitting (araucarian and abietinian). This specimen, BP/16/470, has the features of several abietinian genera, *Podocarpoxylon, Phyllocladoxylon* and *Mesembrioxylon*. These woods have affinities with the Podocarpaceae but *Mesembrioxylon* was erected by Seward (1919) for woods whose cross-field pits are between those of the other two genera. The South African specimen is poorly preserved but is most similar to *M. rajmahalense* from the Jurassic(?) Rajmahal Hills, Bihar, of India (Jain 1964). The Indian wood has mostly uniseriate and contiguous tracheid pitting, 10 x 12 µm in diameter. The rays are 1-10 cells high and there are 1-2 large, simple pits "eiporen" per cross-field, 12-14 µm in diameter, but "sometimes broad, 10 to 20 µm in size". The tracheid pitting in the South African specimen is more regular than the Indian species and a little bigger.

Other specimens have been collected from the Molteno which also appear more podocarpacean than araucarian but the preservation is not good enough to identify them confidently. An example is BP/2/395 from the Burgersdorp Formation. More material needs to be collected and studied.

Fossil woods have also been studied from the Molteno and Clarens Formations but are too poorly preserved to identify to species level. Wood collected by Heidi Anderson from Boesmanshoek and Kannaskop has been distorted and compressed, possibly recrystallized by heat after preservation. The wood is most probably araucarian. John Hancox collected several other samples from the Burgersdorp Formation which also have the same appearance. I collected wood from the Clarens Formation at Rhebokhoek. This wood is unidentifiable because none of the pitting has been preserved but appears to be more like the *Mesembrioxylon* type of wood than araucarian. No wood has been collected and studied from the Elliot Formation.

DISCUSSION

The Karoo Basin vertebrate biostratigraphy has been substantially modified and revised over the last 90 years and in the most recent publication (Rubidge 1995) the ranges of the fish, amphibians and terrestrial vertebrates have been documented within revised Assemblage Zones. No comparable biostratigraphic zonation has been proposed for plant fossils. Although plant material is abundant, most of the material is vegetative which means that the delimitation of taxonomic groups is difficult. In the *Glossopteris* flora for example, there are 40 to 60 leaf species but only half that number of fructifications. These are obviously difficult to reconcile and correlate. The other taxa present are the sphenopsids of which there are several genera, sterile fern fronds, lycopods, ginkgos and gymnosperms of uncertain affinity. As the leaves have not been preserved attached to the wood, the affiliations of dispersed plant organs will remain uncertain.

None of the fossil plant taxa has been thoroughly studied throughout the Karoo of South Africa, and ecological differences also complicate the record, so biostratigraphical correlations have not been made. Fossil woods on the other hand, are more conservative than the leaves, and although they cannot be correlated with any particular plant group, they have a limited distribution through time. The woods, therefore, can be used for a broadscale biostratigraphy.

Based on the fossil woods described above from throughout the Karoo sequence, summarised in Table 2, a preliminary biostratigraphic distribution can be drawn up. *Prototaxoxylon africanum* occurs from the Kookfontein Formation to the Abrahamskraal Formation (Ecca to Lower Beaufort Groups). *Prototaxoxylon uniseriale* is rare and has only been recorded from the Abrahamskraal Formation. *Australoxylon teixeirae* occurs from the Collingham Formation to the Normandien Formation and is very common. *Australoxylon natalense* has been recorded only from the Ecca (Marguerier 1973). *Araucarioxylon africanum* occurs in the Normandien Formation and in even younger sediments (Bamford, unpublished data). *Araucarioxylon karooensis* occurs only in the Normandien Formation. This preliminary biostratigraphy (Table 3) is based on approximately 70 identified woods from known stratigraphic horizons but further collections and studies need to be made in order to check the consistency of this correlation.

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