Resolving the age of Madumabisa fossil vertebrates: palynological evidence from the mid-Zambezi Basin of Zambia

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Abstract

Age estimates for Permian rocks in the mid-Zambezi Basin of Zambia have thus far yielded ambiguous results. Previously studied palynoassemblages from the Madumabisa Formation resemble spore-pollen suites from both the *Cistecephalus* Zone of North Luangwa (Lopingian) and the palynological Assemblage Sub-Zone IV H of Zimbabwe, proposed as Guadalupian. In order to improve age estimates and refine the biostratigraphy of the Madumabisa Formation, this formation together with the underlying Gwembe Formation, were sampled for palynomorphs. Assemblages from the Gwembe Formation are dominated

by trilete spores with less common striate and non-striate bisaccate pollen, whereas the overlying Madumabisa Formation palaeoflora is composed predominantly of striate bisaccates. Ferns, pteridosperms, lycopods, sphenophytes, glossopterids and conifers are represented in the palynofloras. The upper Gwembe Formation palynoassemblage can be correlated with the *Didecitriletes ericianus* Zone of Backhouse (1991), the *Guttulapollenites hannonicus*–*Protohaploxypinus rugatus* Zone (Zone VI) of Aitken (1998), Assemblage Zone III of the mid-Zambezi Basin, Zimbabwe and Biozone KK 3 in the Kalahari Karoo Basin, Botswana, suggesting a Guadalupian (Wordian–Capitanian) age. The upper Madumabisa Formation palynoassemblage can be placed in the upper *Dulhuntyispora parvithola* Zone of Backhouse (1991) / APP5 of Price (1997), dated as Wuchiapingian (Lopingian) and correlates with Assemblage 2 of the Moatize–Minjova Basin, Mozambique and the McKinnon Member palynofloras of East Antarctica. It also resembles *Daptocephalus* Assemblage Zone palynofloras of the lower and middle Balfour Formation in the Karoo Basin, South Africa, and is suggested to be Lopingian (Wuchiapingian–Changhsingian) in age. Although these palynological assemblages place lower and upper age constraints on Madumabisa Formation vertebrate fossils, uncertainty remains as to the exact correlation between the Madumabisa vertebrate assemblages and the assemblage zones of the main Karoo Basin.

Keywords: Permian; Madumabisa Formation; Gwembe Formation; palynology; Karoo; biostratigraphy

1. Introduction and stratigraphic context

The diverse Permian and Triassic fossil vertebrates in the main Karoo Basin of South Africa have facilitated biostratigraphic subdivision of the Beaufort Group (Keyser and Smith, 1977–78; Kitching, 1977; Rubidge *et al.*, 1995), and the Karoo fossil tetrapod record is regarded as the most complete of this age (Rubidge, 2005). The assemblage zones of the Beaufort Group in South Africa have been correlated with analogous faunal assemblages in similar-aged basins throughout southern and eastern Africa (Catuneanu *et al.*, 2005). Karoo-equivalent deposits are widespread in Zambia, occurring in the Luangwa, Luano and Zambezi basins (Drysall and Kitching, 1962; Catuneanu *et al.*, 2005). Angielczyk *et al.* (2014) correlated the upper member of the Madumabisa Formation in the Luangwa Basin to the *Cistecephalus* Assemblage Zone (AZ) of the main Karoo Basin based on its assemblage of dicynodont therapsids (Table 1). This work formed part of a broader, ongoing research project on the Permian and Triassic vertebrates of Zambia (e.g., Peacock *et al.*, 2013; Sidor *et al.*, 2014; Sidor, 2015; Huttenlocker *et al.*, 2015).

<<Insert Table 1>>

Tetrapod fossils were first discovered in the mid-Zambezi Basin in the 1950s (Gair, 1959; Drysdall and Kitching, 1963), but only a small amount of material was collected, and the specimens appear to have been lost (Sidor *et al.*, 2014). Recently, our team has conducted more extensive fieldwork in the Madumabisa Formation of the mid-Zambezi Basin, resulting in the discovery of numerous tetrapod fossils, including temnospondyls, burnetiids, dicynodonts, gorgonopsids, and anteosaurid and tapinocephalid dinocephalians (Sidor *et al.*, 2014). Dinocephalians are currently interpreted to be restricted to the Guadalupian worldwide (Lucas, 2004, 2006; Rubidge, 2005; Benton, 2012; Day *et al.*, 2015b), and this has been

confirmed by radiometric dating, at least in the main Karoo Basin (Rubidge et al., 2013), although the recent discovery of two tapinocephalid dinocephalians from the lowermost Poortjie Member (Teekloof Formation) has extended the range of the *Tapinocephalus* AZ into the late Guadalupian (Day et al., 2015a).

The age of the vertebrate faunas in the Madumabisa Formation in the mid-Zambezi Basin is not well constrained. The palynology of these Permian rocks was previously investigated by Utting (1970, 1978) and Nyambe and Utting (1997), and the taxonomy of spore-pollen suites updated by Barbolini et al. (2016a). Nyambe and Utting (1997) assigned a Cisuralian (Artinskian to Kungurian) age to the Gwembe Formation (= “Gwembe Coal” / “Gwembe Coal Formation” of previous authors), and a Lopingian age to the Madumabisa Formation (= “Madumabisa Mudstone” / “Madumabisa Mudstone Formation” of previous authors). The latter authors interpreted the lower one-third of the Madumabisa Formation to be Tatarian (= Lopingian) on the basis of correlation with palynoassemblages from the *Cistecephalus* Zone of North Luangwa (Utting, 1979) (Table 1). Nyambe and Utting (1997) also correlated the Madumabisa Formation palynoflora with Assemblage Sub-Zone IV H of Zimbabwe (Falcon, 1975) but Bond (pers. comm. to Falcon) proposed that this palynozone was equivalent to the older *Tapinocephalus* Assemblage Zone of South Africa (Table 1). As a result of this discrepancy, our palynological investigation was initiated at existing vertebrate sites in the mid-Zambezi Basin in order to assist with dating and correlation of these rocks, and to reconstruct the palaeoenvironments in which they were deposited (Figure 1).

<<Insert Figure 1>>

2. Materials and Methods

The Madumabisa Formation in the mid-Zambezi Basin comprises gray–green non-carbonaceous mudstones, laminated silty mudstones and siltstones with interbedded calcilutites, sandstones and conglomerates (Nyambe, 1999). It has a gradational contact with the underlying Gwembe Formation that consists of carbonaceous mudstone and siltstone with interbedded coal seams and sandstones (Nyambe and Utting, 1997). The Madumabisa Formation is unconformably overlain by the Triassic Escarpment Grit, a coarse- to very coarse grained unit that has been unproductive for palynomorphs thus far (Nyambe, 1993; Nyambe and Dixon, 2000). Palynological samples were collected at previously unsampled localities in the Bondo and Lusitu areas of the mid-Zambezi Basin, from the Gwembe and Madumabisa formations (Figure 1). Twenty-six samples were processed at the Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg. They were subjected to standard palynological processing techniques including acid preparation, oxidation, and heavy liquid separation (Moore et al., 1991; Traverse, 2007). Residues were mounted in glycerin jelly and prepared slides examined with an Olympus BX51m light microscope. Slides were scanned under 400× magnification and photographs taken under 1000× magnification (oil immersion) to show fine detail. A ColorView Soft Imaging System, AxioCam ICc 1 camera, and Analysis™ software were used for digital photography. All slides are housed at the Evolutionary Studies Institute (ESI), University of the Witwatersrand with slide numbers and co-ordinates of the photographed specimens on record. A species list and images of stratigraphically significant palynomorphs are included in the appendix (Plate I). Two samples from the upper Gwembe Formation and four from the Madumabisa Formation were palynologically productive but pollen and spores were not sufficiently abundant to permit a quantitative analysis, a feature also noted by Utting (1978) and Nyambe and Utting (1997).

3. Results

3.1. Palynology

Assemblages from the upper Gwembe Formation (L190.1 and L190.2) have a slight dominance of striate bisaccate over non-striate bisaccate pollen, together with an abundance of trilete spores and a lesser component of monolete spores, monosaccate, monosulcate and striate non-saccate pollen. Significant taxa include *Alisporites potonieii*, *Chordasporites waterbergensis*, *Striatosporites heyleri*, *Guttulapollenites hannonicus*, *Striatopodocarpites cancellatus*, *Limitisporites*, *Potonieisporites novicus*, five species of *Protohaploxypinus*, *Scheuringipollenites ovatus* and *Vestigisporites ventrisaccatus*.

The assemblage from sample L281 (Madumabisa Formation) was not sufficiently diverse to allow for stratigraphic assignment, while that of sample L229 (middle Madumabisa Formation) did not contain index taxa, but was instead abundant in algal cysts (which are a minor quantitative component of all other assemblages). This sample was from a lignite bed, inferring a waterlogged swampy environment at the time of deposition. Species in the L281 assemblage include *Cycadopites cymbatus*, *C. follicularis*, *Marsupipollenites triradiatus*, *Platysaccus papilionis* and *Weylandites lucifer*. The L229 assemblage contains *Calamospora plicata*, *Cycadopites cymbatus*, *Maculatasporites gondwanensis*, *Pakhapites fusus*, *Quadrисporites* sp. and *Vittatina scutata*.

The assemblages from samples L168.1 and L168.2 (middle Madumabisa Formation) are much more diverse and dominated by taeniate pollen, with a lesser component of non-striate bisaccate pollen, trilete and monolete spores, and monosaccate, monosulcate and striate non-saccate pollen. Significant taxa include *Guttulapollenites hannonicus*, *Klausipollenites schaubergeri*, *Marsupipollenites striatus*, *Platysaccus papilionis*, four species of *Protohaploxypinus*, *Pteruchipollenites landianus*, *Striatopodocarpites cancellatus*,

S. fusus and *Weylandites lucifer*. There are also two unseparated tetrads of *Lundbladispora braziliensis* and a specimen of *Klausipollenites schaubergeri* that appears trisaccate.

3.2. Botanical affinities and palaeoenvironmental reconstruction

The palaeoflora of the upper Gwembe Formation is dominated by trilete spores representing leptosporangiate and eusporangiate ferns, pteridosperms, lycopods and sphenophytes (Table 2). This parent vegetation reflects a swampy alluvial plain (Nyambe, 1993; Nyambe and Utting, 1997) of pteridophytes, lycopods and glossopterids with an upland flora of conifers. The overlying Madumabisa Formation palaeoflora is interpreted to represent a glossopterid woodland with an understorey of leptosporangiate and eusporangiate ferns, lycopods and sphenophytes with sparse peltasperms and conifers (Table 2). The significant presence of various *Protohaploxylinus* and *Striatopodocarpites* species is consistent with the dominance of glossopterids across the Southern Hemisphere during the Permian (e.g., Anderson et al., 1999; Balme, 1995). Less common elements in the Gwembe and overlying Madumabisa formations include various monolete spores, and monosulcate and striate asaccate pollen (Table 2).

<<Insert Table 2>>

3.3. Palynostratigraphy and age assignment

3.3.1. Gwembe Formation

Nyambe and Utting (1997) assigned a Cisuralian (Artinskian to Kungurian) age to the Gwembe Formation on the basis of palynological correlations with Assemblage zone III of the mid-Zambezi Valley, Zimbabwe (Falcon, 1975) and the Mchuchuma Formation (K2) of Tanzania, of “middle Ecce age” (Wopfner and Kreuser, 1986), which would be Kungurian

according to radiometric dates for the main Karoo Basin (Rubidge et al., 2013). MacRae (1988) correlated the upper part of the *Brevitriletes levis*–*Scheuringipollenites maximus* Zone of Zambia with Biozone D of the Waterberg Basin, South Africa, also indicating a late Artinskian to Kungurian age for the Gwembe Formation. As our palynological samples were taken from a higher stratigraphic position than those of previous authors, the Gwembe Formation palynoassemblage of this study is expected to correlate with younger localities. Although it is broadly similar to those of Utting (1970, 1978) and Nyambe and Utting (1997), some stratigraphically significant taxa in our samples were not recovered in previous analyses (Table 3).

<<Insert Table 3>>

Initially, the presence of *Protohaploxypinus rugatus* in the Gwembe Formation palynoassemblages suggests a correlation with the *Protohaploxypinus rugatus* Zone of Backhouse (1991) in the Collie Basin, Western Australia. The two assemblages share abundant *Brazilea scissa*, *Deltoidospora directa* and *Scheuringipollenites ovatus*, together with *Protohaploxypinus rugatus* and eight other taxa present in the *P. rugatus* Zone (Table 4). If the species recovered by Nyambe and Utting (1997) from the Gwembe Formation are also considered, this increases to nineteen shared taxa with the *P. rugatus* Zone (Table 4). However, it must be taken into account that some index palynomorphs, including *P. rugatus*, have diachronous ranges across Gondwana and this complicates correlation between these regions (Barbolini et al., 2014, 2016b). *P. rugatus* appears in South African palynoassemblages during the Capitanian, whereas it is only present in Australia by the Wuchiapingian (Barbolini et al., 2016b). In South America, Balarino and Gutierrez (2006), Di Pasquo et al. (2010) and Césari et al. (2011) identified *P. rugatus* in the Cisuralian FS

Biozone of Argentina. Several other stratigraphically useful Australian taxa that appear in the Guadalupian and Lopingian are rare or absent from other Gondwanan localities, such as *Dulhuntyispora granulata*, *D. dulhuntyi*, and *Bascanisporites undosus* (Anderson, 1977; Backhouse, 1991), and this does not help to refine the stratigraphy of the mid-Zambezi Basin samples. Additionally, the underlying *Didecitriletes ericianus* Zone is extremely similar in composition to the *P. rugatus* Zone, lacking only *P. rugatus* along with some acritarchs, and so the Gwembe Formation palynoassemblage could also correlate with the *D. ericianus* Zone of Australia. Accordingly, palynological correlations are not solely based on first appearance datums, but also overall species associations and the relative proportions of major palynomorph groups sensu Prevec et al. (2010).

There are currently no published radiometric ages for the *P. rugatus* Zone, which is essentially confined to the Collie Basin of Western Australia (Mory and Backhouse, 1997), but the base of the *D. ericianus* spore-pollen Zone (directly below the *P. rugatus* Zone) has yielded four high-precision U-Pb zircon CA-TIMS ages of between 268.63–270.14 Ma, indicating a Roadian age for the base of this zone (Mory et al., 2012). New radio-isotopic ages for the the Guadalupian and Lopingian spore-pollen zones of the Sydney, Bowen and Galilee basins (eastern Australia) by Metcalfe et al. (2015) and Nicoll et al. (2015) suggest that the *D. ericianus* Zone extends up into the Capitanian, and the *P. rugatus* Zone is Wuchiapingian. Therefore, it is probable that the Gwembe Formation palynoassemblage correlates with the Roadian–Capitanian *D. ericianus* Zone, rather than the significantly younger *P. rugatus* Zone of Australia (Figure 2).

<<Insert Figure 2>>

The palynological assemblage from the Gwembe Formation can also be correlated to Zone VI of Aitken (1998) in the northern Karoo Basin, South Africa and the Volksrust Formation assemblage of South Africa recovered by Barbolini (2014) (Figure 2, Table 4). The Gwembe Formation palynoassemblage contains three of the indicator species for Zone VI of Aitken (1998), which ranges through the Volksrust Formation: *Guttulapollenites hannonicus*, *Protohaploxypinus rugatus* and *Chordasporites australiensis* (Table 4). Other palynoassemblages similar to that of the Gwembe Formation (Figure 2, Table 4) include the Mpwashii Carbonaceous Member of the Luwumbu Coal Formation, North Luangwa Valley, Zambia (Utting, 1976), Assemblage Zone III of Falcon (1975) from the mid-Zambezi Basin of Zimbabwe and Seam No. 4 in the Witbank Coalfield, South Africa (Falcon et al., 1984), both suggested as “of upper Middle Ecca age”, and Biozone KK 3 of Modie and Le Hérisse (2009) in the Kalahari Karoo Basin, Botswana, proposed as Roadian. Radio-isotopic ages for the main Karoo Basin indicate a Wordian–Wuchiapingian age for the Volksrust Formation and Zone VI of Aitken (1998) (Rubidge et al., 2013; Day et al., 2015b; Barbolini et al., 2016b), and considered together with the other similar assemblages, support a Guadalupian (Wordian–Capitanian) age for the Gwembe Formation palynoflora (Figure 2).

3.3.2. Madumabisa Formation

Nyambe and Utting (1997) proposed a Lopingian age for the Madumabisa Formation on the basis of correlation with the *Cistecephalus* vertebrate Biozone of North Luangwa (Utting, 1979), which in turn was assigned a Tatarian (= Lopingian) age based on correlation with the *Cistecephalus* Assemblage Zone in the main Karoo Basin. However, based on the newly revised stratigraphic ranges in the main Karoo Basin (Viglietti et al., 2016), the upper Madumabisa Formation in the Luangwa Basin can probably be correlated to near the *Cistecephalus*–*Daptocephalus* zone boundary or even possibly into the *Daptocephalus* zone

(although this would require later survival of *Endothiodon* in Zambia). Based on the occurrence of dinocephalians fossils, Sidor et al. (2014) suggested that the middle of the Madumabisa Formation in the mid-Zambezi Basin was probably Guadalupian in age. The present study shares the characteristic species *Guttulapollenites hannonicus*, *Protohaploxypinus limpidus*, *P. goraiensis*, *Striatopodocarpites cancellatus* and *Weylandites lucifer* with the palynological assemblages of Utting (1970, 1978) and Nyambe and Utting (1997), but like the results from the Gwembe Formation presented herein, new results from this study have recovered some stratigraphically significant taxa not reported in previous works (Table 3).

Foster and Afonin (2005) recorded significant numbers of aberrant trisaccate grains of *Klausipollenites schaubergeri* and *Alisporites* very close to the Permo-Triassic boundary in Russia and China, and Visscher et al. (2004) found regularly unseparated spore tetrads of lycopod spores in East Greenland, particularly *Lundbladispora braziliensis*, at the same stratigraphic level, suggesting global increases land plant mutations as a result of prolonged exposure to greater levels of UV radiation. Looy in Prevec et al. (2010) also recovered trisaccate and tetrasaccate specimens of *Alisporites* and *Klausipollenites schaubergeri* 70 m below the vertebrate-defined Permian–Triassic boundary at New Wapadsberg Pass, South Africa. The presence of both a trisaccate specimen of *Klausipollenites schaubergeri* and unseparated tetrads of *Lundbladispora braziliensis* in the upper Madumabisa Formation is tantalising, but these aberrant grains are not present in significant enough numbers to date this assemblage as latest Permian. Moreover, Lopingian microfloral assemblages of Gondwana are dominated by striate bisaccates such as *Protohaploxypinus* and *Striatopodocarpites*, but this abruptly changes to microfloras typified by aleate bisaccates and cavate spores at the end of the Permian (Collinson et al., 2006; Lindström and McLoughlin, 2007; Prevec et al., 2010; Vajda and McLoughlin, 2007). In Australia, this transformation

occurs at the base of the *Protohaploxylinus microcorpus* Zone and the transition of the APP601 and APP602 subzones (e.g. Helby et al., 1987; Mory and Backhouse, 1997; Price, 1997), most recently dated to 252.54–252.2 Ma by Metcalfe et al. (2014, 2015).

The late (but not latest) Changhsingian (Metcalfe *et al.*, 2008) *Protohaploxylinus microcorpus* Oppel Zone of Helby (1973) is defined by the oldest common occurrence of *Falcisporites* (*Alisporites*) *australis* and *P. microcorpus*, together with *Playfordiaspora velata* and *Triplexisporites playfordii*. Although the upper Madumabisa Formation assemblage (L168) contains both *Falcisporites* (*Alisporites*) *australis* and *P. microcorpus*, it is still dominated by taeniate pollen and, if Zambian microfloras follow the same patterns of overall plant change as most other late Permian localities in Gondwana, then assemblage L168 would be slightly older than the *P. microcorpus* Zone, placing it in the underlying *Dulhuntyispora parvithola* Zone of Backhouse (1991) / APP5 of Price (1997). However, there is already strong evidence that intra-Gondwanan floristic provincialism during the Permian resulted in regional differences in floral composition (e.g., Cúneo, 1996; Prevec et al., 2009; Barbolini et al., 2016b), and so this assumption needs to be corroborated.

In Australia, the first appearance of *D. parvithola* marks the base of this zone (Backhouse, 1991) but unfortunately *Dulhuntyispora* is generally endemic to Australia and *D. parvithola* is not present in the main Karoo Basin at all, complicating correlation to rocks in other parts of Gondwana (Barbolini et al., 2014). However, palynofloral assemblages display a shift from co-dominance of non-taeniate and taeniate bisaccates, to being dominated by taeniate bisaccates within the *D. parvithola* / APP5 Zone, with a concurrent decline in monosaccate pollen (Mory and Backhouse, 1997; Price, 1997). This places the upper Madumabisa Formation assemblage within the younger part of the *D. parvithola* Zone (Figure 2), for which Metcalfe et al. (2015) obtained CA-TIMS tuff ages of 256–254 Ma (Wuchiapingian). This correlates with the *Cistecephalus* and *Daptocephalus* (*Dicynodon*)

293 assemblage zones of the main Karoo Basin, South Africa on the basis of both palynology
294 (Barbolini, 2014) and radiometric ages (Rubidge et al., 2013).

295 The upper Madumabisa Formation palynoflora is most similar to Assemblage 2 of the
296 Matinde Formation, Moatize–Minjova Basin of Mozambique (Pereira et al., 2016), dated as
297 late Changhsingian (Figure 2). The two assemblages share twenty-one taxa, notably
298 *Corisaccites alutas*, *Guttulapollenites hannonicus*, *Klausipollenites schaubergeri*,
299 *Lueckisporites virkkiae*, *Protohaploxypinus goraiensis*, *P. limpidus*, *P. microcorpus*,
300 *Striatopodocarpites cancellatus*, *S. fusus*, and *Weylandites lucifer* (Table 4). The upper
301 Madumabisa Formation palynoassemblage is also particularly similar to the Lopingian
302 McKinnon Member palynofloras of East Antarctica, correlated to Australian upper Stage 5 –
303 *D. parvithola* zone (McLoughlin et al., 1997; Lindström and McLoughlin, 2007) (Figure 2,
304 Table 4).

305 The palynoflora of the upper Madumabisa Formation resembles closely those of the
306 *Daptocephalus* AZ localities Clouston Farm, situated within the northern Normandien
307 Formation of the Karoo Basin, and New Wapadsberg Pass, ranging through the Palingkloof
308 Member of the southern Balfour Formation (Figure 2). The Wuchiapingian palynoflora of
309 Clouston Farm, reported by Looy in Prevec et al. (2009), shares abundant *Protohaploxypinus*
310 and *Striatopodocarpites* with the Madumabisa Formation microflora, including
311 *Protohaploxypinus limpidus*, *Striatopodocarpites cancellatus* and *S. fusus*, as well as
312 *Weylandites lucifer* (Table 4). The latest Permian (late Changhsingian) palynomorphs of New
313 Wapadsberg Pass (Prevec et al., 2010) include *Protohaploxypinus limpidus*, *P. goraiensis*,
314 *Striatopodocarpites cancellatus*, *Lueckisporites virkkiae*, *Guttulapollenites hannonicus*,
315 *Klausipollenites schaubergeri*, *Falcisporites (Alisporites) australis* and *Weylandites lucifer*,
316 which are also common to the Madumabisa Formation assemblage of this study (Table 4).

Other assemblages showing similarity to the upper Madumabisa Formation assemblage (Figure 2, Table 4) include the upper Permian Buckley Formation, Central Transantarctic Mountains (Farabee *et al.*, 1990) correlated to Australian Stage 5 – *P. rugatus* and *D. parvithola* zones, Assemblage Sub-zone H (*Taeniaesporites*–*Guttulapollenites* Assemblage) of Falcon (1975) in the mid-Zambezi Basin of Zimbabwe, considered equivalent to the *Dulhuntyispora* assemblages of Australia, the lower Sakamena Group, Morondava Basin of Madagascar (Goubin, 1965; Wright and Askin, 1987) correlated to the Changhsingian *Playfordiaspora crenulata* Zone in Australia (Foster, 1982), the Chhidru 1 Assemblage of the Salt Range, Pakistan (Hermann *et al.*, 2012) of late Changhsingian age (Schneebeili-Hermann *et al.*, 2015) and the *Vittatina costabilis* and *Lueckisporites virkkiae* zones of the Paraná Basin, Brazil, dated as Asselian to middle Artinskian, and middle Artinskian to Roadian respectively (Mori and Souza, 2012, Mori *et al.*, 2012). These South American biozones are much older than other proposed correlatives of the upper Madumabisa Formation palynoassemblage, which are all Lopingian, and the Madumabisa faunal assemblages provide very strong evidence that this formation cannot be Cisuralian or Roadian (e.g., Angielczyk *et al.*, 2014). This in turn suggests that several palynomorph taxa appear earlier in South America than other Gondwanan localities, a discrepancy that should be explored more fully.

4. Discussion

The correlations outlined above suggest that the mid-Zambezi upper Madumabisa Formation palynoflora closely corresponds with that of the Lower *Daptocephalus* Assemblage Zone (*sensu* Viglietti *et al.*, 2016) of the main Karoo Basin, which encompasses the lower and middle Balfour Formation, rather than the underlying *Cistecephalus* AZ. Unfortunately, as productive pollen samples were not obtained from within the Madumabisa

Mudstone vertebrate-bearing beds, the individual faunal assemblages cannot be assigned to South African assemblage zones based on palynology.

The upper Madumabisa Formation palynoflora is relatively close to dinocephalian-bearing strata, but from an area slightly to the south and evidently up-section. However, there is a perceived long stratigraphic zone that is under recent alluvium, colluvium and modern geomorphic surfaces, which separate the Madumabisa palynofloral strata from the dinocephalian-bearing strata and several faults. The fault blocks separating the zone were recognized to be both upthrown and downthrown; some in excess of 20 m. Furthermore, the similar lithologies (slightly calcareous organic mudrocks, wackestones and fine sandstones) and the regular thicknesses of sedimentary beds and stacking cycles made correlation between fault planes unknown, thus confounding efforts to measure a continuous stratigraphic succession between the Madumabisa palynofloral-bearing and dinocephalian-bearing interval with much accuracy or confidence.

Alternatively, Sidor et al. (2014) proposed the possibility of dinocephalians surviving into the Lopingian of Zambia, perhaps because their preferred lacustrine habitats persisted longer in these basins. Further fieldwork and palynological collecting may help to refine the dating, but the current results indicate that the middle Madumabisa Formation of the mid-Zambezi Basin is of Wuchiapingian–Changhsingian age. Nyambe and Utting (1997), whose samples originated from the lower one-third of the Madumabisa Formation (ranging through 197 – 205 m of the 640 m thick formation), argued that this lower part of the formation was also of Tatarian (= Lopingian) age (Figure 1B). This disagrees with the sedimentology, which suggests that the formation was deposited over an extended period of time (Nyambe and Dixon, 2000). If the entire Madumabisa Formation is Lopingian, then either our palynological samples from the upper Gwembe Formation are late Capitanian, or a hiatus in deposition or missing stratigraphic section exists between the Gwembe and Madumabisa

formation within our study area. Further sampling through the Gwembe Formation is necessary to investigate these alternatives in more detail.

5. Conclusions

The upper Gwembe Formation palynological assemblage can be correlated to the *Didecitriletes ericianus* Zone of Western Australia, the *Guttulapollenites hannonicus* – *Protohaploxypinus rugatus* Zone (Zone VI) of the northern Karoo Basin, South Africa, Assemblage Zone III of the mid-Zambezi Basin, Zimbabwe and Biozone KK 3 in the Kalahari Karoo Basin, Botswana. On the basis of these correlations, the upper Gwembe Formation is assigned a Guadalupian (Wordian–Capitanian) age. The upper Madumabisa Formation palynoflora is most similar to Assemblage 2 of the Moatize–Minjova Basin, Mozambique and the McKinnon Member palynofloras of East Antarctica. It also bears close resemblance to *Daptocephalus* Assemblage Zone palynofloras of the lower and middle Balfour Formation in the Karoo Basin, South Africa, and Assemblage Sub-zone H of the mid-Zambezi Basin of Zimbabwe and is suggested to be Lopingian (Wuchiapingian–Changhsingian) in age. It can be correlated to the upper *Dulhuntyispora parvithola* Zone of Western and eastern Australia, which is radiometrically dated to 256–254 Ma. The vertebrate-bearing beds of the Madumabisa Formation were not productive for palynomorphs and, as such, the individual faunal assemblages cannot yet be correlated with main Karoo Basin assemblage zones based on palynology.

Acknowledgments

NB acknowledges the support of the DST-NRF Centre of Excellence in Palaeosciences (CoE in Palaeosciences) towards this research. Opinions expressed and conclusions arrived at, are those of the authors and are not necessarily to be attributed to the

392 CoE in Palaeosciences. Funding sources had no involvement in study design or any other
393 aspect of the research. The authors thank K. Mwamulowe and J. Museba (NHCC) as well as
394 the rest of the field team members for assistance and companionship. Petrus Chakane and
395 Prosper Bande prepared the samples. Stephen Tolan provided invaluable assistance in the
396 field as well as copies of several important publications. We thank two anonymous reviewers
397 for their constructive comments and David J. Bottjer for editorial handling, which
398 substantially improved the manuscript. Field work in Zambia was supported by National
399 Science Foundation grants EAR-1337569 (to CAS) and EAR-1337291 (to KDA).

400 Appendix: Species list

401

402 **Gwembe Formation**

403 L190.1:

404 *Alisporites potonie* (Lakhanpal, Sah & Dube) Somers 1968

405 *Calamospora plicata* (Luber & Waltz) Hart 1965

406 *Cannanoropollis* sp.

407 *Chordasporites australiensis* de Jersey 1962

408 *Convolutispora* sp. B Modie 2007

409 *Cycadopites nevesi* (Hart) Hart 1965

410 *Deltoidospora directa* (Balme & Hennelly) Norris 1965

411 *Guttulapollenites hannonicus* Goubin 1965

412 *Laevigatosporites vulgaris* (Ibrahim in Potonie, Ibrahim & Loose) Ibrahim 1933

413 *Striatopodocarpites cancellatus* (Balme & Hennelly) Hart 1965

414

415 L190.2:

416 *Alisporites potonie* (Lakhanpal, Sah & Dube) Somers 1968

417 *Apiculatisporis cornutus* (Balme & Hennelly) Høeg & Bose 1960 (= *Brevitriletes cornutus*

418 (Balme & Hennelly) Backhouse 1991)

419 *Brazilea scissa* (Balme & Hennelly) Foster 1975

420 *Cycadopites cymbatus* (Balme & Hennelly) Segroves 1970

421 *Cycadopites follicularis* Wilson & Webster 1946

422 *Cycadopites nevesi* (Hart) Hart 1965

423 *Cyclogranisporites gondwanensis* Bharadwaj & Salujha 1964

424 *Deltoidospora directa* (Balme & Hennelly) Norris 1965

- 425 *Granulatisporites papillosus* Hart 1965
- 426 *Laevigatosporites colliensis* (Balme & Hennelly) Venkatchala & Kar 1968
- 427 *Limitisporites monstruosus* (Luber & Waltz) Hart 1965
- 428 *Limitisporites rectus* Leschik 1956
- 429 *Lophotriletes novicus* Singh 1964
- 430 *Lueckisporites brasiliensis* Cauduro 1970
- 431 ? *Lunatisporites* sp. cf. *L. noviaulensis* (Leschik) de Jersey 1979
- 432 ? *Mabuitasaccites crucistriatus* (Ybert) Playford & Dino 2000
- 433 *Potonieisporites novicus* Bharadwaj 1954 (*Vestigisporites methoris* of Utting 1970)
- 434 *Protohaploxypinus* sp. cf. *P. amplus* (Balme & Hennelly) Hart 1964
- 435 *Protohaploxypinus rugatus* Segroves 1969
- 436 *Protohaploxypinus limpidus* (Balme & Hennelly) Balme & Playford 1967
- 437 *Protohaploxypinus* sp. cf. *P. perfectus* Utting 1970
- 438 *Protohaploxypinus* sp.
- 439 *Pteruchipollenites gracilis* (Segroves) Foster 1979
- 440 *Scheuringipollenites ovatus* (Balme & Hennelly) Foster 1979
- 441 *Striatosporites heyleri* Playford & Dino 2000
- 442 *Thymospora pseudothiessenii* (Kosanke) Wilson & Venkatachala 1963
- 443 *Thymospora thiessenii* (Kosanke) Wilson & Venkatachala 1963
- 444 *Verrucosisporites andersonii* (Anderson) Backhouse 1988
- 445 *Vestigisporites ventrisaccatus* Anderson 1977
- 446
- 447 **Madumabisa Formation**
- 448 L281:
- 449 *Cycadopites cymbatus* (Balme & Hennelly) Segroves 1970

- 450 *Cycadopites follicularis* Wilson & Webster 1946
- 451 *Cyclogranisporites* sp.
- 452 *Deltoidospora directa* (Balme & Hennelly) Norris 1965
- 453 *Laevigatosporites vulgaris* (Ibrahim in Potonie, Ibrahim & Loose) Ibrahim 1933
- 454 *Marsupipollenites triradiatus* Balme & Hennelly 1956
- 455 *Platysaccus papilionis* Potonié & Klaus 1954
- 456 ? *Plicatipollenites trigonalis* Lele 1964
- 457 *Weylandites lucifer* (Bharadwaj & Salujha) Foster 1975
- 458
- 459 L229:
- 460 Alete spore
- 461 *Apiculatisporis* sp.
- 462 *Botryococcus* sp.
- 463 *Calamospora plicata* (Luber & Waltz) Hart 1965
- 464 *Cycadopites cymbatus* (Balme & Hennelly) Segroves 1970
- 465 *Deltoidospora directa* (Balme & Hennelly) Norris 1965
- 466 *Maculatasporites gondwanensis* Tiwari 1965
- 467 *Pakhapites fusus* (Bose & Kar) Menendez 1971
- 468 *Portalites gondwanensis* (Hemer & Nygreen) Souza et al. 2016
- 469 *Striatopodocarpites* sp.
- 470 *Quadrisporites* sp.
- 471 cf. *Verrucosisporites* sp. MacRae 1988
- 472 *Vittatina scutata* (Balme & Hennelly) Bharadwaj 1962
- 473
- 474 L168.1:

- 475 *Brazilea scissa* (Balme & Hennelly) Foster 1975
- 476 *Cyclogranisporites gondwanensis* Bharadwaj & Salujha 1964
- 477 ? *Cannanoropollis densus* (Lele) Bose & Maheshwari 1968
- 478 *Guttulapollenites hannonicus* Goubin 1965
- 479 *Protohaploxypinus goraiensis* (Potonié & Lele) Hart 1964
- 480 *Pteruchipollenites landianus* (Balme 1970) MacRae 1988
- 481 *Striatopodocarpites cancellatus* (Balme & Hennelly) Hart 1965
- 482 ? *Weylandites lucifer* (Bharadwaj & Salujha) Foster 1975
- 483
- 484 L168.2:
- 485 ? *Alisporites australis* de Jersey 1962
- 486 *Convolutispora* sp.
- 487 *Deltoidospora directa* (Balme & Hennelly) Norris 1965
- 488 *Florinites eremus* Balme & Hennelly 1955
- 489 *Granulatisporites* sp.
- 490 *Granulatisporites trisinus* Balme & Hennelly 1956
- 491 *Klausipollenites schaubergeri* (Potonié & Klaus) Jansonius 1962
- 492 *Laevigatosporites vulgaris* (Ibrahim in Potonie, Ibrahim & Loose) Ibrahim 1933
- 493 *Limitisporites* sp.
- 494 *Lueckisporites* sp. cf. *L. virkkiae* Potonié & Klaus 1954
- 495 *Lueckisporites* sp.
- 496 *Lundbladispora braziliensis* Marques-Toigo & Pons 1974
- 497 *Marsupipollenites striatus* (Balme & Hennelly) Foster 1975
- 498 ? *Mehlisphaeridium fibratum* Segroves 1967
- 499 *Platysaccus papilionis* Potonié & Klaus 1954

- 500 *Protohaploxypinus microcorpus* (Schaarschmidt) Clarke 1965
- 501 *Protohaploxypinus* sp.
- 502 *Protohaploxypinus* sp. cf. *P. limpidus* (Balme & Hennelly) Balme & Playford 1967
- 503 *Striatopodocarpites cancellatus* (Balme & Hennelly) Hart 1965
- 504 *Striatopodocarpites fusus* (Balme & Hennelly) Potonié 1958
- 505 *Tetraporina* sp.
- 506 *Thymospora pseudothiessenii* (Kosanke) Wilson & Venkatachala 1963
- 507 *Valialasaccites* sp.
- 508 cf. *Verrucosisporites* sp. MacRae 1988
- 509 *Weylandites lucifer* (Bharadwaj & Salujha) Foster 1975

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745

Figure 1A

Figure 1B

Figure 2

Table 1

Chronostratigraphy			Lithostratigraphy mid-Zambezi Basin, Zambia	Palynozones Nyambe & Utting (1997)	Main Karoo Basin, South Africa Angielczyk et al. (2014)	North Luangwa, Zambia Utting (1979)	mid-Zambezi Basin, Zimbabwe Falcon (1975)
Permian	Lopingian	Changhsingian	Madumabisa Formation	Unnamed			
		Wuchiapingian			<i>Cistecephalus</i>		
						<i>Cistecephalus</i>	? Sub-Zone IV H ?
	Guadalupian	Capitanian	?		<i>Tapinocephalus</i>		
		Wordian					
		Roadian					
	Cisuralian	Kungurian	Gwembe Formation	<i>Brevitriletes levis</i> - <i>Scheuringipollenites maximus</i>			
		Artinskian					

Table 2

	Palynomorph	Botanical affinity
*#	<i>Protohaploxypinus limpidus</i>	The glossopterid sporangium <i>Arberiella</i> has yielded taeniate bisaccate pollen mostly assignable to <i>Protohaploxypinus limpidus</i> , but also <i>Striatopodocarpites cancellatus</i> (Lindström et al., 1997).
*#	<i>Striatopodocarpites cancellatus</i>	
*#	<i>Convolutispora</i>	Both acavate trilete spores been affiliated to the early fern-like order Zygopteridales, the eusporangiate fern order Marattiales and possibly the leptosporangiate fern order Botryopteridales (Balme, 1995; Taylor et al., 2009; Meyen, 2012). <i>Verrucosisporites</i> has also been linked to the isoetalean lycophytes (Balme, 1995).
*#	<i>Verrucosisporites</i>	
*#	<i>Calamospora</i>	The trilete acavate <i>Calamospora</i> is associated with the Lycopodiophyta, Sphenophyta and eusporangiate ferns (Marattiales) (Grauvogel-Stamm, 1978; Balme, 1995; Taylor et al., 2009).
*#	<i>Deltoidospora</i>	The acavate trilete <i>Deltoidospora</i> represents either eusporangiate ferns (Marattiales) or leptosporangiate ferns (Gleicheniaceae, Dipteridaceae, Dicksoniaceae, Schizaeaceae, Polypodiaceae) (Balme, 1995; Taylor et al., 2009).
*#	<i>Apiculatisporis</i>	The trilete acavate <i>Apiculatisporis</i> is also primarily associated with leptosporangiate ferns and sphenophytes (Balme, 1995).
*#	<i>Granulatisporites</i>	The acavate trilete spore <i>Granulatisporites</i> is affiliated to the Lycophyta (Drepanophycales), leptosporangiate ferns (Botryopteridales), and the Sphenophyta (Equisetales) (Balme, 1995).
*#	<i>Cycadopites</i>	The monosulcate pollen <i>Cycadopites</i> has hereto been associated with bennettitaleans, a group first known from the Triassic, although <i>Cycadopites</i> pollen is commonly found in Permian palynological assemblages (e.g., Balme, 1995).
*#	<i>Thymospora</i>	The monoete spores <i>Thymospora</i> and <i>Laevigatosporites</i> may represent ferns (Marattiales, Polypodiaceae) or progymnosperms (Noeggerathians) (Balme, 1995; Taylor et al., 2009).
*#	<i>Laevigatosporites</i>	
*	<i>Alisporites</i>	The bisaccate pollen <i>Alisporites</i> is associated with peltasperms, podocarp and voltzian conifer cones (Balme, 1995). It may also be allied with glossopterids (Lindström and McLoughlin, 2007).
*	<i>Striatosporites</i>	The monoete spore <i>Striatosporites</i> (<i>Columinisporites</i>) is affiliated to equisetalean sphenophytes (Balme, 1995).
*	<i>Lophotriletes</i>	The trilete spore <i>Lophotriletes</i> represents the fern order Botryopteridales (Balme, 1995).
*	<i>Chordasporites</i>	The parent plants of <i>Chordasporites</i> are currently unknown (Prevec et al., 2010).
*	<i>Lunatisporites</i>	The taeniate bisaccate pollen <i>Lunatisporites</i> has been associated with the Podocarpaceae (Balme, 1995; Taylor et al., 2009).
*	<i>Limitisporites</i>	The non-striate bisaccate pollen <i>Limitisporites</i> and the monosaccate pollen <i>Potonieisporites</i> represent coniferophytes (Balme, 1995; Taylor et al., 2009).
*	<i>Potonieisporites</i>	
#	<i>Marsupipollenites</i>	The monosulcate pollen <i>Marsupipollenites</i> and <i>Vittatina</i> are possibly affiliated to the Glossopteridales and Peltaspermales (Balme, 1995).
*#	<i>Vittatina</i>	
#	<i>Weylandites</i>	The taeniate asaccate pollen <i>Weylandites</i> , which has been recovered from the synangium of <i>Rugatheca</i> , has a possible glossopterid affinity (Pant and Basu, 1977; Balme, 1995; Prevec et al., 2010).
#	<i>Florinites</i>	<i>Florinites</i> , <i>Platysaccus</i> and <i>Lueckisporites</i> represent conifers (Balme, 1995).
#	<i>Platysaccus</i>	
*#	<i>Lueckisporites</i>	
#	<i>Lundbladispota</i>	The cavate spore <i>Lundbladispota</i> is associated with pleuromeialean and other lycophytes (Balme, 1995).

Table 3

Gwembe Formation	Madumabisa Formation
<ul style="list-style-type: none"> ● <i>Alisporites potonie</i> ○● <i>Apiculatisporis cornutus</i> (= <i>Brevitriletes cornutus</i>) ○ <i>Apiculatisporis</i> sp. ● <i>Brazilea scissa</i> ○ <i>Brevitriletes levis</i> ● <i>Calamospora plicata</i> ○● <i>Cannanoropollis</i> sp. ● <i>Chordasporites australiensis</i> ○ <i>Circulisporites</i> sp. ○ <i>Converrucosisporites micronodosus</i> (<i>Microbaculispora micronodosa</i>) ○ <i>Converrucosisporites</i> (<i>Pseudoreticulatispora</i>) <i>pseudoreticulatus</i> ● <i>Convolutispora</i> sp. ○● <i>Cycadopites cymbatus</i> ● <i>Cycadopites follicularis</i> ● <i>Cycadopites nevesi</i> ● <i>Cyclogranisporites gondwanensis</i> ○● <i>Deltoidospora directa</i> ● <i>Granulatisporites papillosus</i> ● <i>Guttulapollenites hannonicus</i> ○ <i>Horriditriletes filiformis</i> ● <i>Laevigatosporites colliensis</i> ○ <i>Laevigatosporites minor</i> ● <i>Laevigatosporites vulgaris</i> ● <i>Limitisporites monstruosus</i> ● <i>Limitisporites rectus</i> ● <i>Lophotriletes novicus</i> ○ <i>Lophotriletes</i> sp. ● <i>Lueckisporites brasiliensis</i> ● ? <i>Lunatisporites</i> sp. cf. <i>L. noviaulensis</i> ● ? <i>Mabuitasaccites crucistriatus</i> ○ <i>Pilasporites plurigenus</i> ○ <i>Platysaccus</i> (<i>Pityosporites</i>) <i>leschikii</i> ○ <i>Plicatipollenites indicus</i> ● <i>Potonieisporites novicus</i> (<i>Vestigisporites methoris</i>) 	<ul style="list-style-type: none"> ● ? <i>Alisporites australis</i> ● <i>Apiculatisporis</i> sp. ● <i>Brazilea scissa</i> ○● <i>Botryococcus</i> sp. ● <i>Calamospora plicata</i> ● ? <i>Cannanoropollis densus</i> ● <i>Convolutispora</i> sp. ○ <i>Corisaccites alutas</i> ● <i>Cycadopites cymbatus</i> ● <i>Cycadopites follicularis</i> ● <i>Cyclogranisporites gondwanensis</i> ○● <i>Cyclogranisporites</i> sp. ○● <i>Deltoidospora directa</i> ● <i>Florinites eremus</i> ● <i>Granulatisporites trisinus</i> ● <i>Granulatisporites</i> sp. ○● <i>Guttulapollenites hannonicus</i> ○ <i>Hamiapollenites</i> sp. ● <i>Klausipollenites schaubergeri</i> ● <i>Laevigatosporites vulgaris</i> ● <i>Limitisporites</i> sp. ○ <i>Lophotriletes novicus</i> ● <i>Lueckisporites</i> sp. cf. <i>L. virkkiae</i> ● <i>Lueckisporites</i> sp. ○ <i>Lunatisporites</i> sp. ● <i>Lundbladispota braziliensis</i> ● <i>Maculatasporites gondwanensis</i> ● <i>Marsupipollenites striatus</i> ● <i>Marsupipollenites triradiatus</i> ● ? <i>Mehlisphaeridium fibratum</i> ● <i>Pakhapites fusus</i> ● <i>Platysaccus papilionis</i> ● ? <i>Plicatipollenites trigonalis</i> ○ <i>Polypodiisporites mutabilis</i> ● <i>Portalites gondwanensis</i> ○ <i>Praecolpatites sinuosus</i>

<ul style="list-style-type: none"> ○● <i>Protohaploxypinus amplus</i> ○● <i>Protohaploxypinus limpidus</i> ● <i>Protohaploxypinus rugatus</i> ● <i>Protohaploxypinus</i> sp. ● <i>Protohaploxypinus</i> sp. cf. <i>P. perfectus</i> ● <i>Pteruchipollenites gracilis</i> ○ <i>Punctatisporites gretensis</i> ○● <i>Scheuringipollenites ovatus</i> ○ <i>Scheuringipollenites maximus</i> ○ <i>Striatopodocarpites cancellatus</i> ○ <i>Striatopodocarpites rarus</i> ○ <i>Striatopodocarpites</i> sp. ● <i>Striatosporites heyleri</i> ● <i>Thymospora pseudothiessenii</i> ● <i>Thymospora thiessenii</i> ● <i>Verrucosisporites andersonii</i> ○ <i>Vestigisporites gondwanensis</i> ○ <i>Vittatina saccata</i> ● <i>Vestigisporites ventrisaccatus</i> ○ <i>Weylandites lucifer</i> 	<ul style="list-style-type: none"> ○● <i>Protohaploxypinus goraiensis</i> ● <i>Protohaploxypinus microcorpus</i> ● <i>Protohaploxypinus</i> sp. ○● <i>Protohaploxypinus limpidus</i> ● <i>Pteruchipollenites landianus</i> ● <i>Quadrisporites</i> sp. ○ <i>Reticuloidosporites warchianus</i> ○● <i>Striatopodocarpites cancellatus</i> ● <i>Striatopodocarpites fusus</i> ○ <i>Striatopodocarpites rarus</i> ● <i>Striatopodocarpites</i> sp. ○ <i>Sulcatisporites prolatus</i> ● <i>Tetraporina</i> sp. ○● <i>Thymospora pseudothiessenii</i> (=<i>Reticuloidosporites warchianus</i>) ● <i>Valialasaccites</i> sp. ● <i>Verrucosisporites</i> sp. ○ <i>Vitreisporites pallidus</i> ● <i>Vittatina scutata</i> ○ <i>Vittatina</i> sp. ○● <i>Weylandites lucifer</i>
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Table 4

Madumabisa Formation	<u>Assemblage 2, Moatize–Minjova Basin, Mozambique</u>	<u>McKinnon Member, East Antarctica</u>	<u>Clouston Farm, Karoo Basin, South Africa</u>	<u>Buckley Formation, Central Transantarctic Mountains</u>	<u>Vittatina costabilis Zone, Paraná Basin, Brazil</u>	<u>lower Sakamena Group, Morondava Basin of Madagascar</u>
	<i>Alisporites</i> <i>Calamospora</i> <i>Cycadopites follicularis</i> <i>Corisaccites alutas</i> <i>Deltoidospora</i> sp. <i>Guttulapollenites hannonicus</i> <i>Hamipollenites</i> <i>Klausipollenites schaubegeri</i> <i>Lueckisporites virkkiae</i> <i>Laevigatosporites vulgaris</i> <i>Marsupipollenites triradiatus</i> <i>Pakhapites</i> sp. <i>Protohaploxypinus goraiensis</i> <i>Protohaploxypinus limpidus</i> <i>Protohaploxypinus microcorpus</i> <i>Reticuloidosporites warchianus</i> (=Thymospora pseudothiessenii) <i>Striatopodocarpites cancellatus</i> <i>Striatopodocarpites fusus</i> <i>Verrucosisporites</i> <i>Vittatina scutata</i> <i>Weylandites lucifer</i>	<i>Alisporites australis</i> <i>Corisaccites alutas</i> <i>Cycadopites follicularis</i> <i>Cyclogranisporites</i> <i>Deltoidospora directa</i> <i>Florinites eremus</i> <i>Granulatisporites trisinus</i> <i>Guttulapollenites hannonicus</i> <i>Laevigatosporites</i> <i>Lueckisporites virkkiae</i> <i>Lunatisporites</i> <i>Lundbladispora</i> <i>Marsupipollenites striatus</i> <i>Marsupipollenites triradiatus</i> <i>Plicatipollenites</i> <i>Protohaploxypinus limpidus</i> <i>Protohaploxypinus microcorpus</i> <i>Striatopodocarpites cancellatus</i> <i>Striatopodocarpites fusus</i> <i>Striatopodocarpites rarus</i> <i>Verrucosisporites</i> <i>Weylandites lucifer</i>	<i>Apiculatisporis</i> sp. <i>Calamospora plicata</i> <i>Cyclogranisporites gondwanensis</i> <i>Protohaploxypinus limpidus</i> <i>Striatopodocarpites cancellatus</i> <i>Striatopodocarpites fusus</i> <i>Weylandites lucifer</i> <u>Assemblage Sub-zone H (Taeniaesporites–Guttulapollenites Assemblage), Zimbabwe</u> <i>Deltoidospora directa</i> <i>Florinites eremus</i> <i>Guttulapollenites hannonicus</i> <i>Hamipollenites</i> <i>Lueckisporites</i> <i>Lunatisporites</i> <i>Marsupipollenites striatus</i> <i>Marsupipollenites triradiatus</i> <i>Platysaccus</i> <i>Protohaploxypinus goraiensis</i> <i>Protohaploxypinus microcorpus</i> <i>Striatopodocarpites cancellatus</i> <i>Thymospora pseudothiessenii</i> <i>Vittatina</i> Striates > 50%	<i>Calamospora</i> sp. <i>Cannanoropollis</i> sp. <i>Cycadopites follicularis</i> <i>Deltoidospora directa</i> <i>Laevigatosporites</i> spp. <i>Lunatisporites</i> <i>Marsupipollenites striatus</i> <i>Marsupipollenites triradiatus</i> <i>Protohaploxypinus limpidus</i> <i>Protohaploxypinus microcorpus</i> <i>Striatopodocarpites cancellatus</i> <i>Striatopodocarpites fusus</i> <i>Striatopodocarpites rarus</i> <u>New Wapadsberg Pass, Karoo Basin, South Africa</u> <i>Calamospora</i> sp. <i>Guttulapollenites hannonicus</i> <i>Klausipollenites schaubegeri</i> <i>Falcisporites</i> (Alisporites) australis <i>Lueckisporites virkkiae</i> <i>Protohaploxypinus goraiensis</i> <i>Protohaploxypinus limpidus</i> <i>Striatopodocarpites cancellatus</i> <i>Weylandites lucifer</i>	<i>Brazilea scissa</i> <i>Calamospora plicata</i> <i>Cycadopites</i> <i>Cyclogranisporites gondwanensis</i> <i>Laevigatosporites vulgaris</i> <i>Lundbladispora braziliensis</i> <i>Pakhapites fusus</i> <u>Lueckisporites virkkiae Zone, Paraná Basin, Brazil</u> <i>Brazilea scissa</i> <i>Calamospora plicata</i> <i>Cycadopites</i> <i>Cyclogranisporites gondwanensis</i> <i>Laevigatosporites vulgaris</i> <i>Lundbladispora braziliensis</i> <i>Lunatisporites</i> sp. <i>Lundbladispora braziliensis</i> <i>Marsupipollenites striatus</i> <i>Pakhapites fusus</i> <i>Portalites gondwanensis</i> <i>Protohaploxypinus goraiensis</i> <i>Protohaploxypinus limpidus</i> <i>Striatopodocarpites cancellatus</i> <i>Striatopodocarpites fusus</i> <i>Verrucosisporites</i> sp. <i>Weylandites lucifer</i>	<i>Lueckisporites virkkiae</i> <i>Lunatisporites</i> <i>Platysaccus</i> <i>Protohaploxypinus limpidus</i> <i>Striatopodocarpites fusus</i> <i>Vittatina</i> <i>Weylandites</i> <u>Chhidru Formation 1, Salt Range, Pakistan</u> Alisporites sp. <i>Calamospora</i> <i>Klausipollenites schaubegeri</i> <i>Lueckisporites</i> sp. Non-taeniate bisaccates <i>Protohaploxypinus limpidus</i> Protohaploxypinus spp. <i>Striatopodocarpites</i> spp. Taeniate bisaccates <i>Verrucosisporites</i> sp. <i>Vittatina</i> spp. Weylandites spp.

Gwembe Formation	<u><i>D. ericianus</i> and <i>P. rugatus</i></u> <u>zones, Australia (* = present only</u> <u>in <i>P. rugatus</i> Zone)</u> <i>Alisporites</i> <i>Brazileia scissa</i> <i>Brevitriletes cornutus</i> <i>Cyclogranisporites</i> sp. <i>Deltoidospora directa</i> <i>Laevigatosporites colliensis</i> <i>Limitisporites rectus</i> <i>Plicatipollenites</i> <i>Protohaploxypinus amplus</i> <i>Protohaploxypinus limpidus</i> <i>Protohaploxypinus rugatus</i>* <i>Pteruchipollenites gracilis</i> <i>Scheuringipollenites ovatus</i> <ul style="list-style-type: none"> ○ <i>Brevitriletes levis</i> ○ <i>Circulisporites</i> sp.* ○ <i>Converrucosisporites micronodosus</i> ○ <i>Converrucosisporites pseudoreticulatus</i> ○ <i>Horriditriletes filiformis</i> ○ <i>Pilasporites plurigenus</i> ○ <i>Punctatisporites gretensis</i> ○ <i>Scheuringipollenites maximus</i> ○ <i>Striatopodocarpites cancellatus</i> ○ <i>Weylandites lucifer</i> 	<u><i>Guttulapollenites hannonicus–</i></u> <u><i>Protohaploxypinus rugatus</i></u> <u>Zone (Zone VI), South Africa</u> <i>Chordasporites australiensis</i> <i>Guttulapollenites hannonicus</i> <i>Protohaploxypinus rugatus</i> <i>Alisporites potonieii</i> <i>Apiculatisporis cornutus</i> <i>Calamospora plicata</i> <i>Cycadopites follicularis</i> <i>Deltoidospora directa</i> <i>Granulatisporites papillosus</i> <i>Laevigatosporites vulgaris</i> <i>Limitisporites monstruosus</i> <i>Lophotriletes novicus</i> <i>Lunatisporites</i> sp. <i>Potonieisporites novicus</i> <i>Protohaploxypinus amplus</i> <i>Protohaploxypinus limpidus</i> <i>Scheuringipollenites ovatus</i> <i>Thymospora pseudothiessenii</i> <i>Thymospora thiessenii</i> <ul style="list-style-type: none"> ○ <i>Punctatisporites gretensis</i> ○ <i>Striatopodocarpites cancellatus</i> ○ <i>Weylandites lucifer</i> 	<u>Seam No. 4, Witbank Coalfield, South</u> <u>Africa</u> <i>Alisporites potonieii</i> <i>Apiculatisporis cornutus</i> <i>Calamospora plicata</i> <i>Deltoidospora directa</i> <i>Laevigatosporites colliensis</i> <i>Protohaploxypinus amplus</i> <i>Protohaploxypinus limpidus</i> <i>Scheuringipollenites ovatus</i> <ul style="list-style-type: none"> ○ <i>Converrucosisporites micronodosus</i> (<i>Microbaculispora micronodosa</i>) ○ <i>Platysaccus</i> (<i>Pityosporites</i>) <i>leschikii</i> ○ <i>Striatopodocarpites cancellatus</i> ○ <i>Striatopodocarpites rarus</i> <u>Volksrust Formation, South Africa</u> <i>Calamospora plicata</i> <i>Cannanoropollis</i> sp. <i>Chordasporites australiensis</i> <i>Cycadopites cymbatus</i> <i>Deltoidospora directa</i> <i>Lophotriletes novicus</i> <i>Protohaploxypinus limpidus</i> <i>Scheuringipollenites ovatus</i> <i>Thymospora pseudothiessenii</i> <ul style="list-style-type: none"> ○ <i>Striatopodocarpites cancellatus</i> ○ <i>Striatopodocarpites</i> sp. ○ <i>Weylandites lucifer</i> 	<u>Assemblage Zone III</u> <u>(<i>Densosporites– Gondispora</i></u> <u>assemblage), mid-Zambezi</u> <u>Basin Zimbabwe</u> <i>Apiculatisporis cornutus</i> <i>Calamospora plicata</i> <i>Cycadopites cymbatus</i> <i>Cycadopites nevesi</i> <i>Deltoidospora directa</i> <i>Laevigatosporites colliensis</i> <i>Limitisporites monstruosus</i> <i>Protohaploxypinus amplus</i> <i>Protohaploxypinus limpidus</i> <i>Scheuringipollenites ovatus</i> <i>Thymospora pseudothiessenii</i> <i>Thymospora thiessenii</i> <ul style="list-style-type: none"> ○ <i>Converrucosisporites micronodosus</i> ○ <i>Platysaccus</i> (<i>Pityosporites</i>) <i>leschikii</i> ○ <i>Striatopodocarpites rarus</i> ○ <i>Striatopodocarpites cancellatus</i> 	<u>Mpwashi Carbonaceous Member,</u> <u>North Luangwa Valley, Zambia</u> <i>Apiculatisporis cornutus</i> <i>Cannanoropollis</i> sp. <i>Cycadopites cymbatus</i> <i>Cycadopites nevesi</i> <i>Deltoidospora directa</i> <i>Plicatipollenites indicus</i> <i>Protohaploxypinus limpidus</i> <i>Protohaploxypinus amplus</i> <i>Protohaploxypinus limpidus</i> <i>Protohaploxypinus perfectus</i> <i>Potonieisporites novicus</i> <i>(Vestigisporites methoris)</i> <ul style="list-style-type: none"> ○ <i>Converrucosisporites pseudoreticulatus</i> ○ <i>Converrucosisporites micronodosus</i> ○ <i>Horriditriletes filiformis</i> ○ <i>Platysaccus</i> (<i>Pityosporites</i>) <i>leschikii</i> ○ <i>Scheuringipollenites maximus</i> 	<u><i>Platysaccus papilionis–</i></u> <u><i>Striatopodocarpites fusus</i></u> <u>Assemblage Zone (Biozone KK</u> <u>3), Kalahari Karoo Basin,</u> <u>Botswana</u> <i>Alisporites potonieii</i> <i>Apiculatisporis cornutus</i> <i>Cycadopites follicularis</i> <i>Cyclogranisporites gondwanensis</i> <i>Deltoidospora directa</i> <i>Granulatisporites papillosus</i> <i>Laevigatosporites vulgaris</i> <i>Laevigatosporites vulgaris</i> <i>Limitisporites monstruosus</i> <i>Potonieisporites novicus</i> <i>Protohaploxypinus limpidus</i> <i>Scheuringipollenites ovatus</i> <i>Vestigisporites ventrisaccatus</i> <i>Weylandites lucifer</i> <ul style="list-style-type: none"> ○ <i>Striatopodocarpites cancellatus</i> ○ <i>Striatopodocarpites rarus</i>
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Figure Captions

Figure 1. A, Map of productive palynology sample localities at existing vertebrate sites in the mid-Zambezi Basin, Zambia, with Karoo deposits shaded in dark grey. Tetrapod-bearing areas of the Luangwa Basin (after Angielczyk *et al.*, 2014) are indicated by number: Area 1 = northern Permian localities of Dixey (1937), Boonstra (1938), Drysdall and Kitching (1962, 1963), Kitching (1963) and Attridge *et al.* (1964); Area 2 = Triassic localities of Drysdall and Kitching (1962, 1963), Kitching (1963) and Attridge *et al.* (1964); Area 3 = North Luangwa National Park localities of Kerr (1974) and Kemp (1975); Area 4 = Munyamadzi localities of Kerr (1974) and Kemp (1975). B, a generalised stratigraphic section of the Permian Gwembe and Madumabisa formations in the Bondo district. “L” numbers to the right of the section refer to fixed localities. Locality 281 is not marked on this stratigraphic section because it is situated in the Lusitu district, which comprises a slightly different stratigraphy to that of Bondo.

Figure 2. Correlation of Permian palynological assemblages from the mid-Zambezi Basin of Zambia to the palynozones of Australia (Backhouse, 1991; Price, 1997; Mory and Backhouse, 1997; Mory *et al.*, 2012; Smith and Mantle, 2013; Metcalfe *et al.*, 2015; Nicoll *et al.*, 2015), and assemblages from South Africa (Aitken, 1998; Prevec *et al.*, 2009, 2010), Antarctica (McLoughlin *et al.*, 1997; Lindström and McLoughlin, 2007; Farabee *et al.*, 1990), Zimbabwe (Falcon, 1975), Madagascar (Goubin, 1965; Wright and Askin, 1987), and Tanzania (Hankel, 1987). Dotted lines indicate uncertainty regarding the upper / lower limits of a section. Thickness of formations not to scale. DTM = Dragons Teeth Member.

Plate 1. (Scale bar: 10 μ m). Selected trilete and monolete spores, and monosaccate, bisaccate, monosulcate and striate pollen from the Gwembe and Madumabisa formations of the mid-Zambezi Basin, Zambia.

1. *Thymospora pseudothiessenii* (Kosanke) Wilson & Venkatachala 1963
2. *Deltoidospora directa* (Balme & Hennelly) Norris 1965
3. *Granulatisporites papillosus* Hart 1965
4. *Potonieisporites novicus* Bharadwaj 1954
5. *Alisporites potonie* (Lakhanpal, Sah & Dube) Somers 1968
6. *Marsupipollenites striatus* (Balme & Hennelly) Foster 1975
7. *Lophotriletes novicus* Singh 1964
8. *Guttulapollenites hannonicus* Goubin 1965
9. *Laevigatosporites vulgaris* (Ibrahim in Potonie, Ibrahim & Loose) Ibrahim 1933
10. *Limitisporites monstruosus* (Luber & Waltz) Hart 1965
11. *Weylandites lucifer* (Bharadwaj & Salujha) Foster 1975
12. *Lundbladisporea braziliensis* Marques-Toigo & Pons 1974 (tetrad)
13. *Scheuringipollenites ovatus* (Balme & Hennelly) Foster 1979
14. *Protohaploxypinus rugatus* Segroves 1969
15. *Lueckisporites brasiliensis* Cauduro 1970
16. *Calamospora plicata* (Luber & Waltz) Hart 1965
17. *Limitisporites rectus* Leschik 1956
18. *Cycadopites follicularis* Wilson & Webster 1946
19. *Vestigisporites ventrisaccatus* Anderson 1977
20. *Striatopodocarpites cancellatus* (Balme & Hennelly) Hart 1965
21. *Cycadopites cymbatus* (Balme & Hennelly) Segroves 1970
22. *Striatosporites heyleri* Playford & Dino 2000 (with detached exoexine)

23. *Protophloxypinus limpidus* (Balme & Hennelly) Balme & Playford 1967

Table Captions

Table 1. Correlations of the Gwembe and Madumabisa formations in the mid-Zambezi Basin of Zambia (by previous authors) to other southern African palynological and vertebrate assemblages. Dotted lines represent uncertainty about how far zones extend. Not to scale.

Table 2. Identified pollen and spores from the Gwembe and Madumabisa formations of the mid-Zambezi Basin, Zambia and their botanical affinities with literature references.

Palynomorph taxa in bold, italicised text are abundant in the assemblages, while those in regular, italicised text are less common. * = present in the Gwembe Formation, # = present in the Madumabisa Formation. Only botanical affinities of palynomorphs recovered in this study are included.

Table 3. Comparison of palynoassemblages of this study and those of Nyambe and Utting (1997) from the Gwembe and Madumabisa formations of the mid-Zambezi Basin, Zambia. ○ = present in palynoassemblages of Nyambe and Utting (1997), ● = present in palynoassemblages of this study.

Table 4. Palynological correlations of the Gwembe and Madumabisa formations, mid-Zambezi Basin, Zambia with other Gondwanan assemblage zones and localities. Shared taxa for both palynoassemblages are used to establish correlations, and taxa in bold are either abundant or considered defining index taxa for that zone. ○ = only recovered by Nyambe and Utting (1997).