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A fossil peat deposit from the Late Triassic (Carnian) of Zimbabwe with preserved cuticle of Pteridospermopsida and Ginkgoales, and its geological setting

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Well-preserved cuticular material of Pteridospermopsida and Ginkgoales from the Late Triassic of Zimbabwe is described here for the first time. It is preserved within a brown peat-like lens in the Upper Karoo Angwa Sandstone Formation. The locality is on the Manyima River in the lower portion of the mid-Zambezi Valley of Zimbabwe. Using SEM and light microscopy to identify the taxa, the fragmentary cuticles are of Pteridospermopsida type and have been assigned to *Lepidopteris* sp. (Peltaspermales) and *Dicroidium* sp. A, B, (Corystospermales). Cuticles of the ginkgoalean leaf genus, *Sphenobaiera,* are also described. Well-preserved ovules were found in close association with the cuticles, but as the stomata are not visible they cannot be assigned to any genus. Based on their close similarity to the *Dicroidium* flora of the South African Upper Karoo, the plants are considered to be equivalent to the South African Molteno Formation in age (Carnian). The palynoflora supports this age bracket, as does fauna preserved nearby. The taphonomic process was one of transport, sorting and deposition in a fluvial system.

Keywords: cuticle, Peltaspermales, Corystospermales, ovules, Angwa Sandstone, Late Triassic, Carnian, Molteno, Zambezi Valley.

INTRODUCTION

While prospecting for uranium in the Zambezi Valley of northern Zimbabwe, geologists of the German exploration company Saaberg Interplan Uran GmbH, discovered a coaly outcrop in the bed of the Manyima River (Fig. 1), about 4 km from its confluence with the Angwa River. One of us (T.J.B.) paid an early visit to the site in 1984, at which time the significance of a thin layer of apparently unaltered peat-like plant debris within a carbonaceous shale and mudstone layer was recognized. The locality and its geology were briefly described shortly afterwards by Broderick (1984), and then more formally on a regional basis by Oesterlen (1998). Raath *et al.* (1992) referred to it in their description of the geology and palaeontology of the western Cabora Bassa Basin of the Lower Zambezi Valley, noting that the plant fossils at this locality, and the occurrence in related beds nearby of a diagnostically Late Triassic diapsid reptile, the rhynchosaurian *Hyperodapedon*, supported a Late Triassic (Carnian or younger) age for the beds (see also Lucas & Hancox 2001; Lucas & Heckert 2002). Note, however, that Oesterlen's (1998) map places the rhynchosaur occurrence within the Pebbly Arkose Formation, in a slightly higher stratigraphic position than the Manyima plant locality, which he assigned to the Angwa Sandstone Formation and to which he attached a mid-Triassic age. Yet in an earlier publication (Oesterlen & Millsteed 1994), a palynological assemblage from the Manyima locality confirmed a Late Triassic age for these upper coaly beds within the Angwa Sandstone Formation.

The first description of Triassic fossil plants from Zimbabwe was by Seward & Holttum (1921). Further research was carried out by Walton (1927), du Toit (1927), Lacey (1961, 1970, 1976) and Bond (1965). These authors recorded plants typical of the Molteno Formation, including species of *Dicroidium, Lepidopteris* and *Sphenobaiera* and some other genera of doubtful affinity, from several localities along rivers in the Zambezi Valley. The Manyima leaves are fragmentary but have exceptionally well-preserved cuticles that are described here.

Pollen has also been extracted from the material and it too belongs to the pteridosperms.

GEOLOGICAL SETTING

Geology of the Manyima River fossil locality

The fossil locality is in the bed of the Manyima River in the lower section of the mid-Zambezi Valley, seven kilometres due north of the road bridge across the Angwa River on the main road to Kanyemba (Fig. 1), in sedimentary rocks of Upper Karoo age.

Structurally, this Cabora Bassa section of the mid-Zambezi Valley is an east-trending half-graben, its fundamental active fault being the Zambezi Escarpment Fault flanking the southern margin. Here Upper Karoo rocks and the post-Karoo (Late Jurassic) Dande Formation are in direct contact with Precambrian gneisses of the Zambezi

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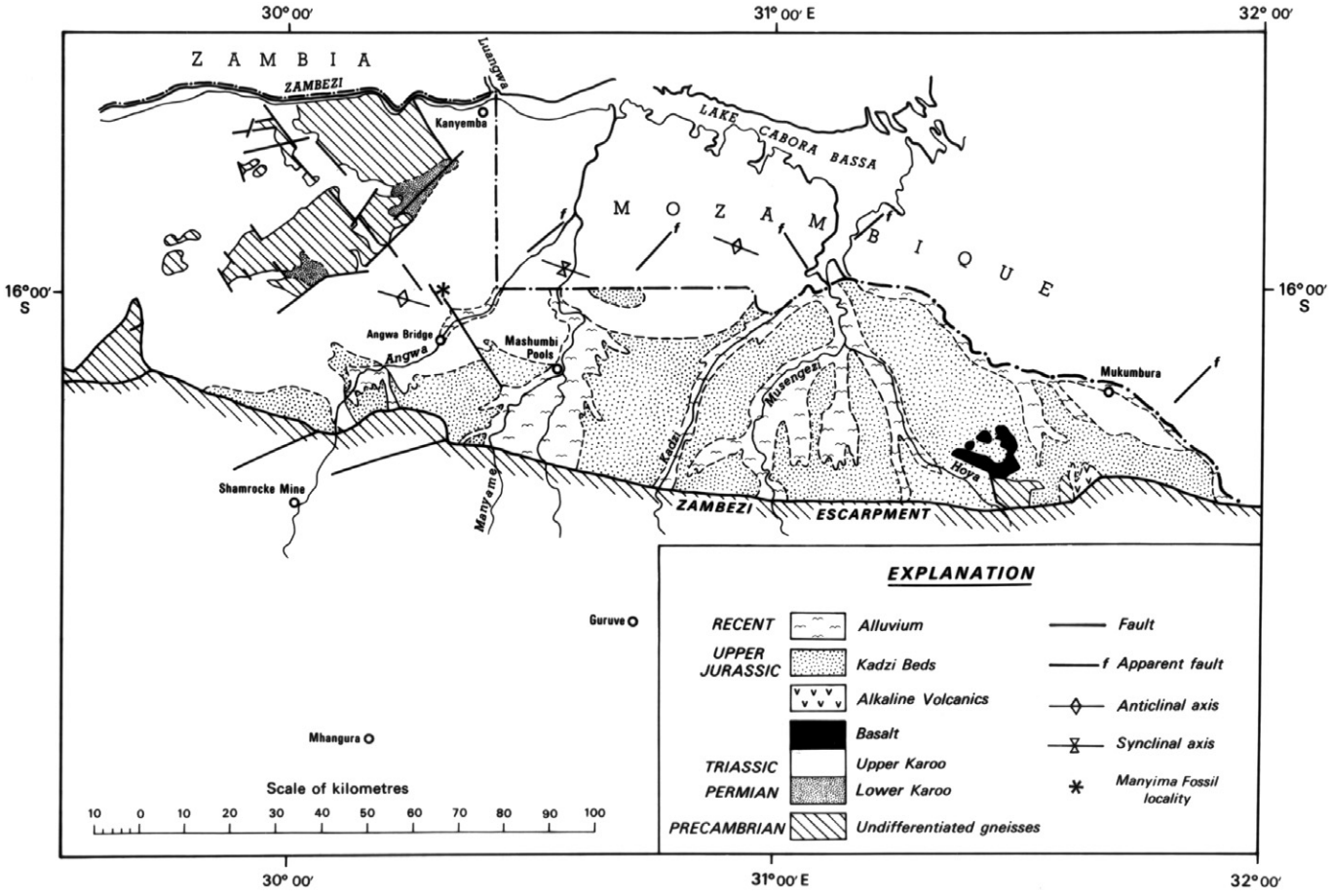


Figure 1. Map showing the geology of the northern portion of the mid-Zambezi Valley, Zimbabwe.

Metamorphic Belt (Fig. 1). Along the northern flank of the Zambezi Valley, in the basin of Lake Cabora Bassa, Lower Karoo glaciogene and Permian coal-bearing sediments appear to overlie the metamorphic basement directly (Broderick 1984). With subsidence, the Karoo sediments have been warped into gentle anticlines and synclines with northwest axial traces lying across the easterly trend of the graben. A number of interference patterns developed within the Upper Karoo sediments, many of them anticlinal or domical and possibly caused by soft sediment slumping during fault movement (L. Zan, pers. comm., 1984). Lower Karoo rocks are rarely exposed in the Zimbabwe section of the Cabora Bassa Basin, but in this area they occur close to and upon gneisses of the Chewore Inliers southwest of Kanyemba (Fig. 1; see also Oesterlen 1998). These horst features were created by northeast and northwest-trending faults operating through post-Karoo times. Farther east, river courses are controlled by northeasterly faults. These may have been responsible for forming secondary cross-graben structures in which a depth to magnetic basement of up to 14 km is reflected (Bosum 1985). Siltstones, sandstones and conglomerates of the post-Karoo Dande Formation have been deposited along the Zambezi Escarpment and over much of the Zambezi Valley east of the Manyame River. Many of the scarp-foot deposits are chaotic boulder conglomerates where the sedimentary sequence has been tilted south towards the Escarpment Fault in the classic roll-back situation found adjacent to graben faulting.

The geology in the vicinity of the Manyima fossil locality is shown in Fig. 2. Upper Karoo sediments underlie the entire area and they show a regional east-southeasterly trend. An older sequence of alternating red to purple or grey mudrocks, commonly ferruginous, and red to brownish-white sandstones are equivalent to the Triassic Molteno Formation of South Africa. They are typical of the Ripple-marked Flags of the Binga District of Zimbabwe and they contain elements of the diagnostic *Dicroidium* flora. Overlying the Molteno-equivalent rocks north of the Manyima bridge are red cross-bedded grits and feldspathic sandstones typical of the Pebbly Arkose Formation of the Middle Zambezi Basin southwest of Kariba. Fine, cross-laminated, biotite-bearing sandstones outcropping at the Manyima site are again seen in outcrop at Angwa Bridge. Two coaly layers were intersected in a water borehole at Chisunga School near the Angwa River 4.5 km east of, and on strike from, the Manyima peat and carbonaceous mudstone outcrop. Four kilometres northeast of the Manyima bridge a domed interference pattern deforms the Karoo sediments. Subsequent faulting has disrupted the Karoo beds and a strong northeast trend is apparent. On the interfluve immediately south of the Manyima River remnants of unconsolidated Kalahari-type or Jesse Sands have been preserved. The river valleys form depositories for thick accumulations of Recent terraced alluvium. However, the Manyima River has incised through this thick cover of alluvium to expose the Karoo sediments in its bed (Fig. 3).

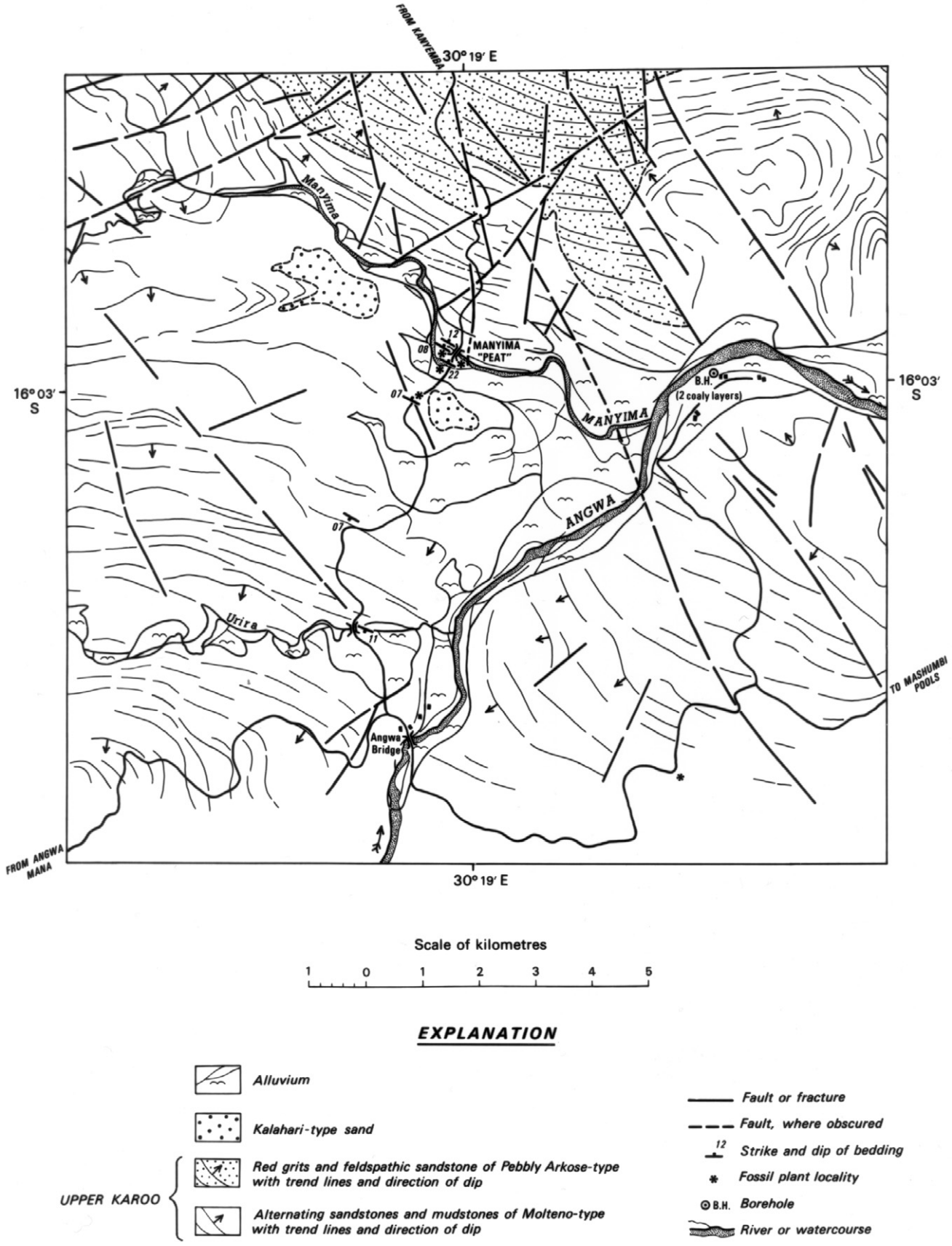


Figure 2. Regional geological map of the area surrounding the Manyima fossil site.

In cliff sections on the meander bends the older dipping sediments are overlain by thick alluvium with an irregular basal contact. A boulder bed about one metre thick marks the base of the alluvium and includes large, disrupted flaggy slabs of the underlying sandstone.

The Karoo beds in the vicinity of the Manyima locality have a consistent strike of 120–125 degrees and they dip at 7–22 degrees to the north-northeast, the greater measurements reflecting oversteepened cross-beds. On the roadside one kilometre south-southwest of the bridge, close to

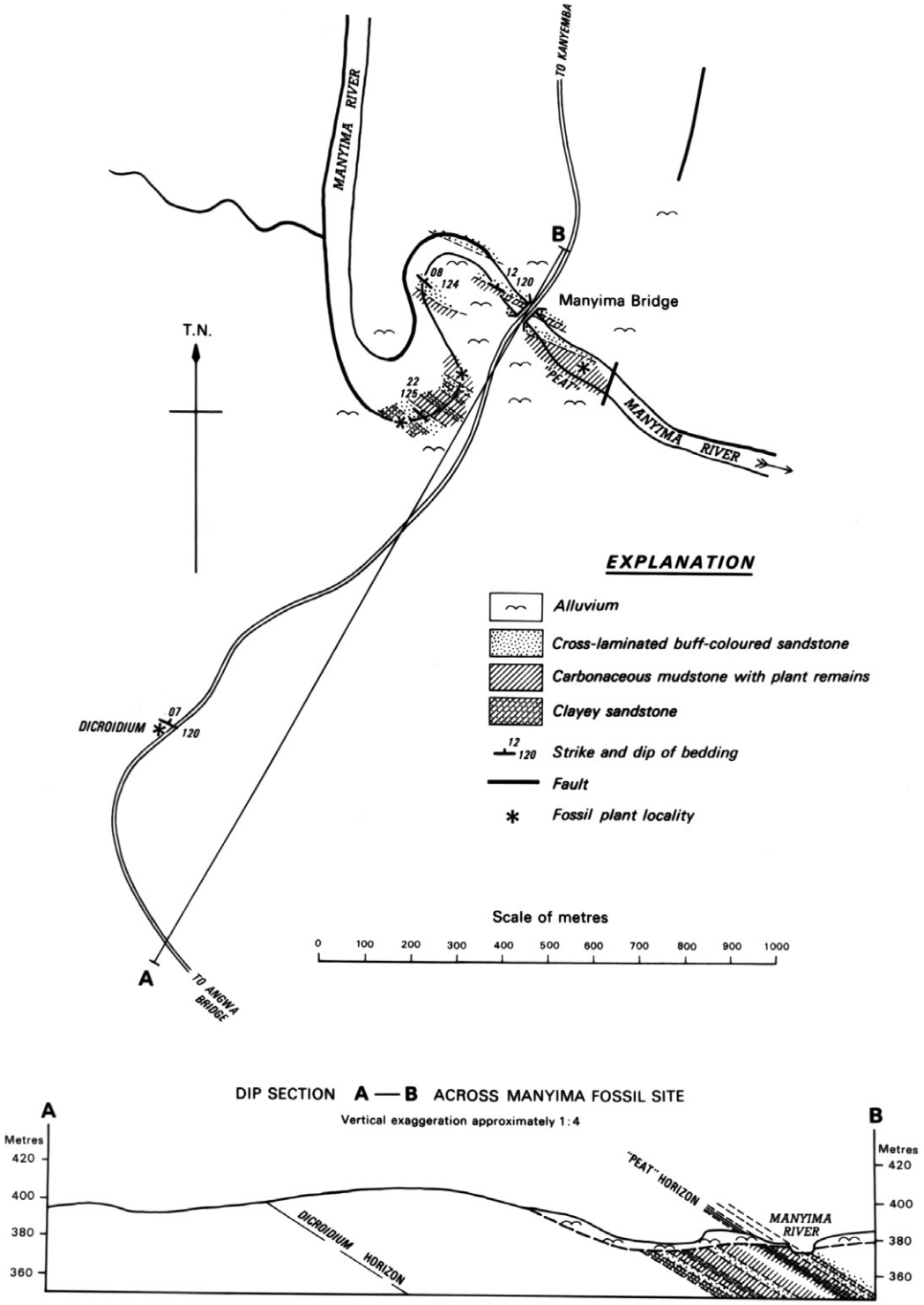


Figure 3. Geological detail at the Manyima fossil locality.

a borrow pit, grey mudstone outcrops with thin fissile, interbedded sandy lenses containing remains of *Dicroidium,* the fructification *Karibacarpon* (Lacey 1976), and *Sphenobaiera.* The relationship of this horizon to the Manyima peat is indicated on the dip section (Fig. 3). The road bridge is founded on two resistant bars of fine- to medium-grained, buff-coloured, finely cross-laminated sandstone in which the laminae are emphasized by the a1ignment of fine flakes of detrital biotite. These sandstones outcrop both upstream and downstream of the bridge and appear as cliff features in the river meander immediately to the northwest. They are flaggy and vertically jointed, which has allowed large slabs to fall away from the face into the river bed. Downstream a north-trending fault with a white siliceous breccia has apparently truncated the sandstone and peat outcrop. The Manyima peat and carbonaceous mudstone unit is sharply overlain by the lower of the two sandstone bars, which is best observed in the river bed and on the right bank directly downstream of the bridge. Here about 1.5 metres of dark grey carbonaceous mudstone gives way downwards to a 1.5 metre-thick layer of finely foliated, friable, carbonaceous material almost entirely made up of plant remains.

An initial examination showed that thin (0.5–2 cm thick) layers and lenses of bright vitrinite having a reflectance value of 0.51 (B. Barber, pers. comm., 1990) are interfoliated within the leafy deposit and, in the more weathered river bank outcrops, they are associated with sulphur encrustation. Vitrinite, indicating diagenesis towards sub-bituminous rank, becomes more apparent towards the base of the plant bed, below which the rock is shaly. Collapse of the overlying sandstone has obscured any further outcrop of the peat in the meander to the northwest, although carbonaceous mudstone was recorded there.

Farther upstream, into the large meander loop which is directed to the south, outcrop has permitted elucidation of the stratigraphy below the peat horizon. The lowest bed exposed comprises a brown, ferruginous clayey sandstone about one metre thick containing poorly preserved specimens of *Sphenobaiera.* This gives way upwards to grey-green mudstone below a 1.5 metre-thick layer of bedded, but weathered, buff-coloured sandstone striking 125 degrees and dipping 23 degrees northeast. A 3.4 metre-thickness of alternating grey and darker carbonaceous mudstone with wedges of fine-grained, yellow, clayey micaceous sandstone occurs below a hard, metre-thick, buff-coloured, cross-bedded and jointed sandstone layer. This jointing has allowed spheroidal weathering to take place and the sandstone beds have broken up in blocky fashion. Above, a thick bed of grey shale containing sandy and carbonaceous lenses is associated with carbon-encrusted plant remains. The relationship of this lower mudstone to the peat horizon above is obscured by alluvium cover.

Palaeoenvironment

There is a repeated sequence of grey to carbonaceous mudstone and shale containing sandy wedges and bars of ripple cross-laminated sandstone in the Manyima deposit. The finer-grained rocks contain abundant plant detritus suggestive of quiet, swampy overbank floodplain and oxbow lake conditions protected by levees, probably in a meandering river system where sandstones are likely to be the product of flood-derived crevasse splays and, to a lesser extent, migrating point bars. The thickest vertical accretion deposit, in which the Manyima peat has been preserved, is in sharp contact with the overlying sandstone. The paucity of well-defined trough cross-bedding, tabular cross-bedding and coarse lag deposits indicates an environment away from any main river channel. The sudden influx of a sand capping allowed for the preservation of the humus-rich accumulation at Manyima, which contains up to 45% of non-combustible ash (W.M. Hamilton, pers. comm., 1984).

MATERIALS AND METHODS

Preservation

The layers of almost pure plant cuticle were collected in blocks upwards through the exposed section by T.J.B. and M.A.R. in 1985.

Their preservation is unusual in that the cuticles have not been lithified and are still brown, flexible and generally translucent. The leaves are fragmentary, the largest ones being incomplete pinnae up to 50 mm long, which is an indication that they have been transported some distance before burial and so represent an allochthonous deposit. The depositional environment was anoxic as there has been little or no degradation of the plant cuticles: there is no evidence of cell wall breakdown, and no discernible fungal, bacterial or insect damage. Mesophyll is absent, but the cuticle fragments are intact.

Preparation of cuticle

The plant material was macerated in the Palaeobotany laboratory of the University of Claude Bernard, Lyon 1, first by addition of 10% HCl to the leaves in a watchglass. Then 20% HF was added in a fume chamber. The material was left in Schultze solution for 3–4 hours to clear the internal organic matter. After neutralising the material with dilute ammonium hydroxide the leaves were carefully teased apart and sorted. Larger leaves were selected because gross morphology is required for identification of taxa. Some leaves were mounted on glass slides in Canada Balsam/glycerine jelly for light microscopy and others were used for SEM.

Scanning electron microscopy

Some pieces of cuticle were selected for observation under the Hitachi S 800 scanning electron microscope at the 'Centre Commun des Microstructures' of the University of Claude Bernard, Lyon 1. After maceration the cuticles were rinsed several times in distilled water. They were mounted on aluminium stubs for SEM by means of double-sided adhesive tape. The samples were then coated with gold in an argon atmosphere to achieve a fine-grained film of 100 Å.

Palynology

Some of the material was prepared for palynological study. It was washed very briefly in 10% HF, neutralized, oxidized with Schultze solution, neutralized with NaOH, then HCl and washed before mounting on glass slides.

SYSTEMATIC STUDY

All the identifiable plant material preserved belongs to the Pteridospermopsida (extinct seed ferns) or the Ginkgoales (maiden hair tree group), which was a more diverse group in the past, with only one species, *Ginkgo biloba* L., remaining today.

Light microscopic study of the cuticular material (Figs 4–23) preceded the SEM studies (Figs 24–32).

Pteridospermopsida
Corystospermales
Dicroidium Gothan 1912

***Dicroidium* sp. A.**, Figs 4 & 5

The fragments of pinnules are broad and show typical venation with a central primary vein and regularly spaced secondary veins arching away to the margins, dichotomising once or twice, close to the midvein and/or close

to the margin. The margins are entire and the pinnae taper gradually to an acute apex. This specimen resembles *D. odontopteroides* forma *odontopteroides* (Anderson & Anderson 1983, plates 32, 54) and *D. dubium* subsp. *dubium* (Anderson & Anderson 1983, plates 33, 52). The laminae are 13 mm wide and those of the specimens illustrated by Anderson & Anderson (1983) range from 4–18 mm, with *D. odontopteroides* forma *odontopteroides* having the wider pinnae. The venation, however, is very similar with a well-developed midrib. *Dicroidium odontopteroides* forma *longifolium* (Anderson & Anderson 1983, plate 66) has similar pinnule widths, but greater lengths than the fragments observed in this collection. The incomplete pinnules without connection to a rachis are impossible to attribute to an established species.

***Dicroidium* sp. B.**, Figs 6 & 7

The Manyima River specimens are 6–8 mm wide, elongate and commonly lack apices. The margins are entire but slightly undulating in some specimens. From the midvein secondary veins depart at an acute angle and bifurcate once before reaching the margin. These narrower and more elongate pinnae resemble *D. odontopteroides* forma *lineatum* (Anderson & Anderson 1983, plates 64–65). The recovered material does not preserve the relation between pinnules on the rachis, so specific attribution is not possible.

Cuticle of *Dicroidium* sp.

The best preserved cuticle fragments are small and without distinctive macromorphological features, so it is difficult to distinguish which cuticle belongs to which leaf type as the two macrofossil species (A and B) are so similar. The general features of the cuticle are described below:

Figures 24–28. The epidermal cells are medium to large, polygonal with 4–6 sides, have straight walls and the haplocheilic, monocyclic stomata are evenly scattered but with a random orientation. Each stoma has 4–5 subsidiary cells, usually with two of these being laterally positioned but sometimes either one or both lateral cells are divided into two. In some cases polar cells are divided into two. Guard cells are more regular in shape. The cuticle is thin and has no ornamentation.

Figure 25 shows one stoma with five subsidiary cells and no clearly positioned lateral or polar cells. The epidermal cell walls are slightly sinuous or just nodular. The stoma in Fig. 26 has two large lateral cells which are aligned with the guard cells, but one of the lateral cells is divided in two. There are two polar cells in Fig. 27 but they are not well aligned. Epidermal cells are large with respect to the guard cells and have more or less smooth walls. The cuticle in Fig. 28 is possibly another type as the guard cells are more prominent and the same size as the epidermal cells.

Peltaspermales

Lepidopteris Schimper 1869

***Lepidopteris* sp.**, Figs 9–13

The pinnae are fragmentary but consist of pieces with up to ten pairs of pinnules in an opposite to sub-opposite arrangement. Pinnules range in size from 1–4 mm wide and 3–8 mm long. The base of each pinnule is attached to the rachis completely and there is even some joining of adjacent laminae for a short distance (Fig. 9). The pinnules are at an acute angle to the rachis and the midveins are simple and central with secondary veins also arising at an acute angle, then travelling straight, or with one dichotomy, which arches slightly downwards, to the entire, undulating or crenate margins. Where present, the small teeth have the secondary vein above this tertiary vein. Between the midvein and most secondary veins there are small resin bodies. Resin bodies are also scattered over the lamina (Fig. 12).

These pinnules are similar to *Lepidopteris ottonis* described by Lundblad in 1950 from the Rhaeto-Liassic flora of Sweden. The specimen in her plate 4, fig. 10, is more complete than our material. However, *L. ottonis* is a typical northern hemisphere species and without fertile structures it is unreasonable to place our specimens in this species.

The specimens assigned to *L. madagascariensis* Carpentier by Anderson & Anderson (1989) on the basis of pinnule size and form are almost identical to the Manyima River material, but there is no preserved cuticle for *L. madagascariensis. Lepidopteris stormbergensis* Anderson & Anderson (*L. natalensis* of Thomas 1933 ex Harris 1926) has mostly larger pinnules and markedly serrate margins and acute apices, but the basal pinnae are smaller, entire and with blunt rounded apices. The cuticle of the Zimbabwe material has strongly papillate sunken stomata with 5–6 subsidiary cells over-arching the aperture (Fig. 23). There are also hair bases or papillae on some of the epidermal cells.

Comparing the Zimbabwe cuticle with other specimens, *L. ottonis* (Harris 1926) has one conspicuous papilla on each epidermal cell. Lundblad (1950) described material attributed to the same species, but it has large epidermal cell papillae which are dark areas with no structure. *Lepidopteris natalensis* (Harris 1926; Thomas 1933, fig. 54) cuticle has the same deeply sunken papillate stomata and sparse papillae on the epidermal cells. The material described here is most similar to *L. natalensis,* but it is too fragmentary for specific designation.

Incertae sedis

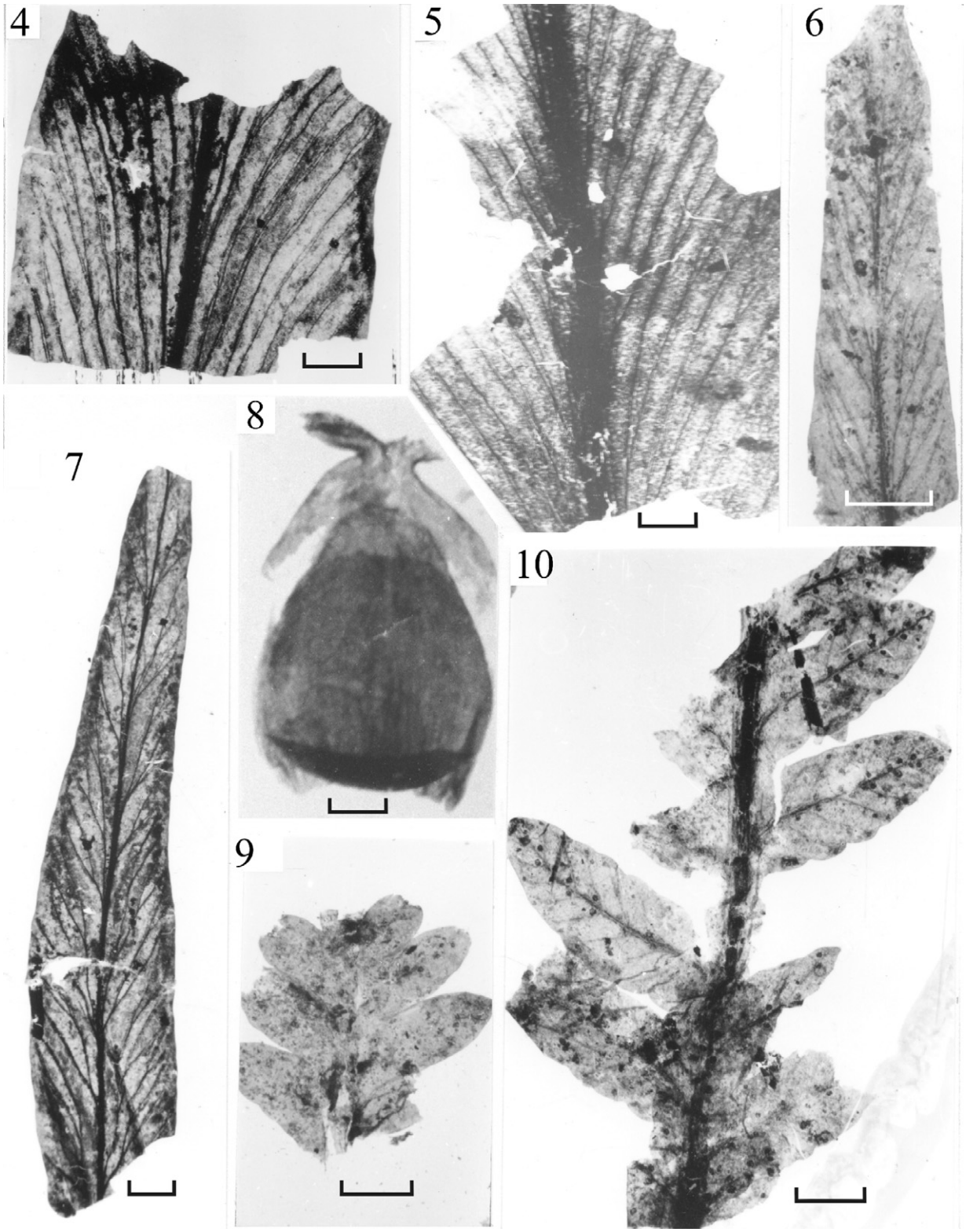
A cross-shaped structure 9 mm in total length, each lobe about 3 mm wide, has a stomatal apparatus identical to that of *Lepidopteris* sp. (Fig. 17) This unknown structure could be a portion of a fertile structure of *Peltaspermum.*

Ginkgoales

Sphenobaiera Florin emend. Harris 1974

***Sphenobaiera* sp.**, Figs 15 & 16

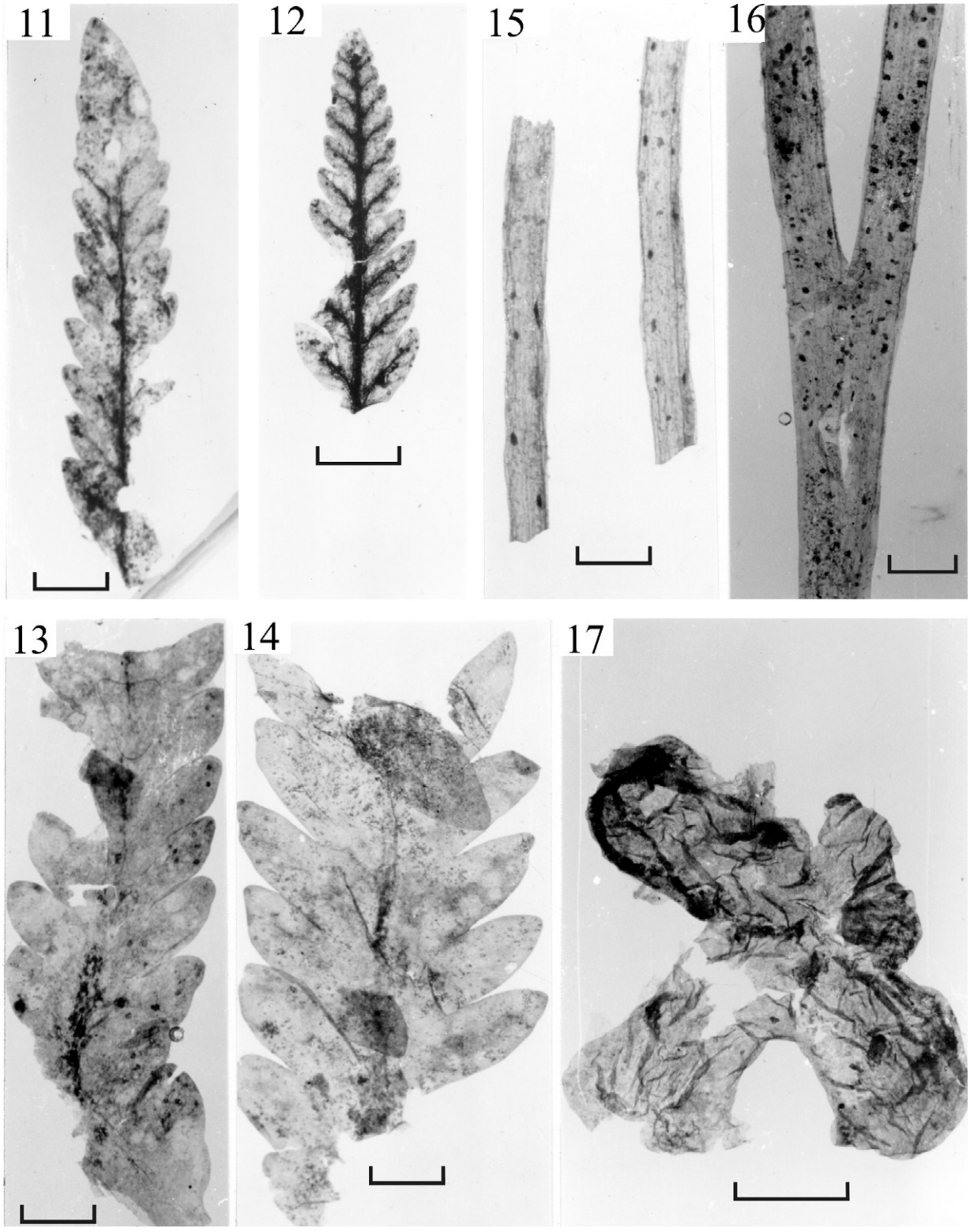
Leaf typically bilobed, narrowly wedge-shaped with basal portion undivided, approximately 10 mm long and 1 mm wide (incomplete fragment). Lobes diverge at about 15 degrees. The lamina is folded longitudinally, so is wider than appears, and no veins are visible. Scattered round to oval resin bodies are present. The cuticle is amphistomatic.



Figures 4–10. Macroplant fossils from the Manyima River. **4**, *Dicroidium* sp. A., fragmentary pinnule showing the venation. **5**, *Dicroidium* sp. A, fragmentary pinnule showing the venation. **6**, *Dicroidium* sp. B., distal part of a pinnule. **7**, *Dicroidium* sp. B., distal part of a pinnule showing venation. **8**, ovule showing the bifid micropylar beak, the integument, nucellus and megaspore. **9**, *Lepidopteris* sp., fragmentary pinna. **10**, *Lepidopteris* sp., fragmentary pinna. All scale bars = 2 mm, except for Fig. 8, which = 500 μm.

Stomata are haplocheilic and arranged in longitudinal bands, probably between veins. Each stoma has elongated subsidiary cells, usually two lateral and two polar, each with rounded or globose papillae over the slightly sunken stoma.

Epidermal cells are also elongated, rectangular, thick and unornamented. Only a few of the epidermal cells are papillate. With the presence of resin bodies in the mesophyll and the linear shape of the leaf, this fragment is characteristic of the Ginkgoales. Because the lamina is divided, the leaf does not belong to the other gingkoalean genera, *Eretmophyllum* Thomas emend. Harris & Millington 1974, *Pseudotoriella* Florin emend. Bose & Manum 1990 or *Nehvidzia* Hlu. *Sphenobaiera* is lobed to

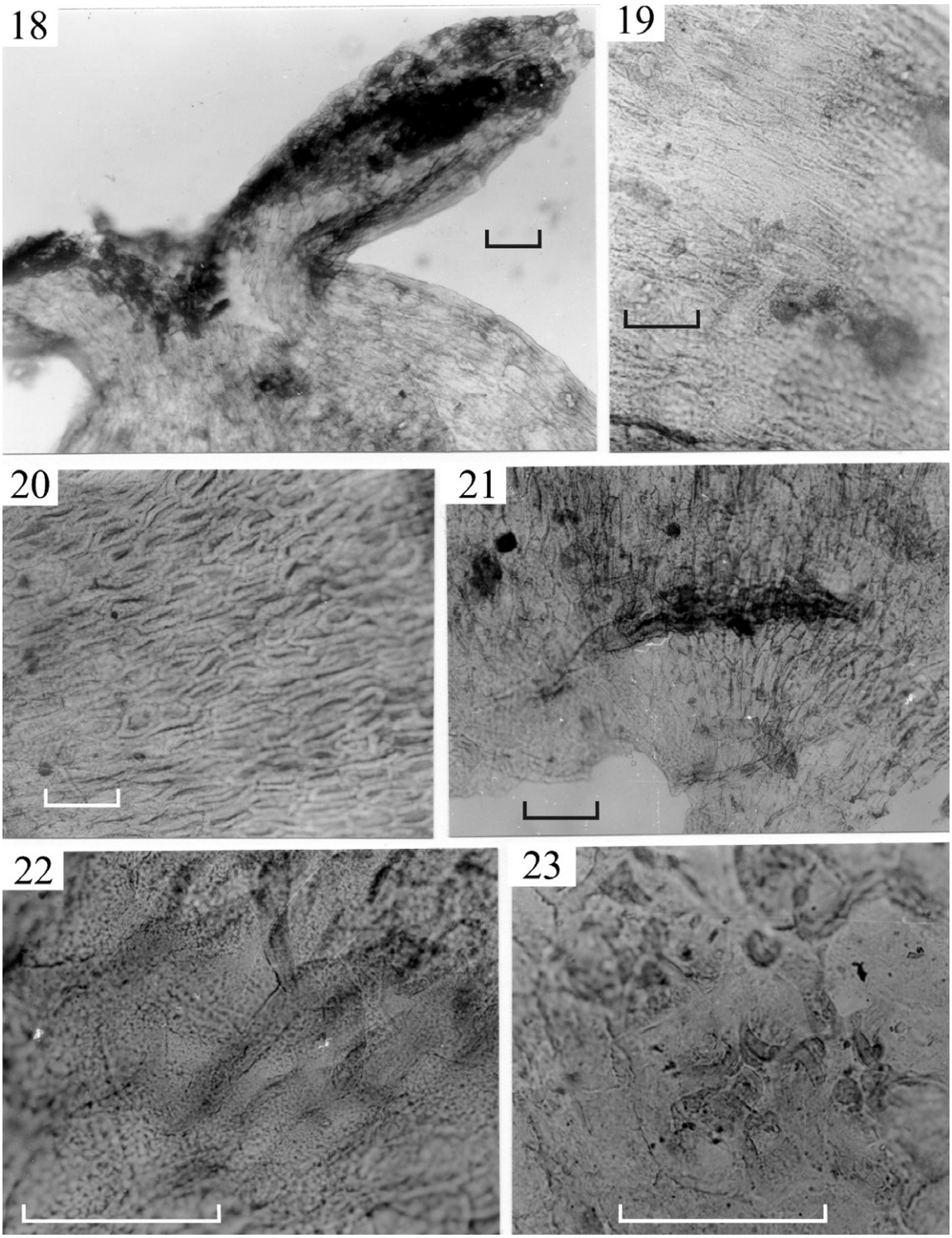


Figures 11–17. Macroplant fossils from the Manyima River. **11**, *Lepidopteris* sp., fragmentary pinna. **12**, *Lepidopteris* sp., fragmentary pinna. **13**, *Lepidopteris* sp., fragmentary pinna. **14**, *Lepidopteris* sp., fragmentary pinna. **15**, *Sphenobaiera* sp., two fragmentary leaves with resin bodies. **16**, *Sphenobaiera* sp., cuticle showing leaf dichotomy with associated resin bodies. **17**, disassociated plant fragment with cuticle showing the characteristics of *Lepidopteris*. All scale bars = 2 mm.

varying degrees. Anderson & Anderson (1989) described many species of *Sphenobaiera,* with six new species from Gondwana. Two of these, *S. pontifolia* and *S. africana* (Baldoni) Anderson & Anderson, have leaves with lobes of the same width. The comparison with northern hemisphere material is more difficult without fertile structures. The cuticles studied here have some affinities with those of *S. africana,* but the stomata seem to differ with the latter having a greater number of subsidiary cells.

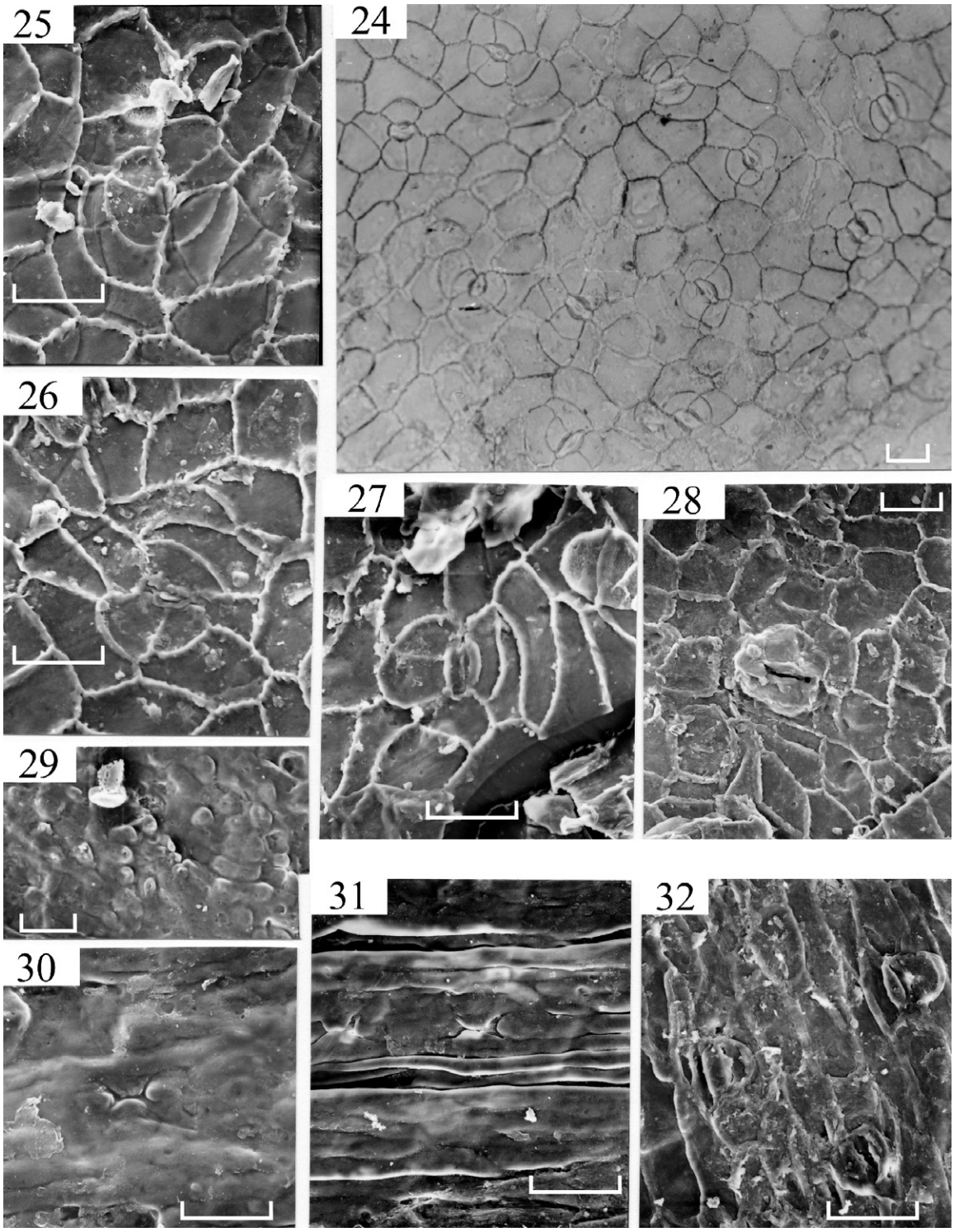
Ovule (Figs 8, 18–22)

These oval structures are 4–7 mm long and 2–4 mm wide, typically with two micropylar beaks at one end, probably flattened (platyspermic) and pear-shaped. Each



Figures 18–23. Cuticular details of the ovule and *Lepidopteris* from the Manyima River. **18**, Epidermal cells near the micropylar beak of the ovule. **19**, integument: epidermal cells of the outer part of the integument. **20**, Nucellus: cells of the nucellus with anticlinal walls. **21**, Integument: the thickened part of the base is of the pollenic chamber. **22**, Megaspore: some folds of the megaspore cuticle are visible but the walls of the cell are not visible. **23**, *Lepidopteris* sp., cuticle showing the stomatal apparatus with papillate subsidiary cells. Scale bars = 100 μm.

ovule consists of an integument with inner and outer cuticles, a nucellus and a megasporangium. Between the inner and outer cuticles of the integument are small resin bodies. The cuticle of the outer integument (Fig. 19) consists of polygonal to rectangular epidermal cells, which at the base of the ovule are irregularly oriented but then converge and eventually are aligned at the micropylar end. The epidermal cells of the inner integument are very delicate. The nucellus comprises polygonal to rectangular cells (3–25 μm wide and 100 μm long), with very thick anticlinal walls (Fig. 20). The base of the pollen chamber is visible as a darker curved ridge or fold (Fig. 21) above which there are pollen grains. The megaspore cuticle is thin and folded but the individual cells are not visible (Fig. 22). The ovules are numerous but not associated with any other particular plant material in this assemblage. In size and shape they strongly resemble seeds of the Corystospermaceae described by Thomas



Figures 24–32. Cuticles of *Dicroidium* and *Sphenobaiera* from the Manyima River. **24**, *Dicroidium* sp., stomatal zone showing numerous scattered stomata (light micrograph). **25**, *Dicroidium* sp., stoma with regular subsidiary cells (internal view of cuticle, SEM). **26**, *Dicroidium* sp., stoma with regular lateral subsidiary and elongated polar subsidiary cells (internal view of cuticle; SEM). **27**, stomata with irregular subsidiary cells (internal view of cuticle; SEM). **28**, *Dicroidium* sp., stoma with broad guard cells (internal view of cuticle; SEM). **29**, *Sphenobaiera* sp., external view of cuticle with papillate epidermal cells (SEM). **30**, *Sphenobaiera* sp., external view of cuticle: stoma with four papillae around the stomatal pit (SEM). **31**, *Sphenobaiera* sp., outer surface of the cuticle showing folds and two stomata with four papillae each (SEM). **32**, *Sphenobaiera* sp., inner surface of the cuticle showing stomata with guard cells (SEM). Scale bars = 50 μm.

(1933, fig. 33) from the Upper Umkomaas Valley in Natal, South Africa. Anderson & Anderson (1983, plate 22) illustrated seeds that have the same morphology, with the characteristic beak and of similar size, but without cuticle preserved. The ovules of *Lepidopteris* figured by Stanislavsky (1976, plate 29, figs 12 & 13) are also similar, but unfortunately they have no preserved cuticle. The ovules described from the Manyima River might also belong to the Peltaspermaceae.

Palynomorphs

Little supra-generic diversity was evident in the assemblage from the Manyima locality, the major miospore component being attributable to non-striate bisaccate

pollen. This group comprised 86.5% of all palynomorphs in the samples studied. The balance was composed of striate bisaccates (8%), trilete spores (3%), plicates (2%) and zonates (0.5%). Identification to species level was hampered by the lack of a well-documented taxonomy for Triassic African miospores. However, identification to genus level was possible for several forms, using Australian references. These included *Pteruchipollenites,* which dominated the non-striate bisaccates (95%), and the striate bisaccate *Lunatisporites.* An interesting palynomorph was *Densoisporites* (*Lundbladispora*) *playfordii,* placed in the Upper Triassic by Balme (1964). Balme (1964) reported that pollen grains of the *Pteruchipollenites*-type become common in continental Triassic microfloras from eastern Australia, and that this palynomorph is overwhelmingly the major component of later Triassic sediments. Many sediments containing this microflora are rich in plant macrofossils of which the most characteristic element is the pteridospermic form-genus of *Dicroidium feistmantel*i-type. Earlier, Thomas (1933) had found occasional specimens of a bisaccate grain resembling *Pteruchus papillatus,* in the Kockatea Shale (Molteno Formation) of Natal. Isolated pollen grains of this type were also recorded by Couper (1958) from the British Jurassic, and were assigned to the genus *Pteruchipollenites.*

In Australia Balme (1964) and Dolby & Balme (1976) recognised two major subdivisions for the Triassic, the *Lunatisporites* (*Taeniaesporite)s* and the *Pteruchipollenites* Microfloral subdivisions. Balme stated that the *Taeniaesporites* Microfloral subdivision presents a major break between Permian and Triassic assemblages, and scarcely has a form in common with the *Dulhuntyispora* Assemblage of the Late Permian. A high proportion and diversity of striate bisaccates is indicative of the Australian Late Permian. This is not true of the Triassic, with only *Lunatisporites (Taeniaesporites*) found in reasonably large numbers. Balme (1964) stated that the occurrence of *Lunatisporites* (*Taeniaesporites)* provides a clear link between the Early Triassic floras of the northern and southern hemispheres. Specialization of this flora is suggested by the lack of diversity and the high pteridophytic component of the miospore assemblage. Such specialization could have been climatically controlled, owing to the change to drier conditions at the end of the Permian.

Pollen of the *Alisporites parvus* de Jersey 1962 type has been recovered from a permineralized *Pteruchus* specimen from Antarctica (Yao *et al.* 1995). The authors reviewed other pollen organs of *Pteruchus* and it appears that the associated pollen types are all bisaccates but with varied ornamentation on the corpus, which for isolated pollen samples would probably be assigned to different taxa.

The oldest occurrence of the *Pteruchipollenites* Microflora reported to date is in the Collaroy Claystone near the top of the Narrabeen Group in the Sydney Basin.(Balme 1964). The abundance of this grain in the Manyima River sediments indicates a correlation with the upper part of the Australian Narrabeen Group. A (tentative) age of 220–230 Ma (Carnian Tethys) is suggested by the Manyima pollen assemblage (Balme 1964) but in more recent publications the Narrabeen Group is Early Triassic (White 1986). *Pteruchus* occurs in middle to Upper Triassic sediments (Yao *et al.* 1995). With such a small sample of pollen it is not possible to attempt closer correlations.

DISCUSSION

The assemblage of plants, determined from the fragmentary macrofossil remains and pollen, is not very diverse as there are only pre-spermatophytes. The presence of typical genera such as *Dicroidium, Lepidopteris* and *Sphenobaiera* is indicative of the classic Carnian Molteno flora. Only the genus *Dicroidium* is typical of Gondwana; the other two genera have a much wider distribution. The association of plants described here is typical of other Molteno-equivalent assemblages already described from Zimbabwe (Lacey 1976), but is less diverse. This is probably a consequence of the fragmentary nature of the plant cuticles, which may not be representative of the whole flora.

The preservation of the material, however, is remarkable, in spite of its fragmentary nature. Plants appear to have been fragmented initially, then transported and sorted before being buried and preserved. The accumulation of leaflets, small stems and ovules evidently represents an assemblage of leaf litter. The fragments appear to have been sorted during transportation, because all are within a limited size range: small pieces of sterile material 1 mm to the largest pinnae 50 mm long occur together with isolated fertile material only a few mm in size. As there is little or no associated sediment within the organic matter, we conclude that the sorting was by gentle water transport rather than by wind.

The sedimentary environment is that of a quiet floodbasin swamp and oxbow lakes associated with a meandering river system. The lenses of organic matter are small and separated by barren sandy lenses, which implies separate events of fluvial activity. More material needs to be collected from different levels and lenses to determine if the depositional setting changed over time. Deposition was under anaerobic conditions and in the absence of microbial and fungal activities. Inclusion of sedimentary particles during deposition of the plants within the peat bed was extremely low. Furthermore, the plant layer consists of cuticle only, so there has been some compression and diagenesis which has removed the mesophyll. The ovules are flattened but have some pollen grains within the pollen chamber. Pollen grains adhere to the outside of some of the cuticle fragments even after chemical treatment.

It would appear that deposition of leaf litter occurred in a low energy environment after transport and sorting by fluvial activity. The concentration of organic material and rapid burial by fluvial sediments has produced this remarkable preservation of Molteno plant fragments.

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