Permo-Triassic palynology and palaeobotany of Zambia: a review

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Permian and Triassic deposits in Zambia have been sporadically researched since the beginning of the 20th century, but there have not been many detailed works on the palaeobotany and palynology of these Karoo-aged rocks. Studies that have been published, suffered from a lack of inter-basinal correlation, which was also hampered by differing stratigraphic subdivisions. We review previous records of palynomorphs, megafloral remains and fossil wood in Zambian Permo-Triassic deposits, present a synthesis of micro- and macrofossil occurrences throughout the country, and propose a standardized subdivision for the Luangwa Valley. This will aid in future correlations between different Karoo basins and act as a framework for future palaeobotanical research in both Zambia and Gondwana.

Keywords: palaeobotany, palynology, Zambia, Permian, Triassic, Karoo.

HISTORICAL SETTING

The famous missionary explorer, David Livingstone, crossed the Luangwa River from the east in December 1866, and reported finding fossil wood in what is now the Munyamadzi Corridor of the Mid Luangwa Valley (Waller 1874). In 1894, the explorer Edward Glave found fossil trees close to the Munyamadzi River and the escarpment in the Mid Luangwa Valley, and another explorer, Cyril Hoste, in 1896, visited the same area and described fossil trees running south for many miles along the foot of the Muchinga Escarpment (Hoste 1898). In 1905, missionary Henry Masters and his wife found fossil trees in the Lukasashi Valley, a minor arm of the Luangwa Valley (Masters & Masters 1920).

Frank Dixey, geologist from the Nyasaland Geological Survey, was the first true fossil hunter to come to the Luangwa Valley. His initial visit in 1928 was a short reconnaissance to the Upper Luangwa Valley around the Sitwe area, collecting a number of Karoo tetrapod and tree fossils (Dixey 1929). In 1935, Dixey returned with a full portered expedition for 4 weeks to the Upper Luangwa Valley, during which time he collected 'well over a ton of fossils', which were carried out on the heads of porters for 60 miles over mountainous country (Dixey 1937). Forty-three samples of fossil wood were sent to the British Museum (Natural History) in London where a report was completed on the fossil wood by W.N. Edwards, entitled 'Fossil woods from the upper Luangwa Valley' (1937).

The Geological Survey Department (GSD) of Northern Rhodesia came into existence in the latter half of 1950 and their geologists were responsible for documenting fossil plants and trees up until the late 1970s. In the early 1950s coal exploration was carried out during the dry season in the mid-Zambezi Valley by GSD geologists Harry Gair and Ron Tavener-Smith. Both men found fossil wood in abundance, Gair in the area of what is now known as Chirundu Fossil Forest, a proposed World Heritage site (Fig. 1), and Tavener-Smith at two areas southeast of Gwembe.

Two GSD geologists, Reichwalder and Brandon, worked in the Luano Valley between 1972 and 1974, where they found fossil plants and silicified trees in Karoo sediments (Reichwalder & Brandon 1978).

Between 1959 and 1973 British biologist William Astle worked with the National Parks & Wildlife Department, and he and his Scouts were responsible for finds of fossil plants and trees in the Mid Luangwa Valley area (Fig. 2), many inside South Luangwa National Park (Astle 1999).

Most recently, Professor Tom Kemp and others carried out a fossil recce in 2000 to several of the fossil tetrapod localities visited by the Oxford University Museum expedition in 1974, and found an extensive fossil tree site between the Mwaleshi and Mulandashi Rivers in North Luangwa National Park (Kemp 2000).

GEOLOGICAL CONTEXT

Karoo-aged deposits are widespread in Zambia, and fossils are known from the Permian and Triassic rocks of the mid-Zambezi and Luangwa-Lukasashi-Lunsemfwa Basins, shaded in dark grey (Fig. 3).

Over the years various authors have made use of slightly different naming conventions for the different sub-divisions of the Luangwa Valley, complicating correlation. In this paper a standardized division of the Luangwa Valley is proposed as follows (Fig. 4):

Figure 1. Transporting pieces of fossil wood from Chirundu Fossil Forest to display outside the Geological Survey Department, Lusaka, Zambia. Photographs by Harry Gair.

Figure 2. Fossil wood in the Mid Luangwa Valley. Photographs by William Astle.

- Upper Luangwa Valley – source (Mafinga Hills) to northern boundary of North Luangwa National Park (NLNP) (='North Luangwa Valley' of Utting).
- Mid Luangwa Valley – North Luangwa National Park (NLNP), Munyamadzi Corridor, South Luangwa National Park (SLNP) to Ndevu Gorge, Kampeketa Range.
- Lower Luangwa Valley – Ndevu Gorge to Zambezi confluence.

The Upper Luangwa Valley was previously subdivided by Banks *et al.* (1995) into a northern and southern sub-basin separated by a wide transfer zone, but the authors did not clearly delineate the southern boundary of the northern sub-basin. The southern sub-basin is shown as ending in the vicinity of the Ndevu Gorge, meaning that the Luangwa deposits south of Ndevu Gorge stretching down to the Zambezi confluence (some few hundred kilometres) were not recognized by Banks and colleagues, despite the fact that extensive Karoo outcrop exists there.

The demarcation of Upper and Mid sections is to create a much-needed division between the classic 'Upper Luangwa Valley' of Drysdall & Kitching, Dixey, and Utting, and the middle reaches of the Luangwa Valley north of the Ndevu Gorge. The northern boundary of North Luangwa NP was chosen to form an expedient physical boundary (within the northern extremity of the 'transfer zone' of Banks *et al.*) to the west of the Luangwa River for the Upper Luangwa Valley division.

Ndevu Gorge is a natural geographical and geological end to the classic rift-like Luangwa Valley upstream of it, in that the wide, flat rift valley-like floor comes to an abrupt end with the Kampeketa range of hills, and the Luangwa is funnelled into a narrow rocky gorge before emerging just upstream of the confluence with the Lunsemfwa River, a major tributary. Accordingly it has been selected to form the southern boundary of the Mid Luangwa Valley.

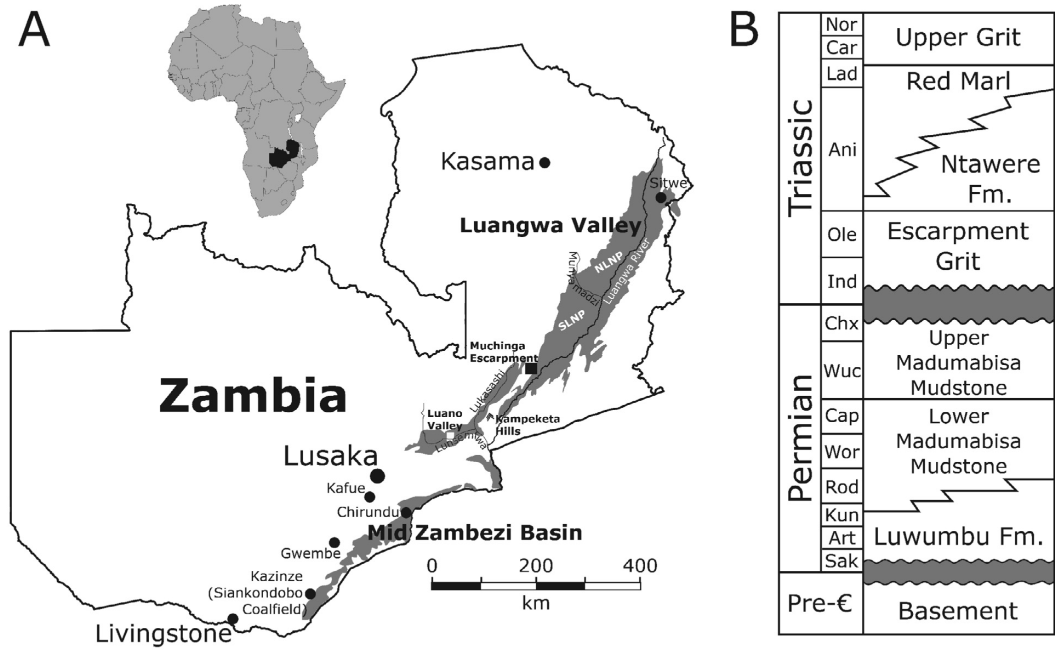

Figure 3. **A**, Map of Karoo fossil localities referred to in the text; **B**, generalized stratigraphy of Permo-Triassic rocks in Zambia (modified from Angielczyk *et al.* 2014 and Sidor *et al.* 2014). Karoo deposits are shaded in dark grey.

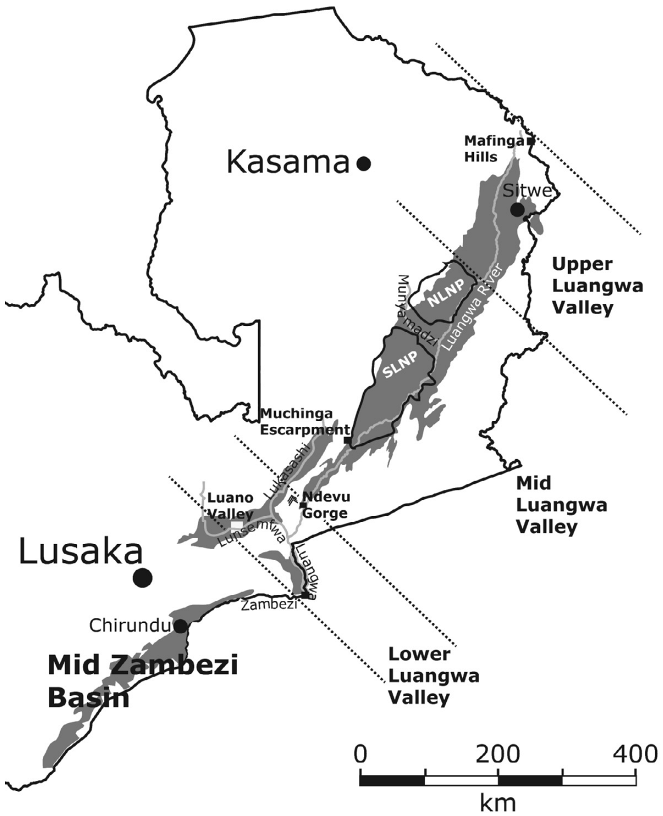

Figure 4. Proposed subdivision for the Luangwa Valley, showing delineations of the Upper, Mid and Lower Luangwa areas. Karoo deposits are shaded in dark grey.

PALYNOLOGY

Palynological research has mostly been carried out in Zambia by John Utting. He did his Ph.D. thesis in 1970 on the stratigraphy and palynology of the Upper Luangwa Valley, and palynology of the Siankondobo coalfield of the mid-Zambezi Valley. As well as pollen samples, Utting also collected megafloral remains, petrified wood and lamellibranchs (Fig. 5; palaeobotany discussed later in the text), of which the former two were identified by C.S. Smith and W.S. Lacey.

Samples from Upper Karoo rocks (Escarpment Grit, Ntawere Formation, Red Marl and Upper Grit; Fig. 3) in the Upper Luangwa Valley were palynologically barren, while the Lower Karoo formations were more productive (Luwumbu Coal Formation and Lower and Upper Madumabisa Mudstone). In the Luangwa Valley, the lowermost productive unit, the Mukumba Siltstone Member, is dominated by monosaccate pollen (approximately 80%) along with trilete spores (13%) and the remainder comprising non-striate bisaccate, monocolpate and alete forms.

The monosaccates *Elilasaccites elilaensis*, *Cannanoropollis obscurus*, *Plicatipollenites indicus* and *Scheuringipollenites ovatus* (*Vesicaspora ovata*) are common, as are *Punctatisporites gretensis*, *Granulatisporites micronodosus*, *Retusotriletes diversiformis*, *Apiculatisporis filiformis*, *Acanthotriletes tereteangulatus* (recombined to *Anapiculatisporites tereteangulatus* by Playford & Dino 2002), *Cycadopites cymbatus* and *Quadrisporites horridus* (Table 1). These forms are also all found in the overlying Mpwashi Carbonaceous Member, but quantitatively this unit is very different. The lower Mpwashi Carbonaceous Member contains trilete, monolete, monosaccate, bisaccate (striate and non-striate) and polyplicate forms, none of which exceeds 25% of the assemblage. This changes in the middle part of the Mpwashi Carbonaceous Member to a predominance of triletes and striate bisaccates, with approximately 10% colpate forms (mainly *Marsupipollenites striatus*). The upper part of the Mpwashi Carbonaceous Member has common bisaccate striate and non-striate forms, the latter of which are mainly *Scheuringipollenites* (= *Vesicaspora*), and triletes make up 20–25% of the assemblages (Table 1).

Borehole samples from the Siankondobo coalfield of the mid-Zambezi Valley, Gwembe Coal Formation were also examined, and this unit displays marked qualitative

Zambian Stratigraphy	Plants	Wood	Vertebrates	Lamellibranchs	Palynomorphs	South African Correlatives
Upper Grit		cf. *Dadoxylon bougheyi* cf. *Araucarioxylon* sp. A				STORMBERG
Red Marl						Molteno
Ntawere Formation	cf. *Schizoneura carreri* cf. *Lepidopteris africanum* cf. *Dicroidium narrabeenensis*					Upper Beaufort *Cynognathus* Zone
Escarpment Grit						Middle Beaufort *Lystrosaurus* Zone
Upper Madumabisa Mudstone	*Glossopteris sp.* *Glossopteris* cf. *indica* ? *Glossopteris decipiens*/ *Gangamopteris cyclopteroides* *Noeggerathiopsis hislopi, N. stoliczkana* *Samaropsis* sp.	cf. *Dadoxylon bougheyi*	Dicynodonts	Lamellibranchs Lamellibranchs	*Guttulapollenites hannonicus* *Lueckisporites nyakapendensis* *Vittatina africana* *Densipollenites indicus*	Lower *Cistecephalus* Zone Beaufort *Endothiodon* Zone *Tapinocephalus* Zone
Lower Madumabisa Mudstone		*Dadoxylon nicolii* *Dadoxylon lukugense*			*Guttulapollenites hannonicus* *Vittatina africana*	
Fimbia Grit Member						
Mpwashi Carbonaceous Member	*Vertebraria indica, V.* sp. *Glossopteris browniana, G.* sp., *G.* cf. *ampla, G. indica, G. stricta* ? *Gangamopteris* *Noeggerathiopsis hislopi, N.* sp. *Paracalamites australis*, cf. *Phyllotheca* *Stellotheca robusta* ? *Schizoneura gondwanensis* *Sphenopteris* sp. *Cordaicarpus* sp. cf. *Annularia sphenophylloides* *Samaropsis* cf. *etheridgei*				*Protohaploxypinus limpidus* *P. amplus* *Pityosporites leschiki* *Striatopodocarpites lemniscata* *S. gondwanensis*	ECCA
Mukumba Siltstone Member					*Elilasaccites* cf. *elilaensis* *Quadrisporites horridus* *Cannanoropollis obscurus* *Plicatipollenites indicus*	DWYKA / ECCA
Musipizi Conglomerate Member	Indet. fragments	Indet. fragments				

Figure 5. Stratigraphic occurrences of palynomorphs, macroplant and vertebrate fossils in Karoo deposits of Zambia (redrawn from Utting 1970 with taxonomic modifications by Lacey & Smith 1972; Lacey 1974).

differences between the upper, middle and lower parts. The lower Gwembe Formation is dominated by trilete spores, with small proportions of monoletes, monosaccates and bisaccates. In the middle Gwembe Formation, triletes decrease markedly and non-striate bisaccate forms, mainly *Scheuringipollenites* (= *Vesicaspora*) are dominant in some samples. The upper Gwembe Formation contains common triletes again as well as alete forms, while all other groups are either present in minor proportions or entirely absent. Utting attributed these marked quantitative changes to a change of facies that occurs from the top to the bottom of the Gwembe Formation. Megaspores were also recovered from the Gwembe Coal formation, and tentatively identified by Dr E. Spinner of the Department of Geology, University of Sheffield. Taxa include *Carruthersiella* cf. *trivedii* Pant and Srivastava, 1962 (= *Biharisporites trivedii* (Dykstra) Pierart 1961), *Duosporites* sp., *Cystosporites* sp., and *Mammilaespora* cf. *superba* Pant and Srivastava, 1961.

The Lower Madumabisa Mudstone is quantitatively very different from the underlying Mpwashi Carbonaceous Member and dominated by *Guttulapollenites hannonicus* and *Vittatina africana*, along with other bisaccate striate and non-striate taxa such as *Protohaploxypinus amplus*, *P. limpidus*, *P. goraiensis*, *Striatopodocarpites lemniscata* and *Scheuringipollenites ovatus* (Table 1). Upper Madumabisa Mudstone samples were from the area mapped by Drysdall and Kitching in 1963, said to be from the *Cistecephalus* zone. They are dominated by taxa such as *Lueckisporites nyakapendensis*, *Vittatina africana*, *Guttulapollenites hannonicus*, *Protohaploxypinus limpidus* and *Densipollenites indicus* (Table 1). Both the Lower and Upper Madumabisa assemblages are similar in species composition, but can be differentiated on the high proportion of *L. nyakapendensis* in the Upper unit.

The Mukumba Siltstone assemblage can be correlated with that of the Elila River glacial and periglacial beds, Congo (Bose & Kar 1966). Palynomorphs of the Mpwashi Carbonaceous Member in the Luangwa Valley are similar to those of the lower and middle Gwembe Coal Formation, mid-Zambezi Valley, Zambia. The upper Mpwashi Carbonaceous Member and lower to middle Gwembe Coal Formation are palynologically comparable to the K_2e_2 complex, Ketewaka-Mchuchuma coalfield, Tanzania (Hart 1965), and the lower part of the Mpwashi Carbonaceous Member is similar to K_2e_1. Assemblages from the upper part of the Gwembe Coal Formation resemble those from the Black Shales of Lukuga, Congo (Kar & Bose 1967). Palynomorphs of the Madumabisa Mudstone assemblages can be correlated with those from the Lower Sakamena Beds of Madagascar (Goubin 1965). In particular, the *Cistecephalus* zone of the Upper Madumabisa Mudstone has been tentatively correlated with zone IsC in the upper part of the Lower Sakamena beds, Madagascar.

Utting (1976) extended his doctoral research by sampling the type sections of the Mpwashi Carbonaceous and Mukumba Siltstone members of the Upper Luangwa Basin. In a paper published in 1976 he described two distinct palynological assemblages, with the lower Mukumba Siltstone Member dominated by the monosaccates *Cannanoropollis* and *Plicatipollenites*, and the overlying Mpwashi Carbonaceous Member (containing thin coal seams) yielding a diverse microflora dominated by striate and non-striate bisaccate pollen and trilete spores, but also containing monosaccates, polyplicates, colpates, monolete and alete spores (Table 2). The most common taxa are *Protohaploxypinus*, *Scheuringipollenites* (= *Vesicaspora*) and *Acanthotriletes*, while *Cannanoropollis* is abun-

Table 1. Palynomorphs of the Upper Luangwa and mid-Zambezi Valleys. Redrawn from Utting (1970).

	LUANGWA VALLEY		MID-ZAMBEZI VALLEY	LUANGWA VALLEY	
	Mukumba Siltstone Member	Mpwashi Carbonaceous Member	Gwembe Coal Formation	Lower Madumabisa Mudstone	Upper Madumabisa Mudstone
Anapiculatisporites tereteangulatus Playford & Dino 2002 (= *Acanthotriletes tereteangulatus* Balme & Hennelly 1956)	X	X	X		
Anaplanisporites levis Balme & Hennelly 1956		X	X		
Baculatisporites bharadwaji Hart 1963		X	X		
Brevitriletes cornutus (Balme & Hennelly) Backhouse 1991 (= *Apiculatisporis cornutus* (Balme & Hennelly) Høeg and Bose 1960)		X	X		X
Boutakoffites elongates Bose & Kar 1966		X	X		
Cannanoropollis (= *Virkkipollenites*) *corius* Bose & Kar 1966			X		
Cannanoropollis janaki Potonié & Sah 1960 (= *Virkkipollenites obscurus* Lele 1964)	X	X	X		
Converrucosisporites pseudoreticulatus (Balme & Hennelly) Modie 2007 (= *Verrucosisporites pseudoreticulatus* Balme & Hennelly 1956; *Pseudoreticulatispora pseudoreticulata* (Foster & Waterhouse) Millsteed 1999)		X	X		
Cycadopites cymbatus (Balme & Hennelly) Segroves 1970	X	X	X		
Cycadopites nevesii (Hart) Hart 1965		X	X		
Deltoidospora lukagaensis (Kar & Bose) Falcon 1975 (= *Leiotriletes lukagaensis* Kar & Bose 1967)			X		
Deltoidospora directa (Balme & Hennelly) Norris 1965 (= *Leiotriletes directus* Balme & Hennelly 1956)		X	X		
Densipollenites indicus Bharadwaj 1962					X
Diatomozonotriletes sp. (Naumova) Playford 1963			X		
Elilasaccites elilaensis Bose & Kar 1966	X	X			
Granulatisporites micronodosus Balme & Hennelly 1956	X	X	X		
Granulatisporites trisinus Balme & Hennelly 1956		X	X		X
Greinervillites sp. Bose & Kar 1967			X		
Guttulapollenites hannonicus Goubin 1965				X	X
Horriditriletes filiformis (Balme & Hennelly) Backhouse 1991 (= *Apiculatisporis filiformis* Balme & Hennelly 1956; *Acanthotriletes filiformis* (Balme & Hennelly 1956) Tiwari 1965)	X	X	X		
Horriditriletes ramosus (Balme & Hennelly) Bharadwaj & Salujha 1964 (= *Neoraistrickia ramosa* (Balme & Hennelly) Hart 1960)		X	X		
Incertae sedis A			X		
Incertae sedis B			X		
Kraeuselisporites apiculatus Jansonius 1962		X	X		
Laevigatosporites desmoinesensis (Wilson & Coe) Schopf, Wilson & Bentall 1944		X	X		
Lophotriletes rectus Bharadwaj & Salujah 1964		X	X		
Lueckisporites nyakapendensis Hart 1960		X		X	X
Lycospora sp. A Schemel 1951			X		
Marsupipollenites striatus (Balme & Hennelly) Hart 1965		X			
Microbaculatisporites gondwanensis Bharadwaj 1962			X		
Parasaccites sp. Bharadwaj & Tiwari 1964	X	X	X		
Pilasporites calculus Balme & Hennelly 1956		X	X		

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Table 1 (continued)

	LUANGWA VALLEY		MID-ZAMBEZI VALLEY	LUANGWA VALLEY	
	Mukumba Siltstone Member	Mpwashi Carbonaceous Member	Gwembe Coal Formation	Lower Madumabisa Mudstone	Upper Madumabisa Mudstone
Pityosporites fuscus Utting 1970				X	X
Pityosporites leschiki Hart 1964		X	X		
Plicatipollenites indicus Lele 1964	X	X	X		
Potonieisporites granulatus Bose & Kar 1966		X	X		
Primuspollenites levis Tiwari 1964		X	X		
Protohaploxypinus amplus (Balme & Hennelly) Hart 1964		X	X	X	X
Protohaploxypinus goraiensis Hart 1964		X	X	X	X
Protohaploxypinus limpidus (Balme & Hennelly) Balme & Playford 1967		X	X	X	X
Protohaploxypinus perfectus (Naumova ex Kara-Murza) Samoilovich 1953			X		
Protohaploxypinus samoilovichii (Jansonius) Hart 1964		X			
Punctatisporites gretensis Balme & Hennelly 1956	X	X	X		
Quadrisporites horridus (Hennelly) Potonié & Lele 1961	X		X		
Retusotriletes diversiformis (Balme & Hennelly) Bharadwaj 1962	X	X	X		
Scheuringipollenites maximus (Hart) Tiwari 1973 (= *Vesicaspora potoniei* Lakhanpal, Sah & Dube 1960)		X	X	X	X
Scheuringipollenites ovatus (Balme & Hennelly) Foster 1979 (= *Vesicaspora ovata* (Balme & Hennelly) Hart 1960)	X	X	X	X	X
Striatopodocarpites communis (Wilson) Hart 1964		X			X
Striatopodocarpites gondwanensis (Lakhanpal, Sah & Dube) Hart 1964		X	X		
Striatopodocarpites lemniscata (Wilson) Hart 1964		X	X	X	X
Striatopodocarpites secretus (Bharadwaj) Hart 1964		X			
Striomonosaccites sp. Bharadwaj 1962					X
Tetraporina horologia (Staplin) Playford 1963			X		
Triquitrites verrucosus Alpern 1958			X		
Verrucosisporites trisecatus Balme & Hennelly 1956			X		
Vestigisporites hennellyi Hart 1960		X			
Vestigisporites methoris Hart 1960		X	X		
Vestigisporites thomasi (Pant) Hart 1960		X			
Vittatina africana Hart 1966		X		X	X
Vittatina africana Hart 1966 (withdrawal of intexine)					X
Vittatina subsaccata (Samoilovich) Jansonius 1962		X			
Zinjispora zonalis Hart 1963		X			

dant in the lower section of the younger assemblage. The microfloras show similarities to the upper part of the Lower Coal Measures of the Ketewaka/Mchuchuma coalfield of Tanzania, but an age for the Luwumbu Coal Formation was not able to be confidently determined based on the palynology.

A species comparison of the palynological assemblages obtained by Utting in 1970 and 1976 (Table 3) shows 8 species in common for the samples from the lower Mukumba Siltstone (combined total of 43 species), and 26 species in common from the overlying Mpwashi Carbonaceous Member (combined total of 107 species). This low overlap of taxa suggests localized microhabitats in the Luangwa Valley during Permian times.

Utting (1978) recorded the palynology of three boreholes in the Lower Karoo Siankondobo Sandstone and Gwembe Coal formations (comprising the Maamba Sandstone Member, Main Coal Seam and Carbonaceous

Table 2. Qualitative comparison of the Mukumba and Mpwashi assemblages of the Upper Luangwa Valley. Redrawn from Utting (1976).

	Mukumba Siltstone Member	Mpwashi Carbonaceous Member
Botryococcus sp. Kützing 1849	+	–
Cannanoropollis densus (Lele) Bose & Maheshwari 1968	+	–
Høegiasaccites transitus Bose & Kar 1966	+	–
Lunatisporites brevis Bose & Kar 1966	+	–
Pityosporites cf. *P. lucidus* Hart 1965	+	–
Plicatipollenites trigonalis Lele 1964	+	–
Converrucosisporites naumoviae (Hart) Backhouse 1991 (= *Verrucosisporites naumovae* Hart 1963)	+	–
Vittatina sp. Luber ex Jansonius 1962	+	–
? *Granulatisporites trisinus* Balme & Hennelly 1956	+	+
Anapiculatisporites tereteangulatus Playford & Dino 2002 (= *Acanthotriletes tereteangulatus* Balme & Hennelly 1956)	+	+
Cannanoropollis (= *Virkkipollenites*) *corius* Bose & Kar 1966	+	+
Cannanoropollis mehtae (Lele) Bose & Maheshwari 1968	+	+
Cannanoropollis janaki Potonié & Sah 1960 (= *Virkkipollenites obscurus* Lele 1964)	+	+
Cycadopites cymbatus (Balme & Hennelly) Segroves 1970	+	+
Cyclogranisporites gondwanensis Bharadwaj & Salujha 1964	+	+
Deltoidospora directa (Balme & Hennelly) Norris 1965 (= *Leiotriletes directus* Balme & Hennelly 1956)	+	+
Deltoidospora lukagaensis (Kar & Bose) Falcon 1975 (= *Leiotriletes lukagaensis* Kar & Bose 1967)	–	+
Deltoidospora (= *Leiotriletes*) *plicatus* Maheshwari & Bose 1969	+	+
Granulatisporites micronodosus Balme & Hennelly 1956	+	+
Horriditriletes filiformis (Balme & Hennelly) Backhouse 1991 (= *Apiculatisporis filiformis* Balme & Hennelly 1956; *Acanthotriletes filiformis* (Balme & Hennelly 1956) Tiwari 1965)	+	+
Neoraistrickia congoensis Kar & Bose 1967	+	+
Parasaccites bilateralis Tiwari 1965	+	+
Pilasporites plurigenus Balme & Hennelly 1956	+	+
Plicatipollenites gondwanensis Lele 1964	+	+
Plicatipollenites indicus Lele 1964	+	+
Protohaploxypinus limpidus (Balme & Hennelly) Balme & Playford 1967	+	+
Punctatisporites gretensis Balme & Hennelly 1956	+	+
Punctatisporites minutus (Kosanke) Peppers 1964	+	+
Scheuringipollenites ovatus (Balme & Hennelly) Foster 1979 (= *Vesicaspora ovata* (Balme & Hennelly) Hart 1960)	+	+
Converrucosisporites pseudoreticulatus (Balme & Hennelly) Modie 2007) (= *Verrucosisporites pseudoreticulatus* Balme & Hennelly 1956; *Pseudoreticulatispora pseudoreticulata* (Foster & Waterhouse) Millsteed 1999)	+	+
Vestigisporites methoris Hart 1960	+	+
Zinjisporites eccensis Hart 1965	+	+
Acanthotriletes bellus Bose & Kar 1966	–	+
Acanthotriletes sp. Naumova ex Potonié & Kremp 1954	–	+
Brevitriletes cornutus (Balme & Hennelly) Backhouse 1991 (= *Apiculatisporis cornutus* (Balme & Hennelly) Høeg and Bose 1960)	–	+
Baculatisporites bharadwaji Hart 1963	–	+

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Table 2 (continued)

	Mukumba Siltstone Member	Mpwashi Carbonaceous Member
Brevitriletes levis (Balme & Hennelly) Bharadwaj & Srivastava 1969 (= *Apiculatisporis levis* Balme & Hennelly 1956)	–	+
Cirrabaculisporites praeclarus Maheshwari & Bose 1969	–	+
Cirratriradites africanensis Hart 1963	–	+
Cycadopites nevesii (Hart) Hart 1965	–	+
Grandispora dwykensis Hart 1963	–	+
Greinervillites sp. Bose & Kar 1967	–	+
Hamiapollenites karrooensis Hart 1964	–	+
Hamiapollenites sp. (Wilson) Tschudy & Kosanke 1966	–	+
Laevigatosporites minor Loose 1934	–	+
Latosporites colliensis (Balme & Hennelly) Bharadwaj 1962	–	+
Lueckisporites nyakapendensis Hart 1960	–	+
Marsupipollenites striatus (Balme & Hennelly) Hart 1965	–	+
Horriditriletes ramosus (Balme & Hennelly) Bharadwaj & Salujha 1964 (= *Neoraistrickia ramosa* (Balme & Hennelly) Hart 1960)	–	+
Piceapollenites sp. Potonié 1931	–	+
Pityosporites leschikii Hart 1964	–	+
Protohaploxypinus amplus (Balme & Hennelly) Hart 1964	–	+
Protohaploxypinus goraiensis Hart 1964	–	+
Protohaploxypinus micros Hart 1964	–	+
Retusotriletes diversiformis (Balme & Hennelly) Bharadwaj 1962	–	+
Scheuringipollenites maximus (Hart) Tiwari 1973 (= *Vesicaspora potoniei* Lakhanpal, Sah & Dube 1960)	–	+
Striatoabieites sp. (Zoricheva & Sedova) Hart 1964	–	+
Striatopodocarpites cancellatus (Balme & Hennelly) Hart 1965	–	+
Striatopodocarpites communis (Wilson) Hart 1964	–	+
Striatopodocarpites indicus (Bharadwaj) Hart 1964	–	+
Striatopodocarpites lemniscata (Wilson) Marques-Toigo 1972	–	+
Striomonosaccites brevis Bose & Kar 1966	–	+
Thymospora cicatricosus (Balme & Hennelly) Hart 1965	–	+
Thymospora sp. Wilson & Venkatachala 1963	–	+
Vesicaspora milvinus (Balme & Hennelly) Hart 1965	–	+
Vestigisporites gondwanensis (Mehta) Hart 1965	–	+
Vestigisporites hennellyi Hart 1960	–	+
Vittatina africana Hart 1966	–	+
Vittatina saccata (Hart) Jansonius 1962	–	+
Welwitschiapites simplex Tiwari 1965	–	+

Mudstones), Kazinze, mid-Zambezi Basin. A threefold zonation was erected (Fig. 6) and these zones were correlated to the lower and upper units of the Luwumbu Coal Formation, 1000 km to the northeast, in the Upper Luangwa Valley, Zambia. Utting noted that it was not possible to recognize the three subdivisions of Zone 1 of Falcon (1975) in either the Kazinze or Upper Luangwa areas.

The Siankondobo Sandstone Formation (Zone IO) is dominated by monosaccates (*Cannanoropollis* and *Plicatipollenites*) with smaller proportions of trilete spores (Fig. 6). These proportions are reversed in the Maamba Sandstone Member and the base of the Main Coal Seam, which are dominated by *Punctatisporites*, *Acanthotriletes* and *Apiculatisporis* (Zone LP). In the remainder of the Main Coal Seam and overlying Carbonaceous Mudstones, striate and non-striate bisaccates become common, particularly *Protohaploxypinus* and *Scheuringipollenites* (= *Vesicaspora*), respectively (Zone LP). The topmost beds of

Table 3. Species common to both investigations (Utting 1970, 1976) of the Mukumba Siltstone and Mpwashi Carbonaceous members of the Luangwa Valley.

MUKUMBA SILTSTONE MEMBER	MPWASHI CARBONACEOUS MEMBER
Anapiculatisporites tereteangulatus (= *Acanthotriletes tereteangulatus*)	*Anapiculatisporites tereteangulatus* (= *Acanthotriletes tereteangulatus)*
Cannanoropollis janaki (= *Virkkipollenites obscurus*)	*Brevitriletes cornutus* (= *Apiculatisporis cornutus*)
Cycadopites cymbatus	*Baculatisporites bharadwaji*
Granulatisporites micronodosus	*Cannanoropollis janaki* (= *Virkkipollenites obscurus*)
Horriditriletes filiformis (= *Apiculatisporis filiformis; Acanthotriletes filiformis*)	*Converrucosisporites pseudoreticulatus* (= *Verrucosisporites pseudoreticulatus*)
Plicatipollenites indicus	*Cycadopites cymbatus*
Punctatisporites gretensis	*Cycadopites nevesii*
Scheuringipollenites ovatus (= *Vesicaspora ovata*)	*Deltoidospora directa* (= *Leiotriletes directus)*
	Granulatisporites micronodosus
	Granulatisporites trisinus
	Horriditriletes filiformis (= *Apiculatisporis filiformis; Acanthotriletes filiformis*)
	Lueckisporites nyakapendensis
	Marsupipollenites striatus
	Neoraistrickia ramosa
	Pityosporites leschiki
	Plicatipollenites indicus
	Protohaploxypinus amplus
	Protohaploxypinus goraiensis
	Protohaploxypinus limpidus
	Punctatisporites gretensis
	Retusotriletes diversiformis
	Scheuringipollenites ovatus (= *Vesicaspora ovata*)
	Scheuringipollenites maximus (= *Vesicaspora potoniei)*
	Vestigisporites hennellyi
	Vestigisporites methoris
	Vittatina africana

GS 31 (Zone AV) contain an incursion of acritarchs (referred to as Incertae sedis by Utting) including *Tetraporina* sp., *Circulisporites* sp., *C. parvus*, *Pilasporites plurigenus*, *Quadrisporites horridus* and *Peltacystia* sp., as well as zonotrilete spores such as *Gondisporites vrystaatensis* (Fig. 6). Rare elements include the bisaccates *Alisporites tenuicorpus* and *Hamiapollenites* sp., and the polyplicate pollen *Vittatina africana*. This zone is not recognized in the Upper Luangwa and most likely represents a localized damp terrestrial environment (Barbolini 2014).

The work of Utting (1978) was supplemented by further palynological investigations by Nyambe & Utting (1997) who also sampled the younger Madumabisa Mudstone and Interbedded Sandstone and Mudstone formations as well as the subordinate Karoo formations of Kazinze area, mid-Zambezi Basin, Zambia. Monosaccate palynomorphs dominate the *Plicatipollenites indicus–Cannanoropollis obscurus* Zone, encompassing the basal Siankondobo Sandstone Formation (Fig. 7). Utting (1978) correlated this lowermost zone to Zone 1 of Falcon (1975); however, Césari (2007) suggested that due to the presence of *Vittatina* sp. and *Converrucosisporites confluens*, Zone IO is better correlated with Subzone C, Zimbabwe (Falcon 1975). The overlying *Apiculatisporis levis–Vesicaspora potoniei* (LP) Zone of Utting (1978), which spans the Gwembe Coal Formation, is renamed the *Brevitriletes levis –Scheuringipollenites maximus* Zone by Nyambe & Utting (1997) to reflect updated taxonomy (Fig. 7). Microfloras indicate ages of late Carboniferous (Gzhelian) to early Permian (Asselian to early Sakmarian) for the Siankondobo Sandstone Formation, early Permian (Artinskian to Kungurian) age for the Gwembe Coal Formation, late Permian (Lopingian) age for the Madumabisa Mudstone, and early or Middle Triassic (late Scythian or Anisian) age for the Interbedded Sandstone and Mudstone (Nyambe & Utting 1997). The early Permian (Artinskian to Kungurian) age assigned to the Gwembe Coal Formation stems from palynological correlations with Assemblage zone III of the mid-Zambezi Valley, Zimbabwe (Falcon 1975) and the Mchuchuma Formation (K2) of Tanzania, of middle Ecca age (Wopfner & Kreuser 1986). MacRae (1988) correlated the upper part of the *Brevitriletes levis–Scheuringipollenites maximus* Zone with Biozone D of the Waterberg, South Africa, indicating a late Artinskian to Kungurian age for the Gwembe Coal Formation. The late Permian age assigned to the overlying Madumabisa Mudstone, which can be correlated with the Tatarian-aged *Cistecephalus* reptile zone of the Upper Luangwa (Utting 1979), is equivalent to strata in southern Africa on the basis of microfloral correlation, including the Madumabisa Shale Formation of Zimbabwe (Nyambe & Utting 1997).

PALAEOBOTANY

Megafloras

The first account of Permian fossil plants in Zambia seems to have been Molyneux (1909), who reported species

Plicatipollenites indicus - Cannanoropollis obscurus Zone (IO)	*Apiculatisporis levis – Vesicaspora potoniei* Zone (LP)	*Vittatina africana - Gondisporites vrystaatensis* Zone (AV)
Anapiculatisporites tereteangulatus (=*Acanthotriletes*) *tereteangulatus*	*Horriditriletes filiformis* (= *Acanthotriletes filiformis*)	Alete type I
Brevitriletes cornutus (= *Apiculatisporis cornutus*)	*Acanthotriletes* sp.	*Alisporites tenuicorpus*
Cannanoropollis (= *Virkkipollenites*) *corius*	*Baculatisporites bharadwajii*	*Circulisporites parvus*
Cannanoropollis (= *Virkkipollenites*) *densus*	*Brevitriletes levis* (= *Apiculatisporis levis*)	*Circulisporites* sp.
Cannanoropollis janaki (= *Virkkipollenites obscurus*)	*Cirratriradites africanensis*	*Gondisporites vrystaatensis*
Cycadopites cymbatus	*Cycadopites nevesii*	*Hamiapollenites* sp.
Deltoidospora directa (= *Leiotriletes directus*)	*Granulatisporites* sp.	*Ouadrisporites horridus*
Granulatisporites micronodosus	*Laevigatosporites colliensis*	*Peltacystia* sp.
?*Granulatisporites trisinus*	*Lophotriletes rectus*	*Vittatina africana*
Laevigatosporites minor	*Marsupipollenites striatus*	
Incertae sedis A	*Horriditriletes ramosus* (= *Neoraistrickia ramosa*)	
Parasaccites bilateralis	*Pityosporites leschikii*	
Pilasporites plurigenus	*Potonieisporites granulatus*	
Plicatipollenites indicus	*Protohaploxypinus amplus*	
Plicatipollenites trigonalis	*Protohaploxypinus diagonalis*	
Protohaploxypinus limpidus	*Protohaploxypinus lemniscata*	
Protohaploxypinus goraiensis	*Retusotriletes diversiformis*	***(species) = form common, but less frequent than dominant group**
Protohaploxypinus micros	*Scheuringipollenites maximus* (= *Vesicaspora potoniei*)	
Striatopodocarpites sp.	*Striatopodocarpites cancellatus*	
Protohaploxypinus varius	*Striatopodocarpites rarus*	
Punctatisporites gretensis	*Striomonosaccites* sp.	
Scheuringipollenites ovatus (= *Vesicaspora ovata*)	*Vitreisporites pallidus*	
Tetraporina sp.	*Vittatina saccata*	
Converrucosisporites pseudoreticulatus (= *Verrucosisporites pseudoreticulatus*)		
Vestigisporites methoris		
Vittatina sp.		
Zinjisporites eccensis		

Monosaccates *(triletes)	**Triletes *(monosaccates)**	**Triletes and bisaccates dominant**		**Incertae sedis *(triletes)**
Siankondobo Sandstone Formation	**Maamba Sst Member**	**Main Coal Seam**	**Carbonaceous mudstones with thin coal seams**	
77m	**58m**	**53m**	**47m**	**13m 0m**

Figure 6. Concurrent range zones of the Siankondobo Sandstone and Gwembe Coal formations, Kazinze, mid-Zambezi Basin, Zambia. Redrawn from Utting (1978).

of *Gangamopteris* McCoy 1847, *Glossopteris* Brongniart 1828 and *Schizoneura* Hartig 1837 from the Luano area, and *Glossopteris indica* (Brongniart) Schimper 1869 from the Lufua River valley and its tributaries south of Kafue in the mid-Zambezi Valley. *Glossopteris* and *Gangamopteris* specimens from Zimbabwe, Zambia and Malawi are small compared to those from South Africa (Arber in Andrew & Bailey 1910; Lacey 1961), possibly due to climatic amelioration in the more northerly areas of Gondwana.

Later authors recorded macroplants from various locali-

System		Stage	Lith. Unit	Palynomorph Zone	Characteristic Taxa	Rock Unit
				?		
Triassic	Mid	Anisian	Stormberg	Unnamed	*Pityosporites* sp., *Falcisporites stabilis, Alisporites* sp., *Sulcatisporites* sp., *Platysaccus queenslandi, Rimaesporites aquilonis, Lunatisporites pellucidus, Apiculatisporis* sp., *Calamospora* sp., *Verrucosisporites* sp., *Uvaesporites* sp., *Aratrisporites fischeri, Playfordiaspora crenulata (Guthoerlisporites cancellosus)*	Interbedded Sandstone and Mudstone Fm
Triassic	Early	Scythian				
Permian	Late	Tatarian	Beaufort	Unnamed	*Guttulapollenites hannonicus, Corisaccites alutas, Protohaploxypinus limpidus, Protohaploxypinus goraiensis, Striatopodocarpites* sp., *Sulcatisporites prolatus, Vitreisporites pallidus, Reticuloidosporites warchianus, Polypodiisporites mutabilis, Weylandites lucifer, Botryococcus* sp.	Madumabisa Mudstone Fm
Permian	Late	Kazanian				
Permian	Late	Ufimian				
Permian	Early	Kungurian	Mid-Ecca	*Brevitriletes levis - Scheuringipollenites maximus*	*Punctatisporites gretensis, Deltoidospora directa, Cirratriradites africanensis, Brevitriletes levis, Horriditriletes filiformis, Protohaploxypinus limpidus, Protohaploxypinus amplus, Striatopodocarpites cancellatus, Striatopodocarpites rarus, Plicatipollenites indicus, Scheuringipollenites maximus, S. ovatus, Vittatina saccata, Cycadopites cymbatus, Pilasporites plurigenus, Circulisporites* sp.	Gwembe Coal Fm
Permian	Early	Artinskian				
Permian	Early	Sakmarian	Dwyka	*Plicatipollenites indicus - Cannanoropollis obscurus*	*Plicatipollenites indicus, Cannanoropollis obscurus, Brevitriletes cornutus, Acanthotriletes tereteangulatus, Zinjisporites eccensis, Microbaculispora micronodosa, Converrucosisporites pseudoreticulatus, Cycadopites cymbatus*	Siankondobo Sandstone Fm.
Permian	Early	Asselian				
Carboniferous	Late	Gzhelian				
				?	?	?

Figure 7. Palynozones of the Dwyka, Ecca, Beaufort and Stormberg groups of the mid-Zambezi Valley, southern Zambia (redrawn from Nyambe & Utting 1997). Dotted lines represent uncertainty about how far zones extend. Not to scale.

ties, including the Upper Luangwa (Dixey 1937), Lower and Upper Karoo beds at Gwembe (Gair 1959; Tavener-Smith 1958, 1960), and the Western Luano (Gair 1960). Gair (1959) recorded *Glossopteris* sp. from the Gwembe Coal Formation. Bond (1954) and Gair (1959, 1960) reported *Glossopteris indica* from the Lower and Upper Beds of the Madumabisa Mudstone in the Luano and Luangwa areas, along with *Phyllotheca* sp. Brongniart 1828 in the Upper Bed. Drysdall & Kitching (1963) identified *Schizoneura* sp. and *Phyllotheca* sp. from the Luwumbu Coal Formation and lowest beds of the Madumabisa Mudstone in the Upper Luangwa Valley.

Bond (1954, 1955) described lamellibranchs in association with a *Glossopteris* flora in limestones from the Gwembe area, and Lacey (1974) noted a similar assemblage from the Kafue Valley, consisting of paper shales with poorly preserved leaves (cf. *Taeniopteris* sp. Brongniart 1828) and lamellibranchs of *Palaeomutella oblongata*, *P. neglecta* and *Palaeanodonta wadei* (det. Bond).

Lacey and Smith (1972) and Lacey (1974) made slight modifications of the Ecca flora originally described by Utting (1970), consisting of 17 taxa from the Luwumbu Coal Formation and the Lower Member of the Madumabisa Mudstone in the Upper Luangwa Valley. These taxonomic modifications are presented earlier in the text (Fig. 5). The discovery of the fossil tentatively identified as *Annularia sphenophylloides* Zenker 1833 (Utting 1970; discussed by Lacey 1974) represented the first occurrence of a late Carboniferous–early Permian Russian/North American/European species in an African *Glossopteris* flora at the time. *Annularia* has since been identified in Permian deposits of South Africa (Anderson & Anderson 1985; le Roux & Anderson 1977; Prevec *et al.* 2010), Zimbabwe (Bond 1973) and Argentina (Archangelsky & Cúneo 1984). Other fossil plants collected in the Luwumbu Coal Formation are generally similar to those of other African Ecca-equivalent assemblages, but Utting (1970) and later authors (e.g. Lacey & Smith 1972; Lacey 1974) considered the presence of *Noeggerathiopsis hislopi* Feistmantel 1879 in the Upper Madumabisa Mudstone (correlated with the Lower Beaufort) to be anomalous, being that this species was thought to be restricted to the Ecca Group. To date, *N. hislopi* has been found in the Lower Beaufort Estcourt Formation (Anderson & Anderson 1985) and in Indian Permian coal fields (Srivastava & Agnihotri 2013) so cannot be used as a biostratigraphic marker.

Fragmentary fossil plants were occasionally noted in the boreholes studied by Utting (1978), and a well-preserved *Glossopteris damudica* Feistmantel 1879 leaf was identified by W.S. Lacey in borehole GS 70 of the Siankondobo Coalfield (Gwembe Coal Formation). Lacey & Lucas (1984) listed 9 fossil taxa from new collecting in the Upper Luangwa Valley: *Glossopteris indica*, *G. browniana* Brongniart 1892, *G.* cf. *communis* Feistmantel 1876, *G.* cf. *stricta* Bunbury 1861, *G.* cf. *ampla* Dana 1849, *G.* cf. *damudica*, cf. *Gangamopteris* sp., cf. *Noeggerathiopsis hislopi*, and *Neomariopteris* (= *Sphenopteris*) cf. *polymorpha* (Feistmantel) Maithy 1974. Megafloral remains indicate an Upper Ecca–Lower Beaufort age and probably derive from the Lower Madumabisa Mudstone.

Less diverse assemblages have been recovered from Triassic deposits in Zambia. Du Toit (1954) made reference to 'typical species of *Dicroidium*' present in the mid-Zambezi Kafue Valley (Upper Karoo), and the Western Luano Valley. Utting (1970) recorded unidentifiable plant fragments from the Ntawere and Upper Grit formations in the Upper Luangwa Valley. Lacey & Smith (1972) noted fragments similar to *Schizoneura carreri* Zeiller 1903 (= *Neocalamites carrerei* (Zeiller) Halle 1908[1]), *Lepidopteris africanum* (Du Toit) (= *L. stormbergensis* (Seward) Townrow 1956[1]) and *Dicroidium* (= *Thinnfeldia*[1,2]) *narrabeenensis* (Walkom) Jakob & Jakob 1950 in the Triassic Ntawere Formation, and these taxa are known from Middle Triassic 'Molteno' beds in other Karoo deposits of Africa (Lacey 1974). This is confirmed by the extensive records published by Anderson & Anderson (1983, 1985).

Lacey & Lucas (1984) suggested a Triassic age for deposits in the Mid Luangwa Valley on the presence of cf. *Paracalamites australis* Rigby 1966 and *Dadoxylon* cf. *sclerosum* Walton (syn. *Kaokoxylon* cf. *sclerosum* (Walton) Kräusel 1956). *Dicroidium* cf. *odontopteroides* (Morris) Gothan 1912 and *D.* cf. *zuberi* (Szajnocha) Archangelsky 1968 (= *Zuberia zuberi* Frenguelli 1943; Artabe 1990; illustrated in Fig. 8), *Neocalamites* cf. *foxii* Lele 1956, *N.* cf. *carrerei* and *N.* cf. *horensis* (Schimper) 1908 were collected from the Luano Valley and Lacey & Lucas (1984) thought these specimens probably indicated a 'Molteno age' for the deposits (the Molteno Formation is currently thought to be Carnian – Hancox 1998).

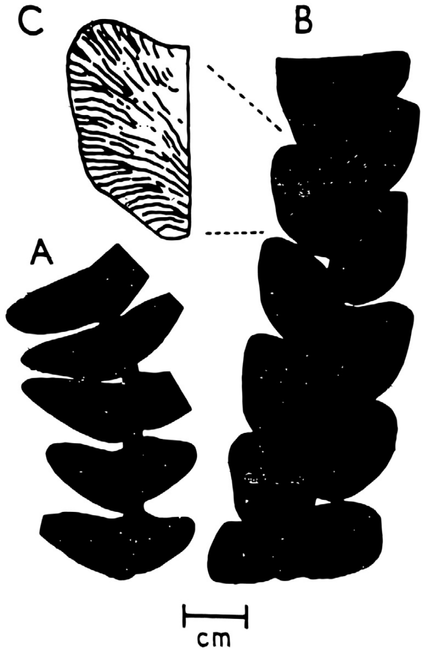

Figure 8. *Dicroidium* from the Luano Valley (reproduced from Lacey & Lucas 1984). **A**, *Dicroidium* cf. *odontopteroides* (Morris) Gothan 1912. **B**, *Dicroidium* cf. *zuberi* (= *Zuberia zuberi* Frenguelli 1943, Artabe 1990). **C**, enlargement of a single pinna from (**B**), illustrating shape of the pinna, wide basal attachment with numerous veins entering the pinna and dichotomous branching of the veins. Scale bar: 1 cm.

[1]Synonym according to Lacey & Lucas (1972), who did not publish figures of the fossil material for re-evaluation by the present authors

[2]The genus *Thinnfeldia* was historically used for *Dicroidium*-like foliage until Doludenko (1971) demonstrated that the holotype for the type species was a *Pachypteris*. However, Kirchner & Müller (1992) suggested retention of the genus due to unique reproductive structures that differ slightly from those associated with *Pachypteris* (Taylor *et al.* 2009).

Fossil wood

Early geologists described fossil wood in the Luangwa Valley formations: L.A. Wallace (1907) reported 'much silicified wood' in the Mlembo and Lukasashi valleys, J.C. Molyneux (1909) reported that, 'silicified wood in fragments, or in prostrate trunks as long as 9 feet, is found in all [Karoo System] beds up to the Forest Sandstone'.

F.P. Mennell (1930) reported that silicified wood occurs in some abundance in the Upper Shales above the coal seams at various localities, particularly the Lufua River in the mid-Zambezi Valley, and stated that '[s]ilicified wood occurs in these beds in some abundance … Near the Lusangashi River pieces can be picked up full of holes made by boring insects and looking so exactly like ordinary bits of decayed timber that their weight always gives one a sensation of surprise'.

In 1931, George Reed Downs, an American geology student, spent several months walking in the Lukasashi Valley and found Permian therapsid fossils, as well as well-preserved fossil wood (Downs 1935). He states: '[s]ilicified wood is especially abundant in the district north and northwest of Manchiti. One specimen from half a mile north of N'Kanga village along the Boma path as identified by Mr. Eltar Nielson as representing a primitive cordaitales genus'.

Dixey (1937) described 'large masses of fossil wood' from the Grey Shales and Sandstones, and the Red Pebbly Grits and Grey Grits of the Upper Luangwa Valley (thought by Lacey (1961) to be equivalent to the upper Ecca / base of the Beaufort and the lower and upper Escarpment Grit, respectively). Woods were identified by Edwards (1937) as *Dadoxylon sclerosum* (Walton) Kräusel 1956 and *Dadoxylon arberi* Seward 1919. The genus *Rhexoxylon* Bancroft 1913 was not represented. Dixey also noted abundant fossil wood material in the Red Sandstones of the Upper Luangwa Valley, equivalent to the Forest Sandstones of other areas (Lacey 1961).

In 1941, T.D. Guernsey wrote a report on the geology of the concession areas of Luangwa Concessions (N.R.) Limited, 'based on data gathered by 166 geologists who prospected and mapped approximately 156,000 square miles within Northern Rhodesia'. In the Zambezi-Kafue section of Karoo sediments, the report mentions 'fossil wood … up to 7 ft. in diameter and 100 ft. long, is abundant'. (However, it is believed by the authors that these figures are exaggerated or a mistake).

Fossil wood was also noted by Gair (1959) and Tavener-Smith (1960) in the Madumabisa Mudstone and Escarpment Grit formations exposed in the Gwembe valley. Gair reported 'abundant fossilised logs, up to 4 feet in diameter, probably including *Dadoxylon* sp. Endlicher 1847 and *Rhexoxylon africanum* Bancroft 1913', and Tavener-Smith describes 'abundant silicified tree-trunks, up to 2 feet in diameter, with annual rings and radial structures well preserved, spread over many acres' in the Escarpment Grit Formation (The authors visited Tavener-Smith's main site in 2015 and found far bigger specimens.) Additionally, Gair (1960) noted fossil wood in Lower Karoo beds of the Western Luano Valley.

Petrified wood collected by Utting (1970) from the Lower Madumabisa Mudstone was rarely found *in situ*, explaining why the different species suggest varying ages. *Dadoxylon sclerosum* Walton (syn. *Kaokoxylon* cf. *sclerosum* (Walton) Kräusel 1956) and *D. bondii* have been found elsewhere in Africa from Triassic beds, whilst *Dadoxylon nicolii* Seward 1917, nom. illeg. (= *Dadoxylon arberi* Seward 1919) has been found in Permian localities of Gondwana. *D. bougheyi* Williams was one of the only specimens to be found *in situ* from the Upper Madumabisa Mudstone.

In the Kafue Valley, Lacey (1974) noted *Rhexoxylon africanum* Bancroft from the sandstone/grit unit overlying the cf. *Taeniopteris*–lamellibranch assemblage contained in a paper shale unit. As *Rhexoxylon* was considered to be consistent with an 'Upper Madumabisa Mudstone age', the sandstone/grit unit was thought by Lacey (1974) to be the equivalent of the Escarpment Grit elsewhere in Zambia.

Most recently, Lacey & Lucas (1984) recorded *Dadoxylon* cf. *sclerosum* from Triassic deposits in the Mid Luangwa Valley. These woods need to be revised because the genus *Dadoxylon* is now treated as a junior synonym of *Agathoxylon* Hartig (Rößler *et al.* 2014) and there is confusion over *D.* (= *Kaokoxylon) sclerosum* and its age range.

CONCLUSIONS

The Karoo deposits of Zambia preserve a rich record of fossilized plants, pollen and wood. John Utting investigated the palynology of both the mid-Zambezi and Luangwa Valleys, while William Lacey was mainly responsible for publications on Permian and Triassic fossil plants. The fossil wood has not been comprehensively researched, with only a few identifications made by Edwards and Lacey, but for the most part, simply noted as occurring over wide areas throughout the country. The palaeobotanical record of Zambia would benefit greatly from a detailed study into both Permian and Triassic woods, as well as further research on the macroplants and pollen to augment existing studies. A new standardized subdivision for the Luangwa Valley is proposed herein, which clarifies naming discrepancies in previous works and should assist in future correlations between different Gondwana basins.

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