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GEOLOGY AND PALAEOBIOLOGY OF THE CENTRAL AND SOUTHERN NAMIB

VOLUME 2:
PALAEONTOLOGY OF THE ORANGE RIVER VALLEY, NAMIBIA

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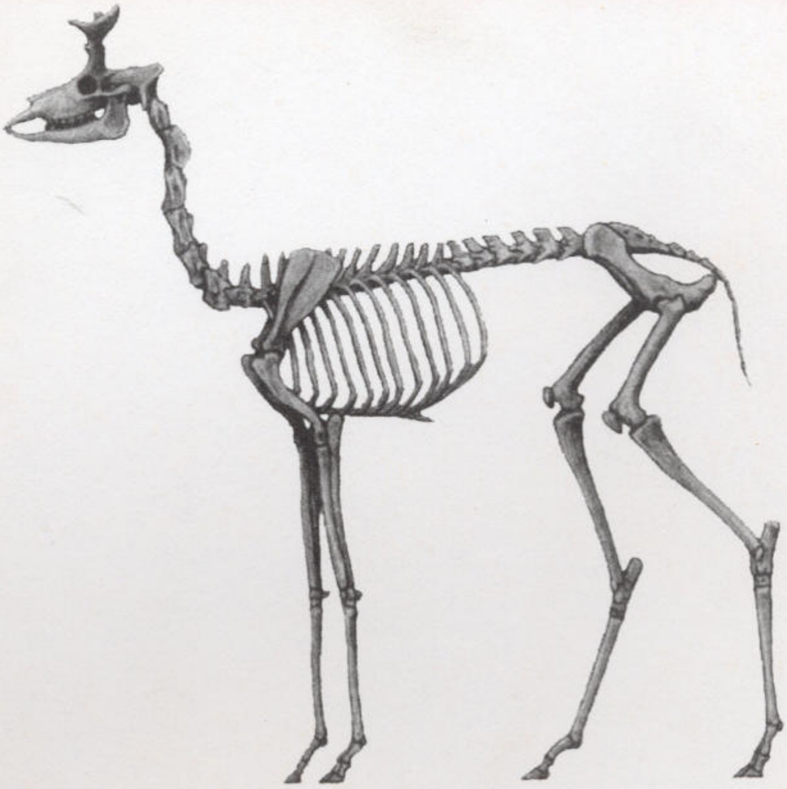
Martin Pickford and Brigitte Senut



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VOLUME 2: PALAEONTOLOGY OF THE ORANGE RIVER VALLEY, NAMIBIA

by

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Fossil woods from Auchas and their palaeoenvironment

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During mining activities fossil woods have been recovered from the abandoned palaeochannels of the Orange River, in the sections known as Auchas and Auchas Main. They are of Early Miocene age based on the associated faunal remains. Some very large logs are over I m in diameter but most specimens are 10 - 20 cm in diameter, and have been washed downstream and deposited as lag channel deposits. Some of the woods have been identified as members of the Combretaceae: *Combretoxylon namaensis* Bamford sp. nov., *Terminalioxylon crystallinum* Bamford sp. nov. and *T. orangensis* Bamford sp. nov. The new species *Burseroxylon africanum* Bamford of the Burseraceae is also described here. These fossil woods have been closely compared with equivalent modern woods of known climatic tolerances and it is suggested that the Early Miocene climate along the Orange River was wetter than today's and probably more humid with little seasonality. Comparisons of the calculated Vulnerability Index and Conductivity with other floras indicates that the woods were from a mesic to dry megathermal forest.

Version française abrégée

Au cours des travaux miniers á Auchas, on rencontre fréquemment des troncs d'arbres pétrifiés dans les dépôts de terrasses du Miocène inférieur liées à la proto-Oranje qui se trouvént à 50 km en amont d'Oranjemund dans Ie sud de la Namibie (Pickford & Senut, 1999). Des sections fines du bois fossile provenant de ces troncs ont été préparées dans les trois orientations standard - transversale, longitudinale radiale et longitudinale tangentielle. Les sections ont été examinees avec un microscope pétrographique Zeiss et les spécimens comparés avec les bois modernes. Les mesures sont établies à partir de 25 comptages pour lesquels les moyennes et les variations sont présentées dans le texte.

Les identifications ont été faites à partir de la littérature (Metcalfe & Chalk, 1950), des programmes d'identification des bois assistes par ordinateur (Wheeler *et al.*, 1986; Ilic, 1987) et quand cela était possible, les données étaient comparées avec des diapositives de la xylothèque de Tervuren (Belgique) et Forestek (Afrique du Sud).

Quatre espèces d'arbres appartenant à deux familles, les Combretaceae et les Burseraceae ont été reconnues. Elles sont toutes nouvelles. Dans la première famille, trois nouvelles espèces sont décrites - *Combretoxylon namaensis*, *Terminalioxylon crystallinum* et *Terminalioxylon orangensis*, et dans la seconde une nouvelle espèce est érigée, *Burseroxylon africanum*. Ces espèces sont comparées aux autres des mêmes genres.

Les bois fossiles fournissent des données utiles sur la Paléoclimatologie. Non seulement, certains spécimens d'Auchas sont très grands, indiquant un climat favorable de croissance, probablement dans des forêts où des pays boisés, mais ils ne présentent pas d'anneaux de croissance, ce qui implique des conditions de croissance favorable tout au long de l'année, bien que l'on ait quelques preuves de stress hydrique. Les relations entre l'anatomie du bois et le climat ont été quantifiées par plusieurs auteurs (Carlquist, 1975; Wolfe & Upchurch, 1987; Weimann *et al.*, 1998). La capture d'eau par les vaisseaux est fonction du diamètre de ces derniers et de leur fréquence. L'indice de vulnérabilité (VI) est le rapport du diamètre tangentiel moyen des vaisseaux sur Ie nombre des vaisseaux par mm^2. Des valeurs élevées indiquént un climat mésique et des faibles un climat plus xérique. La conductivité est calculee par la formule $C=r^4/10^6$ x nombre de vaisseaux par mm^2, où "r" est Ie rayon tangentiel moyen des vaisseaux. On trouvé des valeurs de la conductivité supérieures à 500 exclusivement dans les bois de grande taille et des valeurs supérieures à 200 seulement dans des bois de taille moyenne où grands.

L'étude de l'indice de vulnérabilité et de la conductivité des bois d'Auchas indiqué que le climat était sec, mégathermal, ce qui signifie que la moyenne des températures annuelles était supérieure à 20°C, les pluies saisonnieres et les précipitations inférieures à 1650 mm par an. Cette conclusion concorde avec les reconstitutions basées sur les mammifères et les reptiles des dépôts de la proto-Oranje à Auchas et Arrisdrift.

Introduction

The mighty Orange River has not always flowed along the same channels in the past, nor through such dry terrain, as it does today. Evidence for these changes lie in the sediments, abandoned river channels with pebble clasts, and the fossils trapped within. The exploration and extensive mining operations along the river have yielded evidence of the past fauna, flora and climatic conditions that have existed at various times in the past. Details of the past fluctuations are described by Pickford & Senut (1999) who also give sketch maps of the particular abandoned channels of the Auchas mine (Figures 4-1, 4-14, ibid) in which an abundance of Lower Miocene fossil wood has been discovered.

I first visited the sites in November 1990 with Ian Corbett, Mike de Wit, and John Ward (all of De Beers) and Roger Smith (South African Museum) when excavations had only just begun in the section known as AM02. The mechanical excavators unearthed several large fossil trunks, over 2 m long and 1.3 m in diameter. These logs were lying at 45° to the horizontal in a layer of sediment on Level 43 (43 m above sea level) and were surrounded by a green, clayey substance. Numerous other fossil trunks but with diameters of 6.2' - 0.5 m and lengths up to 2 m were found in other layers above and below, the trunks in each cluster aligned in the same direction. The separate clusters were not aligned. These log accumulations may represent different flood events (Corbett & Burrell 2001). During excavating activities these trunks were broken up into much smaller pieces as the material was hard but brittle.

Continuing excavations have produced an enormous pit exposing much of the bedrock below the gravel deposits of the abandoned proto-Orange River meander loops. Wood throughout the sequence has been stockpiled. Externally all the silicified tree trunks and stumps look the same, a rough, cream outer layer and fine dark brown inner part, but under the microscope the differences are evident. By comparing the detailed cellular structure of the fossil woods with modern woods it is possible to identify the taxa. Since the distribution and climatic tolerances of the modern woods are well documented, and based on the assumption that the fossil woods had the same tolerances as their modern counterparts, it is possible to reconstruct the palaeoenvironment of the fossil woods.

The Auchas deposits have been dated as Early Miocene based on faunal remains including mammals (Pickford & Senut 1999). Auchas is a bit older than Arrisdrift, being about 19 Ma. Trace fossils at Arrisdrift, about 4 km south of Auchas, indicate that the sea level was some 40 m higher than it is at present. They postulated that the sea level dropped after 17.5 Ma (the age of the faunal remains at Arrisdrift) and so the Orange River incised a new channel in the alluvial plain, leaving the gravel terrace deposits with fossilised wood and bones on either side of the new channel (ibid.).

There are other deposits of fossil wood and vertebrates at Baken, a more recently discovered site only a few kilometres away, which is the same age as Auchas (Pickford & Senut 1999). Offshore and onshore deposits of Lower Cretaceous woods occur north of the present Orange River (Bamford & Corbett, 1994, 1995). An Upper Cretaceous submerged forest has been recorded on the Namaqualand middle shelf (Bamford & Stevenson, in press). All these trees are conifers and not comparable with the angiospermous woods described here. Eocene woods have been collected from Bogenfels in Namibia (Bamford 2000) but the fossil record for the Tertiary has many gaps.

Materials and Methods

The trunks, stumps and branches of fossil wood, have been recovered from the gravels during mining operations and dumped nearby. From these stockpiles samples have been selected and sectioned at the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg. Very large specimens and ones which were distorted or replaced with large crystal inclusions were avoided. Each selected sample was cut with a diamond blade into blocks with one face in each of the following three directions: transverse, radial longitudinal and tangential longitudinal sections. The surfaces were polished and mounted onto petrographic glass slides with epoxy resin and the rest of the block cut off in the discoplan. Finally the newly cut surface was ground and highly polished to a thickness of 30-50 µm.

The thin sections were studied, measured and photographed under a Zeiss petrographic microscope and the wood structure compared with that of modern woods. The measurements given in the descriptions below are based on a minimum of 25 counts and the averages and ranges are presented.

Identifications were made using the literature, particularly Metcalfe & Chalk (1950), and two computer-aided wood identification programmes (Wheeler *et al.* 1986, Ilic 1987). Where possible the wood identifications have been checked with slides of modern woods from the xylarium in Tervuren, Brussels (Musée Royal de l'Afrique Centrale) and Forestek (CSIR, Pretoria) and specific published articles.

Description of fossil woods

Family Combretaceae Loefl.
Genus *Combretoxylon* Lemoigne 1978
Type species *Combretoxylon desrotoris*
***Combretoxylon namaensis* Bamford sp. nov.**
Figures: 1-7

Specimen: BP/16/496

Locality: Auchas Main, Orange River, Namibia

Stratigraphy: Early Miocene river gravels.

Other specimens: BP/16/375, 381, 499, 501, 785, 791.

Etymology: from the name of the country.

The piece of silicified wood is 27 cm long and 7 x 5 cm wide, and has a rough, creamy outer layer. The internal part is dark brown and fine grained. The wood is diffuse porous and no growth rings were observed in the thin section. There are two sizes of vessel elements (fig. 1). In transverse section the larger ones are oval in outline, solitary or more commonly in low radial multiples of 2-3-(4) members, sometimes in clusters with small vessels or tracheids (fig. 2). The proportions are 20% solitary, 40% paired, 30% groups of three and 10% groups of four or more large vessel elements. The mean tangential diameter is 120 µm (range 62 - 155 µm) and average length of 300 µm. The latter are difficult to measure because of the abundance of tyloses. Small vessel members have a mean tangential diameter of 30 µm (range 22 - 42 µm). Of the large vessels there are 13 per mm^2. The perforation plates are simple and horizontal to slightly oblique. Inter-vessel pitting is alternate, crowded and 2.5 x 5 µm (fig. 3). Vessel-parenchyma pitting was not preserved. Included phloem of the foraminate type is present in rare clumps (fig. 4).

Parenchyma is paratracheal and vasicentric to aliform, occasionally linking closely adjacent vessel multiples (figs 1-2). Fibres are thick-walled and non-septate. Rays are mostly biseriate, sometimes uniseriate or triseriate (figs 5-6) and 6-15-20 cells high (width: 15 - 40 - 50 µm; height: 195 - 335 - 500 µm). There are 9 rays per mm and they are heterocellular with the central cells mostly procumbent and the 1 - 2 - 4 rows of marginal cells are square. Uniseriate rays tend to be made up mostly of square to upright cells with some shorter procumbent cells (fig. 7). Square to rhomboidal crystals of calcium oxalate occasionally occur in the enlarged marginal cells or idioblasts.

***Terminalioxylon* (Schönfeld) Mädel-Angeliewa & Müller-Stoll 1973.**
Type species: *T. naranjo*
***Terminalioxylon crystallinum* Bamford sp. nov.**
Figures: 8-11

Specimen: BP/16/502

Locality: Auchas Main, Orange River, Namibia

Stratigraphy: Early Miocene river gravels

Other specimens: BP/16/792, 794.

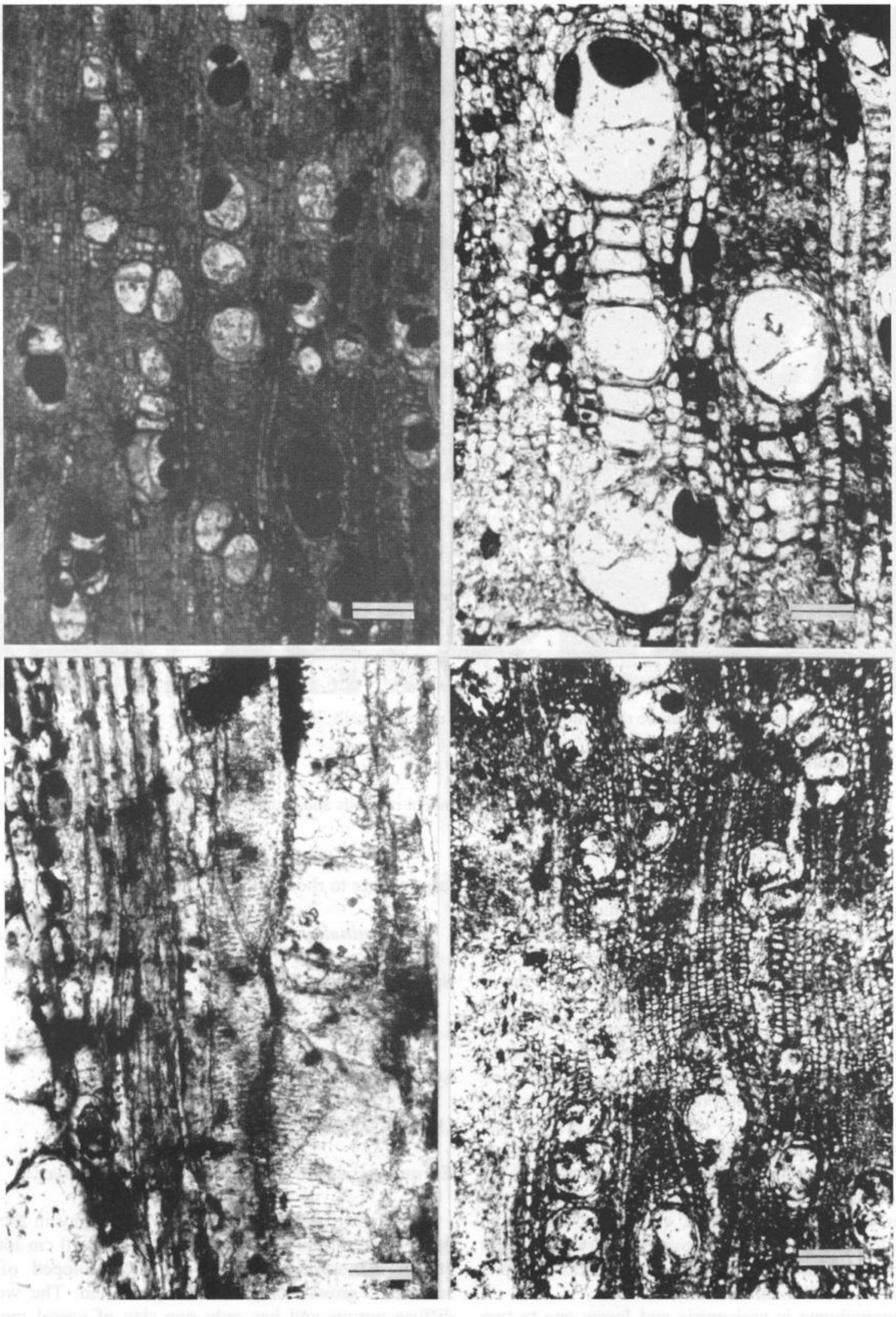


Figure 1. - *Combretoxylon namaensis* Bamford sp. nov. BP/16/496.
TS (= transverse section) showing low radial multiples of vessel elements. Some large vessels have a dark substance. Scale bar = 200μm.

Figure 2. - TS enlarged to show details of a solitary vessel and a radial multiple of three large vessels in line with 7 small vessels and tracheids. Note the thick-walled fibres, and vasicentric parenchyma. Scale bar = 66μm.

Figure 3. - TLS (= tangential longitudinal section) with inter-vessel pitting in the centre. Scale bar = 33μm.

Figure 4. - TS showing foraminate phloem. Scale bar = 200μm.

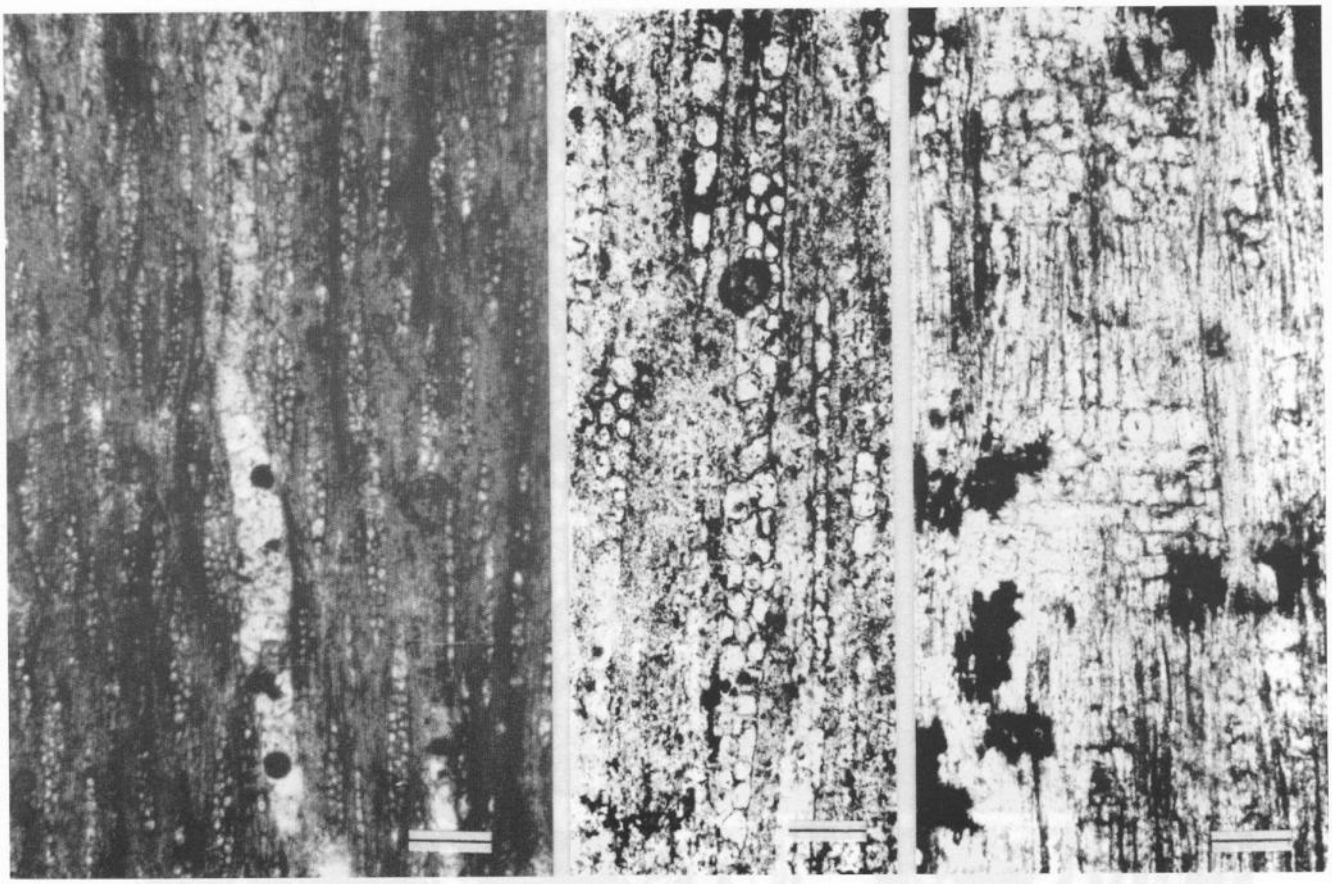


Figure 5. - TLS. Uniseriate rays and biseriate rays with long "tails" of uniseriate cells. Scale bar = 200μm.

Figure 6. - TLS. Details of rays. Scale bar = 66μm.

Figure 7. - RLS (= radial longitudinal section). Note the short procumbent ray cells and square marginal cells of the rays. Scale bar = 66μm.

Etymology: species name refers to the prominent crystals in the marginal ray cells

The piece of silicified wood is 15 cm long and 13 cm in diameter. Although the outer layers are white to ochre and brittle, the inner part is black and fine-grained. Growth rings were not observed and the wood is diffuse porous (fig. 8), with large round to oval vessel members solitary or arranged in low radial multiples of 2-3-4, (20% solitary, 20 % pairs, 54 % threes and 6 % in lines of 4 vessels). The vessels have a mean tangential diameter of 103 μm (range 75 - 138 μm). It is not possible to measure the length of the vessel members because of numerous tyloses. There are 17 vessels per mm^2 and they have simple, horizontal to oblique perforation plates. Inter-vessel pits are alternately arranged, crowded and 5 μm wide. Vessel-parenchyma pits were not observed. Phloem was not observed.

Axial parenchyma is vasicentric and forms one to two rows of cells around the vessels, but sometimes is aliform (fig. 8). Thick-walled fibres form the ground tissue and they are sinuous in tangential longitudinal section (fig. 10.) Rays are short and wide (figs 9-10): mostly biseriate, occasionally uniseriate or triseriate. (25 - 40 - 50 μm) and 3-9-14 cells high (125 - 180 - 200 μm). There are 9 rays per mm and they are weakly heterocellular with short procumbent central cells and 1-2 rows of square to upright marginal cells, some of which are idioblasts containing large square to rhomboidal crystals (fig. 11).

***Terminalioxylon orangensis* Bamford sp. nov.**

Figures: 12-17.

Specimen: BP/16/789

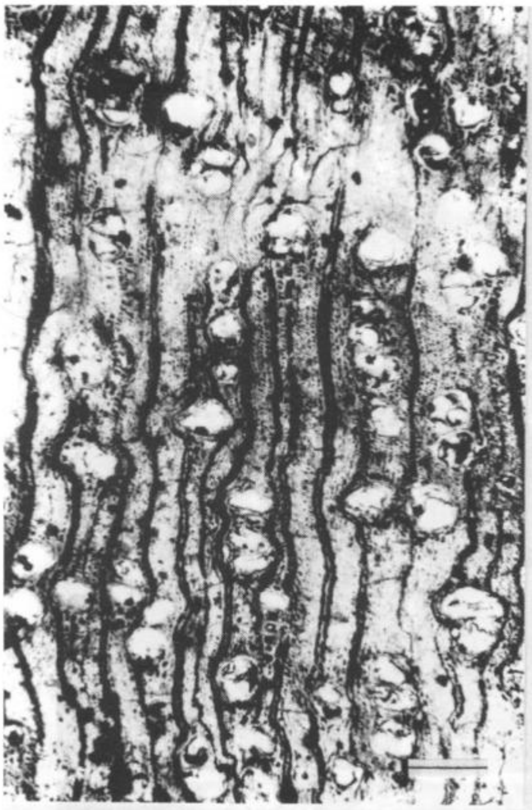
Locality: Auchas Main, Orange River, Namibia

Stratigraphy: Early Miocene river gravels

Other specimens: none.

Etymology: species name From the Orange River.

The fossil tree trunk, which is on display in the mine offices, is a bright green colour and about 50 cm long, 18 cm in diameter. A small piece was chipped off and sectioned: growth rings are not preserved. The wood is diffuse porous and has only one size of vessel members which are in low radial multiples of (1-)2-3(-4) members (figs 12-13). Their mean tangential diameter is 118 μm and their range is 90 - 150 μm. On average the vessels are 325 μm long, filled with tyloses and there are 16 per mm^2. Perforation plates are simple and horizontal to oblique. Inter-vessel pitting is alternate and crowded, 2.5 x 5.0 μm, and vestures are not seen (fig. 14). Vessel - ray parenchyma pitting is random (fig. 15), without a border and 10-15 μm in diameter.



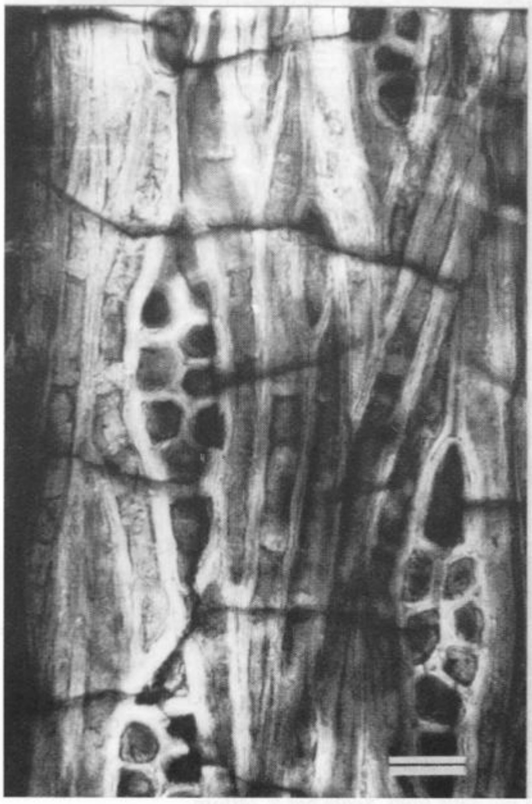
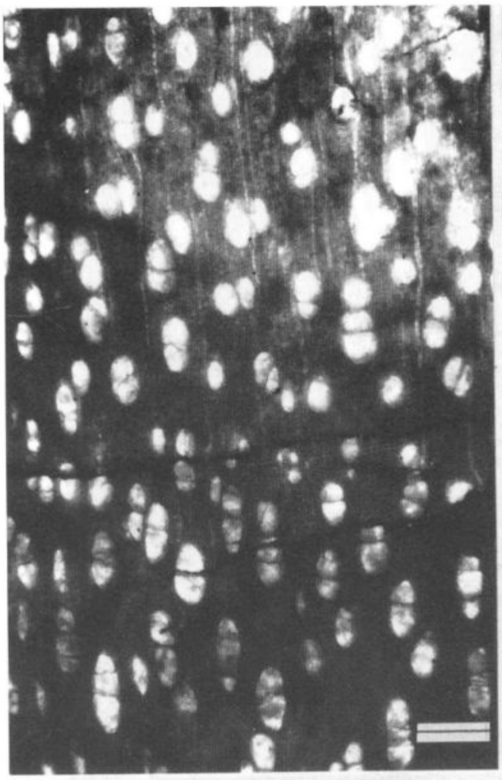


Figure 8. - *Terminalioxylon crystallinum* Bamford sp. nov. BP/16/502.
TS. Solitary and low radial multiples of vessels with dark rays and vasicentric parenchyma. All vessels are of a similar size. Scale bar = 200μm.

Figure 9. - TLS. Dark-celled rays are distributed between fibres (light background) and tylosed vessels in longitudinal section. Scale bar = 200μm.

Figure 10. - TLS. Detail of rays and fibres. Scale bar = 50μm.

Figure 11. - RLS. In the upright or square marginal cells of the rays are idioblasts containing crystals. The central cells are procumbent. Scale bar = 66μm.



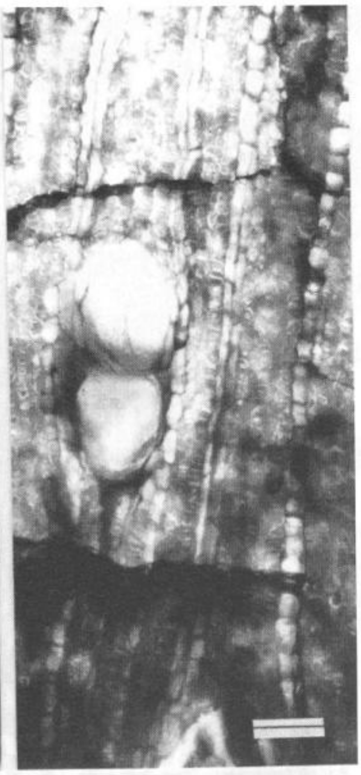
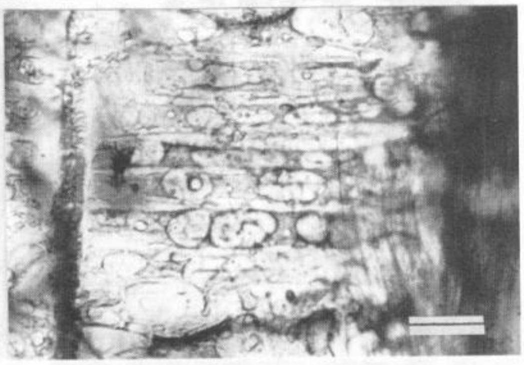
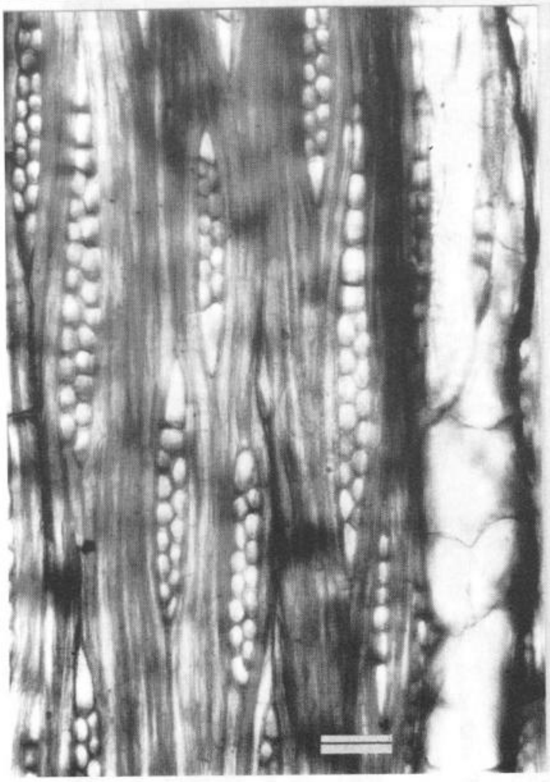
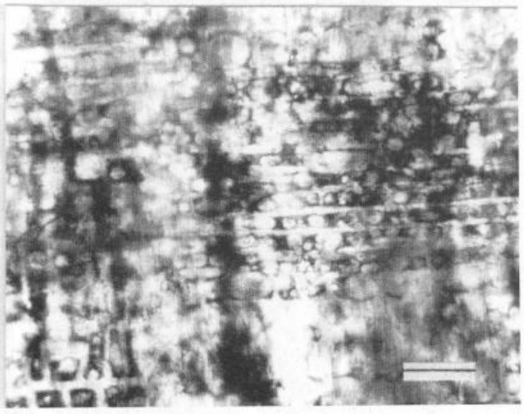





Figure 12. - *Terminalioxylon orangensis* Bamford sp. nov. BP/16/789.
TS. Vessels are solitary or in low radial multiples. Fibres are dark and ray cells light. Scale bar = 240μm.

Figure 13. - TS. Detail showing two vessels, very little paratracheal parenchyma, thick walled fibres and the parallel bands of ray cells. Scale bar = 50μm.

Figure 14. - RLS. Inter-vessel pitting is crowded and alternate, and the pits are oval with slit-like apertures. Scale bar = 33μm.

Figure 15. - RLS. Vessel-ray parenchyma pits are oval, thin-walled, randomly arranged and vary in size from 4-10-15 μm. Scale bar = 15μm.

Figure 16. - TLS. Rays are mostly biseriate, occasionally uniseriate. Tyloses are visible in the vessels. Scale bar = 66μm.

Figure 17. - RLS. Ray cells are procumbent in the central portion and square or upright in the margins. Scale bar = 66μm.

Fibres are thick-walled, rarely septate and appear very neat and regular in tangential longitudinal section.

Parenchyma is sparse, scanty paratracheal with one incomplete row of cells around the vessels. Rays are biseriate, narrow, neat and mostly 14 cells high (fig. 16), heterocellular, with central procumbent cells and 1-4 rows of square marginal cells or one row of more upright marginal cells, (average width 25µm, height 125 - 360 - 500µm (fig. 17). There are 10 rays per mm. No crystals were seen in the ray parenchyma cells.

Family: Burseraceae Jacq.
Genus and type species: *Burseroxylon preserratum* Prakash & Tripathi 1973.
***Burseroxylon africanum* Bamford sp. nov.**
Figures: 18-23.

Specimen: BP/16/382

Locality: Auchas Main, Orange River, Namibia.

Stratigraphy: Early Miocene river gravels.

Etymology: species name from the continent.

This piece of wood was part of a large diameter tree, at least 50 cm wide. The vessels are solitary or arranged in low radial multiples of 1-2 (-3-4) vessels, oval when solitary, distorted when in larger groups (fig. 18). The wood is diffuse porous and there are 17 pores per mm^2. Vessel mean tangential diameter is 191 µm with a range of

110 - 230 µm. Average vessel member length is 272 µm (range 185 - 350 µm) with abundant thin-walled tyloses. Perforation plates are simple. Inter-vessel pitting is alternate, crowded with a diameter of 5 µm. Vessel-parenchyma pits are a little bigger, 10-15 µm, simple and randomly arranged (fig 19). Thin-walled fibres form the ground tissue and may be gelatinous but this could be an artefact of preservation.

Scanty vasicentric parenchyma surrounds the vessels but is not abundant. Biseriate rays are most common but some uniseriate ones do occur with square to upright cells (figs 20 -21). Triseriate rays are very rare. Ray width varies from 25 - 45 - 60 µm for the 1 - 2 - 3 - seriate rays respectively. Height ranges from 5 - 11 - 25 cells (average 471 µm) and there are 9 rays per mm. Rays are heterocellular with central short procumbent cells and 1 ¬2 - 4 rows of marginal cells which are most commonly square (fig. 22). The rays have dark cellular contents which contrast with the clear fibres. No crystals, phloem or small vessels were observed. In the outer part of the trunk there is evidence of damage to the wood before preservation; there is frass in some vessels from some kind of boring insect, and also fungal hyphae in other cells (fig. 23).

Discussion

Identification of woods

<u>Combretaceae</u>:

Woods which have included phloem of the foraminate type occur in some genera in the following 10 families: Bixaceae, Chenopodiaceae, Combretaceae, Gonostylaceae, Loganiaceae, Melastomataceae, Nyctaginaceae, Onagraceae, Thymeliaceae, and Urticaceae. Of these only the Combretaceae has genera with crystalliferous cells within the marginal ray cells (Ilic 1987).

There are some 19 genera and about 600 species in the Combretaceae, of cosmopolitan distribution in the tropics and sub-tropics (Metcalfe & Chalk, 1950; Wickens, 1973; Carr, 1988). Of these only members of the subtribe Combretinae (Excell & Stace 1966) have vessels of two sizes. Only four of these genera have included phloem, namely most species of *Guiera*, *Thiloa* and *Calycopteris*, and some species of *Combretum* (van Vliet 1978). In the latter genus included phloem is restricted to species with a shrub or tree habit and one liana. This is further restricted to those members which are in the subgenus *Combretum* and occur in Africa (van Vliet 1978). These four genera have very similar wood anatomical structures but *Thiloa* and *Calycopteris* have only uniseriate rays. *Guiera* has biseriate rays but they are numerous and narrow, and the vessel members are extremely short, less than 200 µm. Thus only *Combretum* has the same combination of characters as the fossil wood specimen BP/16/496: vessel members of two sizes, included phloem of the foraminate type, bi- to triseriate heterogeneous rays with idioblasts in the marginal cells, scanty paratracheal to vasicentric parenchyma. Only the inter-vessel pitting is not well enough preserved to determine whether or not it is vestured. Vestured pitting is characteristic of the Combretaceae and a number of other families.

Amongst the modern species of *Combretum* the specimen BP/16/496 can be compared with those species with included foraminate phloem. *C. erythrophyllum* (Forestek slide No: 649) has phloem but the rays are exclusively uniseriate. *C. krausii* (FT 652), *C. acutifolium* (Tervuren wood collection, TW 28653), *C. apiculatum* (FT 645), *C. molle* (FT 1364) and *C. psidioides* (TW 28540) also have only uniseriate rays. The latter two species have included phloem which is distributed in a concentric pattern, but this could be mistaken in small sections of fossil wood for foraminate included phloem. 14 species are listed with foraminate phloem (Metcalfe & Chalk 1950, Lebacq & Dechamps 1964, Dechamps 1971, Dechamps unpub.) but I do not have access to the rest of the material.

There are relatively few species of fossil woods of *Combretoxylon* described. Lemoigne (1978) erected this genus for woods resembling the modern genus but he did not mention the two sizes of vessel elements which occurs in all species, nor the presence of included phloem which occurs in some species. These characters, however, may not always be preserved or observed and emending the diagnosis to include them would require the re-examination of Lemoigne's type material from Omo, Ethiopia. The specimens described here have the combination of features of the modern species but not of anyone particular species, so a new fossil species is erected here, *Combretoxylon namaensis* Bamford sp. nov. The suffix "-oxylon" is used because no exact match was found and also it is not possible to tell if the vessel pitting of the fossil is vestured.

The most noticeable feature of the specimen BP/16/502 is the idioblasts, each containing a single large crystal, amongst the square marginal cells of the rays (Fig. 11). There are 19 families which have crystals in idioblasts in ray cells but only four of these have the combination of features of simple perforation plates, paratracheal parenchyma with no banding and rays two or more cells wide (Hie 1987). The Anacardiaceae has these features but has large inter-vessel pitting;

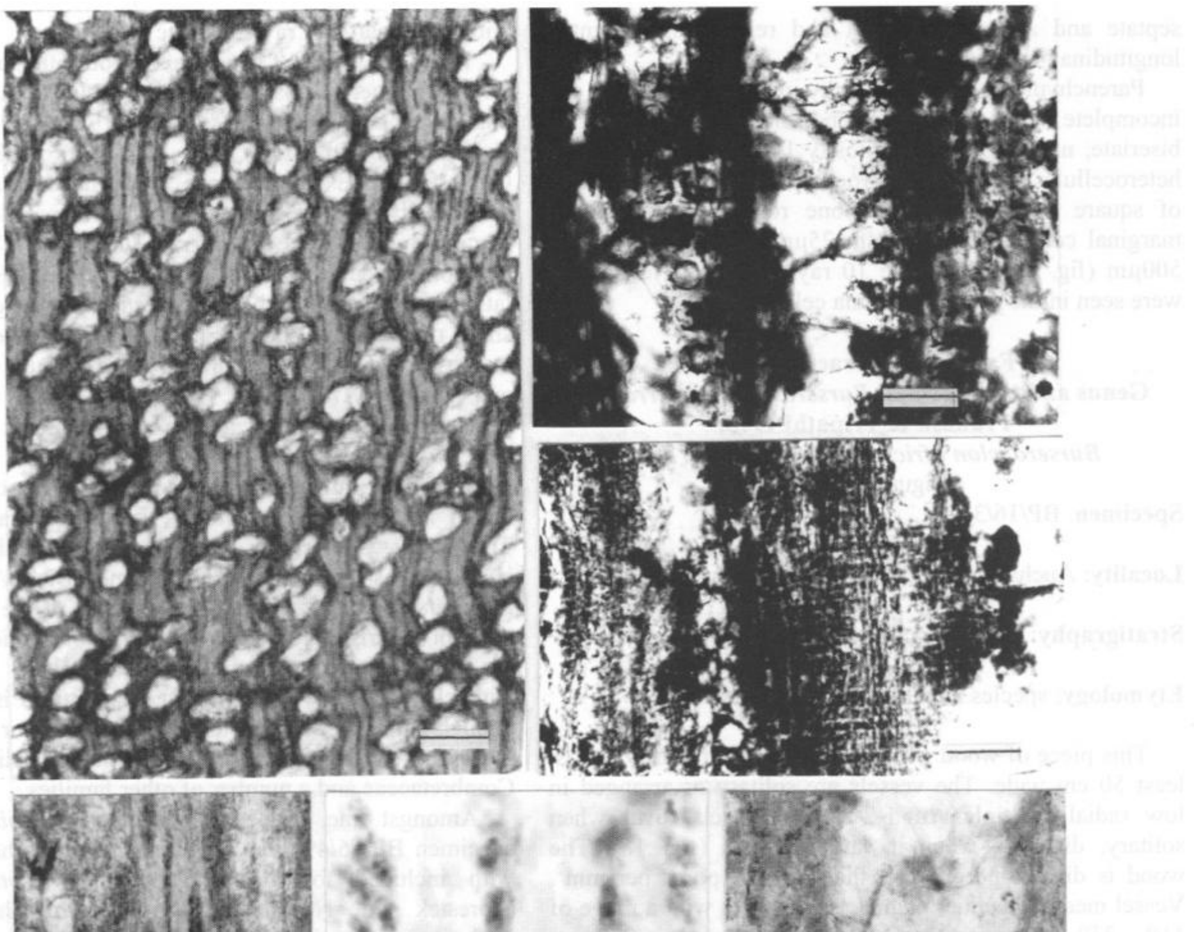


Figure 18. - *Burseroxylon africanum* Bamford sp. nov. BP/16/382.
TS. Vessels are mostly solitary but also in low radial multiples. They are somewhat distorted. Rays have dark cells. The scanty paratracheal parenchyma cells form incomplete sheaths around the vessels. Scale bar = 240µm.

Figure 19. - RLS. Faint vessel-ray parenchyma pits are just visible. Thick walled tyloses present. Scale bar = 100µm.

Figure 20. - TLS. Dark celled uniseriate and biseriate rays and tylosed vessels present. Scale bar = 200µm.

Figure 21. - TLS. Detail of ray cells and ?gelatinous fibres. Scale bar = 66µm.

Figure 22. - RLS. Poorly preserved rays with procumbent central cells and square to upright marginal cells. Scale bar = 200µm.

Figure 23. - RLS. Frass (insect faecal pellets) and fungal hyphae in the cavity of a vessel element. Scale bar = 66µm.

the Dilleniaceae differs in having predominantly solitary vessels and some genera have scalariform perforation plates; the Ochnaceae differ in having very heterogeneous rays. This leaves the Combretaceae.

In the Combretaceae ray cells with crystalliferous idioblasts occur in *Combretum*, *Guiera* and *Finetia* (van Vliet 1978) and *Terminalia* (Ilic 1987). The first two genera have two sizes of vessels, and the third has only uniseriate rays. This leaves *Terminalia* which typically has vessels which are of one size class, solitary or in low radial multiples, simple perforation plates, crowded and alternate inter-vessel pitting which is vestured, no included phloem, paratracheal parenchyma and narrow, heterocellular rays with idioblasts.

There are about 250 species of *Terminalia* with a wide distribution in warm regions. In South Africa there are about 9 species of trees or shrubs which are widespread except for the Cape and Free State. The fossil wood, BP/16/502, is very similar to *Terminalia sericea* (Forestech sample no. 242) which has a mean vessel tangential diameter of 120µm (range 70-150µm) 15 vessels per mm^2, alternate and crowded inter-vessel pitting 7.5µm in diameter, vasicentric to aliform parenchyma, short wide rays which are 2 cells wide and 11-19 cells high (28µm; 225-275 µm respectively), weakly heterocellular with central procumbent cells and 1-2 rows of marginal square cells. This modern wood, however, does not have idioblasts with crystals; these are found in several species in Asia and Malaysia only (van Vliet 1978).

Comparing the fossil wood BP/16/789 with modern species it shows some similarities with *Terminalia grandiflora* which has a slightly smaller mean vessel tangential diameter of 114µm, 15 vessels per mm^2, mean vessel length of 320µm, thick-walled fibres and very similar rays and parenchyma. The inter-vessel pits of *T. grandiflora* have coalescing apertures which is not evident in the fossil. The modern wood occurs in Australasia and not Africa.

Some of the fossil woods of *Terminalioxylon* described in the literature are very similar to the specimens described here, for example *T. primigenium* and *T. intermedium* from the Oligo-Miocene of Europe and Temperate Asia (Mädel-Angeliewa & Müller-Stoll 1973). *T. primigenium* differs in having exclusively uniseriate rays, and *T. intermedium* has uni- to triseriate rays and growth rings. *T. coriaceum* from the Mio-Pliocene of Assam, India (Prakash & Awasthi 1969) is similar in some respects only to BP/16/789. In *T. coriaceum* the idioblasts containing crystals are amongst the procumbent cells of the homocellular rays whereas they are amongst the square marginal cells of the Namibian material. Also the Indian material has some banded parenchyma and there is no evidence of this feature in any of the Namibian material. *T. coriaceum* has been compared with the extant *Terminalia coriacea* which grows on rocky and gravelly soils in drier and other parts of Madras State and Central India (Prakash and Awasthi 1969).

BP/16/789 is similar to BP/16/502 in the distribution of the vessels and parenchyma, and the inter-vessel pitting. Both have heterocellular rays but those of BP/16/502 are short and wide (125-200µm high; 25 - 50µm wide) and in BP/16/789 they are long and narrow (125 - 5.00µm high; 25µm wide). BP/16/502 has crystals in the marginal ray cells but BP/16/789 has none.

As there are no published woods with, the same characteristics, these two specimens are given new species names, *Terminalioxylon crystallinum* Bamford sp. nov. for BP/16/502 and *Terminalioxylon orangensis* Bamford sp. nov. for BP/16/789.

Burseraceae:

The combination of wood features of BP/16/382, diffuse porous, simple perforation plates, vessels solitary or in low radial multiples, tyloses, scanty paratracheal parenchyma, 1-5 seriate heterocellular rays with marginal upright cells, medium sized, crowded inter-vessel pitting and bigger vessel-parenchyma pitting are common to several families, namely Anacardiaceae, Burseraceae, Euphorbiaceae, Flacourtiaceae and Lauraceae (Metclafe & Chalk, 1950). In the Anacardiaceae, however, the inter-vessel pitting is larger than that of the fossil. The Phyllanthoideae section of the Euphorbiaceae has rays of two sizes whereas the rays in section Crotonoideae are much more heterocellular. Rays of the Flacourtiaceae are also much more heterocellular, and oil and mucilage cells are very common in the Lauraceae. This leaves the Burseraceae which generally have very little parenchyma and sometimes have radial canals within the rays.

There are about 16 genera and over 500 species in the family Burseraceae, widely distributed in tropical countries. *Commiphora* is typical of the more arid regions of southern Africa today with its spiny branches and peeling bark. About 20 of the approximately 200 species occur in this region. *Boswellia* is also a genus of dry savanna trees but other African members of the family, *Santiria*, *Dacryodes*, and *Canarium*, are large forest trees (Gillett, 1990).

Comparing the fossil with extant genera of the Burseraceae, it is most similar to *Bursera* on the basis of the size of the vessels, the presence of tyloses, sparse parenchyma and thick-walled fibres (Webber 1941, Metcalfe & Chalk 1950). Without comparative material it is not possible to determine the species affinities with any confidence.

Not many fossil woods of the Burseraceae have been described. Awasthi & Srivastava (1989) summarised the taxa from India (*Boswellioxylon indicum*. *Burseroxylon preserratum*, *Burseroxylon garugoides*, *Canarioxylon ceskobudejoviense*, *Canarioxylon indicum* and *Canarium paleoluzonicum*) and they are all very similar to each other. Several other taxa, *Canarioxylon shahpuraensis* (Trivedi & Srivastava 1985), *Canarioxylon* sp. (Lemoigne 1978) and *Sumatroxylon molli* (Den Berger 1923 in Awasthi & Srivastava 1989) are also very difficult to distinguish. Awasthi and Srivastava (1989) suggested combining all these fossil wood genera into *Burseraceoxylon*. This would simplify the taxonomy but lose any biogeographical and palaeoclimatic interpretations. More reference material needs to be studied. The woods of the Burseraceae are very close to the Anacardiaceae and there may be misidentified fossil woods (Wheeler 1991).

BP/16/382 is most similar to *Burseroxylon preserratum* (Prakash & Tripathi 1973) from the Upper Miocene of eastern India. The Indian fossil wood has mostly solitary vessels, heavily tylosed and 80-200µm tangential diameter, 12-18 per mm^2 , 300-640µm long; alternate inter-vessel pitting 8-10µm wide, scanty paratracheal parenchyma usually only one cell wide, and rays which are 1-6 seriate, homocellular (upright cells) or heterocellular with central procumbent cells and marginal upright cells. The differences are in the rays and vessel parenchyma pitting. The Namibian wood has rays which are 1-2 cells wide, very rarely triseriate and do not contain crystals. Vessel-parenchyma is poorly preserved but the thin walled (simple), round to oval, large and randomly arranged pits can be seen in some areas, 10-15µm wide. These differences are considered to be significant enough to place the Namibian wood in a new species, *Burseroxylon africanum* Bamford sp. nov.

Palaeoclimatic implications

The most striking feature of the woods in general is the enormous size of some of the logs and their abundance. This alone indicates that there was a favourable climate for the growth of large trees, either in a forest of some type or woodland. Considering the wood tissue with the fairly numerous and medium-sized vessels, diffuse porosity, and no growth rings, implies that there may have been suitable growing conditions all year round but with some water stress. The relationship of wood anatomy to climate has been quantified by Carlquist (1975), Wolfe & Upchurch (1987) and Weimann *et al.* (1998). Water uptake by vessels is a function of the diameter of vessels as well as their frequency. If a wood with a few large diameter vessels loses the function of one of the vessels, due to blockage by an embolism for example, the overall effect would be much greater than that for a wood with numerous smaller vessels if one vessel was rendered useless. The wood with a few large diameter vessels is more vulnerable to water stress. A measure of this is the Vulnerability Index where VI = vessel mean tangential diameter / number of vessels per square mm. High values indicate a mesic climate and low values a more xeric climate. Vessel diameter and number, however, are also a function of the size of the woody plant so shrubs and small trees have VI values much smaller than large trees. The conductivity of the vessels is calculated as $C = r^4/10^6$ x number of vessels per square mm, where "r" is the average tangential radius of the vessels. High Conductivity values indicate the size of the tree; C values over 500 are found only in large trees and C values over 200 are known only in medium-sized or large trees (Wolfe & Upchurch 1987).

Comparisons of woods from different climates for both modern and fossil plant assemblages have been done by Wolfe & Upchurch (1987) using large sample sizes. The sample size is important for overcoming biases and Weimann *et al.* (1998) recommend a minimum size of 25. The sample size here for the Auchas woods is very small so the interpretation should be treated with caution. Nonetheless if the calculated values for the Auchas woods (Table 1) are compared with those of Wolfe & Upchurch (1987) it indicates that the climate was a dry megathermal one. This means that the mean annual tem-

Table 1: Calculations for Vulnerability Index and Conductivity for the Auchas woods.
VI = Vessel mean tangential diameter / number of vessels per square mm.
C = (mean vessel radius) $r^4/10^6$ x number of vessels per square mm.

Catalogue N° BP/16/--	Identification	Vessel diameter µm	N° of vessels per mm^2	VI	C
382	*Burseroxylon africanum*	191	17	11.2	1410
496	*Combretoxylon namaensis*	120	13	9.2	168
375	*C. namaensis*	97	9	10.7	42
381	*C. namaensis*	93	17	5.4	76
499	*C. namaensis*	109	17	6.4	144
501	*C. namaensis*	95	19	5	93
785	*C. namaensis*	100	13	7.6	81
791	*C. namaensis*	113	12	9.4	126
502	*Terminalioxylon crystallinum*	103	17	6	119
792	*T. crystallinum*	82	17	4.8	48
794	*T. crystallinum*	128	7	18.3	117
789	*Terminalioxylon orangensis*	118	16	7.3	194
377	unidentified	128	3	42.6	50
379	unidentified	78	21	3.7	48
497	unidentified	97	12	8.1	63
498	unidentified	81	11	7.3	28
500	unidentified	109	16	6.8	136
786	unidentified	104	14	7.4	102
	Average	108	13	9.8	169

perature was more than 20°C, rainfall was seasonal and less than 1650 mm per annum. From Table VI in Wolfe & Upchurch (1987), the average vessel diameter of the Auchas fossil woods is closest to that of a modern megathermal semi-deciduous dry forest, and Palaeocene and Late Cretaceous megathermal forests. The number of vessels per square mm, the vulnerability index and the conductivity of the Auchas woods is the same as those for Palaeocene forests. Comparing the Auchas figures with those compiled by Wolfe and Upchurch (1987) from the literature, the figures are within the ranges of those for large and medium sized trees in mesic and dry megathermal forests.

This scenario correlates well with the data from the taxonomic comparisons: there is no question of the size of the Auchas trees. Rainfall is less easily interpreted from the wood anatomy alone. Riverine vegetation can take up water from the river whose catchment may be quite distant. A large river needs a considerable source and rainfall to sustain it and may induce a more humid local climate. Mean annual temperature is not easy to determine but there is virtually no latewood. Broad bands of latewood are typical of temperate climates and the absence of latewood is common in tropical climates. Both families have deciduous and non-deciduous members. Overall it is feasible that the trees grew in a mesic to dry megathermal forest somewhere inland from Auchas.

Conclusion

The woods from the Orange River gravel deposits at Auchas in southern Namibia are dated at 19 Ma on the basis of the associated faunal remains (Pickford & Senut 1999). They have been identified as members of two common African families, the Combretaceae and the Burseraceae. As the woods are not identical to modern species they are given generic names for fossil woods with the suffix "-oxylon", namely *Combretoxylon*, *Terminalioxylon* and *Burseroxylon*. They are not identical to any described fossil species so are given new species names.

The woods have been transported down the palaeo-Orange River and deposited in a log jam and then preserved. Preservation occurred after burial because the mineralogy of the pieces of wood is the same and some of the pieces are very large. Transportation of already fossilised wood would result in breakage and not whole logs. Two approaches are used to interpret the palaeoclimate of the region where the trees grew. Comparison of the fossil taxa with modern analogues indicates that the trees grew in wet or drier climates and so is not conclusive. The second approach was to look at the structure of the wood itself. As the function of plant vascular systems is the transport of water, their efficiency should be reflected in their structure. Data have been collected from modern and fossil woods (Wolfe & Upchurch 1987) and by comparing the Auchas woods with this data base it shows that the trees are typical of mesic to dry megathermal forests (Mean Annual Temperature over 20°C, mean annual precipitation of 1650 mm, non-seasonal). The Auchas wood sample is fairly small with 17 woods but they give an indication of the climate.

The fauna from Auchas also indicates a sub tropical environment as crocodiles and large tortoises have been found (Pickford & Senut, 1999; this volume).

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