Botanical remains from a coprolite from the Pleistocene hominin site of Malapa, Sterkfontein Valley, South Africa

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A coprolite probably from a carnivore described in this paper was recovered from the decalcified sediments of Facies D, close to the cranium of a hominid child, *Australopithecus sediba,* at Malapa, and is dated at 1.95–1.78 Ma based on a combination of faunal, U-Pb and palaeomagnetic dating techniques. Maceration of the coprolite yielded wood fragments and pollen of *Podocarpus* sp. as well as phytolith morphotypes that occur in leaves of *Podocarpus* and many other woody taxa. The Malapa site today is in the Grassland Biome, close to the transition to the Savanna Biome. *Podocarpus/Afrocarpus* occurs about 30 km distance in the Northern Afromontane Forest Biome and is restricted to small patches in the mountain kloofs or small canyons (altitude: 1500–1900 m). The occurrence of this vegetation at Malapa in the past implies that the cooler, moister forest vegetation was more widespread.

Keywords: *Podocarpus*, pollen, wood, phytoliths.

INTRODUCTION

The late Pliocene to Pleistocene cave deposits in the Cradle of Humankind World Heritage Site (South Africa) represent one of the world's most important geological settings, hosting hominin fossils and associated faunal and archaeological remains. The recently discovered site of Malapa in the Cradle of Humankind, 15 km NNE of Sterkfontein (Fig. 1), has yielded a remarkable array of fossil hominins attributed to the species *Australopithecus sediba* (Berger *et al.* 2010) together with remains of well-preserved fauna (Dirks *et al.* 2010). The hominin fossils, one juvenile male and one adult female, occur together with the other faunal remains in near-articulated state in the sedimentary remains of a deeply eroded cave system. The hominin remains were deposited in the cave by a single debris flow which occurred shortly after the death of the animals. The fossils of *Au. sediba* are exceptionally well preserved and represent a transitional form, maybe the best yet found, between early australopithecines and early members of the genus *Homo,* thereby replacing other candidates such as *Homo habilis* as our distant ancestor (Berger *et al.* 2010). A reconstruction of the full environment in which *Au. sediba* lived is therefore of great importance.

However, finding fossil plant remains in calcareous hominin sites for reconstructing environments is extremely difficult (Scott & Bonnefille 1986; Carrión & Scott 1999). Amongst the fossils a coprolite, most likely belonging to a carnivore, was discovered during the course of excavations in 2009. Research by Bryant (1974), Scott (1987), Carrión *et al.* (2001), Horrocks *et al.* (2002, 2003), Gonzalez-Samperiz *et al.* (2003) and Ghosh *et al.* (2008) have shown that coprolites may contain preserved pollen, phytoliths and other macerated plant remains. These remains can be from ingestion of plants directly, from ingestion of herbivores by carnivores or from airborne pollen or plant litter that adhered to the fresh, moist faeces before being buried rapidly and preserved. The coprolite from Malapa preserves evidence of floral remains and provides important clues about the local vegetation and environment in which *Au. sediba* lived and died.

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SITE DESCRIPTION

Geological setting

Cave deposits in the Cradle of Humankind are hosted by stromatolite-rich dolomite of the late Archaean (2.64–2.5 Ga) Malmani Subgroup (Eriksson *et al.* 2006) which is subdivided into five formations based on stromatolite morphology, chert content and the presence of shale and chert-breccia horizons (Eriksson & Truswell 1974). From base to top these formations are: the Oaktree, Monte Christo, Lyttelton, Eccles and Frisco Formations. The Malapa site occurs in well-bedded, chert-free dolomite in the stratigraphic top of the 155 m-thick Lyttelton Formation.

Malapa is positioned within the steep-sided valley of the Grootvleispruit, at an altitude of 1442 masl, and represents an erosion remnant of a de-roofed cave. Dating of the land surface around the fossil site constrains the minimum and maximum erosion rates of the land surface to 4 m/My and 55 m/My, respectively (Dirks *et al.* 2010). This illustrates the dynamic nature of the landscape and indicates that at the time the Malapa fossils were buried, the cave was over 30 m deep (Dirks *et al.* 2010).

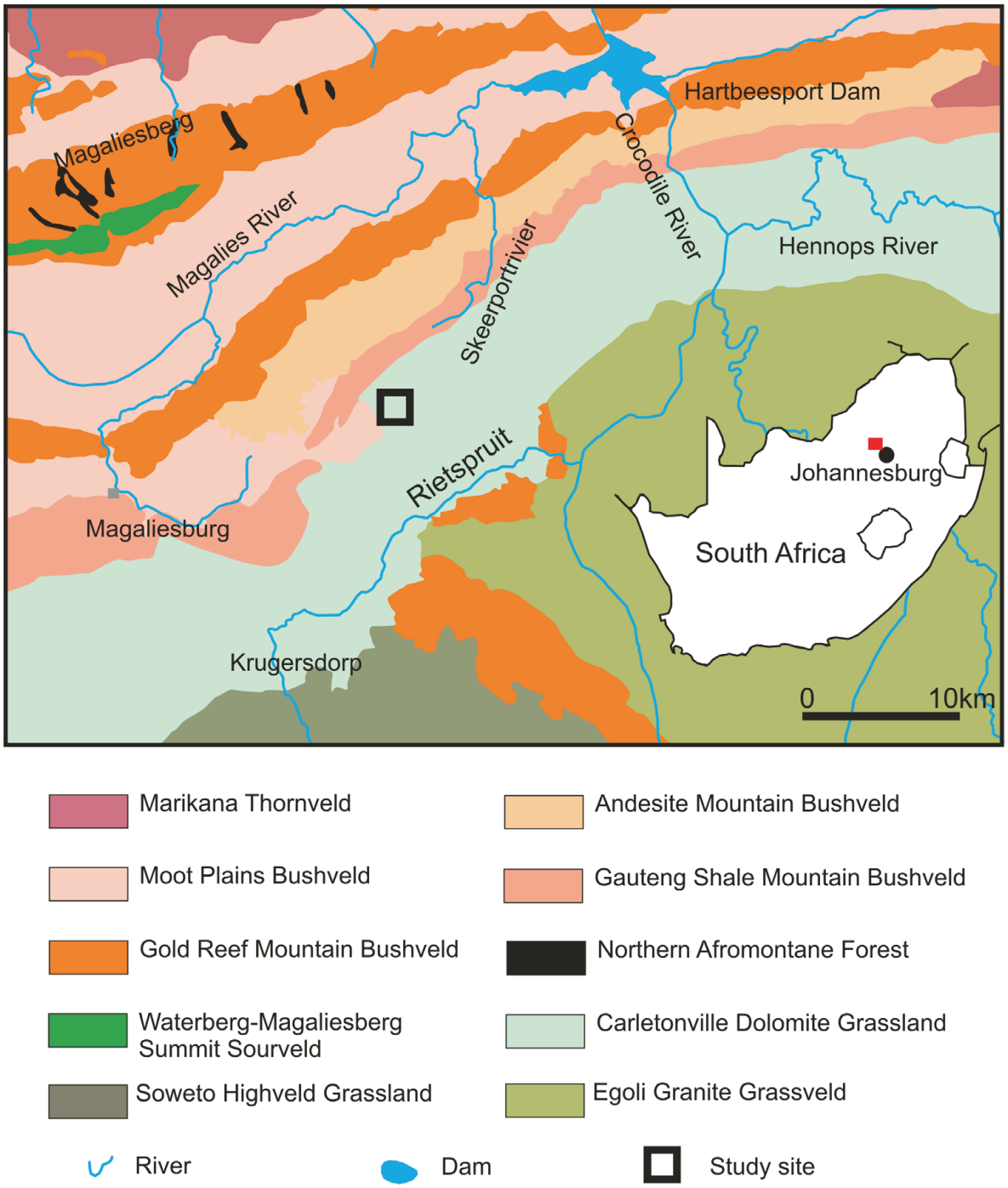

Figure 1. Map of locality with the vegetation biomes indicated (from Mucina & Rutherford 2006).

The fossil remains of *Au. sediba* and associated fauna occur predominantly in two sedimentary facies named Facies D and Facies E (Fig. 2 of Dirks *et al.* 2010) which are positioned stratigraphically above a central flowstone. The fauna includes an unusual abundance of carnivores, several in near-articulated state (Dirks *et al.* 2010). The coprolite described in this paper was recovered from the decalcified sediments of Facies D, close to the child's cranium and probably belonged to a carnivore. The order Carnivora is represented in Facies E and D by four families: Canidae, Felidae, Hyaenidae and Herpestidae. The family Canidae is represented by a single species, *Lycaon pictus*; Felidae is represented by *Dinofelis* sp., *Megantereon whitei* and *Felis silvestris; Parahyaena brunnea* is the sole species representing the Hyaenidae; and Herpestidae is represented by *Atilax mesotes* and *Mungos sp.*

Through a combination of faunal, U-Pb and palaeomagnetic dating techniques the age of the rocks encasing the fossils has been determined at 1.95–1.78 Ma (Dirks *et al.* 2010). Dating involved a U-Pb date for a flowstone sheet below the hominin-bearing sediments of Facies D, and yielded an age of 2.026 ± 0.021 Ma. Paleomagnetic analysis further constrained the age of the fossil-bearing layers above the flowstone to the period coinciding with, or immediately following, a palaeomagnetic reversal at 1.95 Ma (Dirks *et al.* 2010).

Ecological setting

The Malapa site today occurs within the grassland biome, close to the transition to the savanna biome (Fig. 1).

Table 1. Microbotanical remains of the Malapa coprolite.

Micro remains	Outer layer (? local plant debris)	Core (? ingested material)
Wood	2 *Podocarpus/Afrocarpus* sp. 1 dicot wood	1 piece conifer charcoal 1 larger piece with cross-fields 12 woody fragments (indeterminate)
Palynomorphs	1 *Podocarpus* sp. 1 unidentified	barren
Phytoliths	Not tested (insufficient material)	12 orbicular nodulose 6 sub-orbicular nodulose 5 orbicular psilate 3 orbicular rugulose 2 lanceolate psilate 2 tabular psilate 1 irregular nodulose

The hilly region features heavily degraded vegetation due to human activities. Precipitation is around 600 mm per annum (Avery 2001; Mucina *et al.* 2006). The remains of the cave lie within the Carletonville Dolomite Grassland. Poaceae are dominant and species-rich, *Anthospermum rigidum* subsp. *pumilum, Rhus Magalismontana* and *Ziziphus zeyheriana* are typical shrubs (Mucina *et al.* 2006). To the south Egoli Granite Grassland can be found on

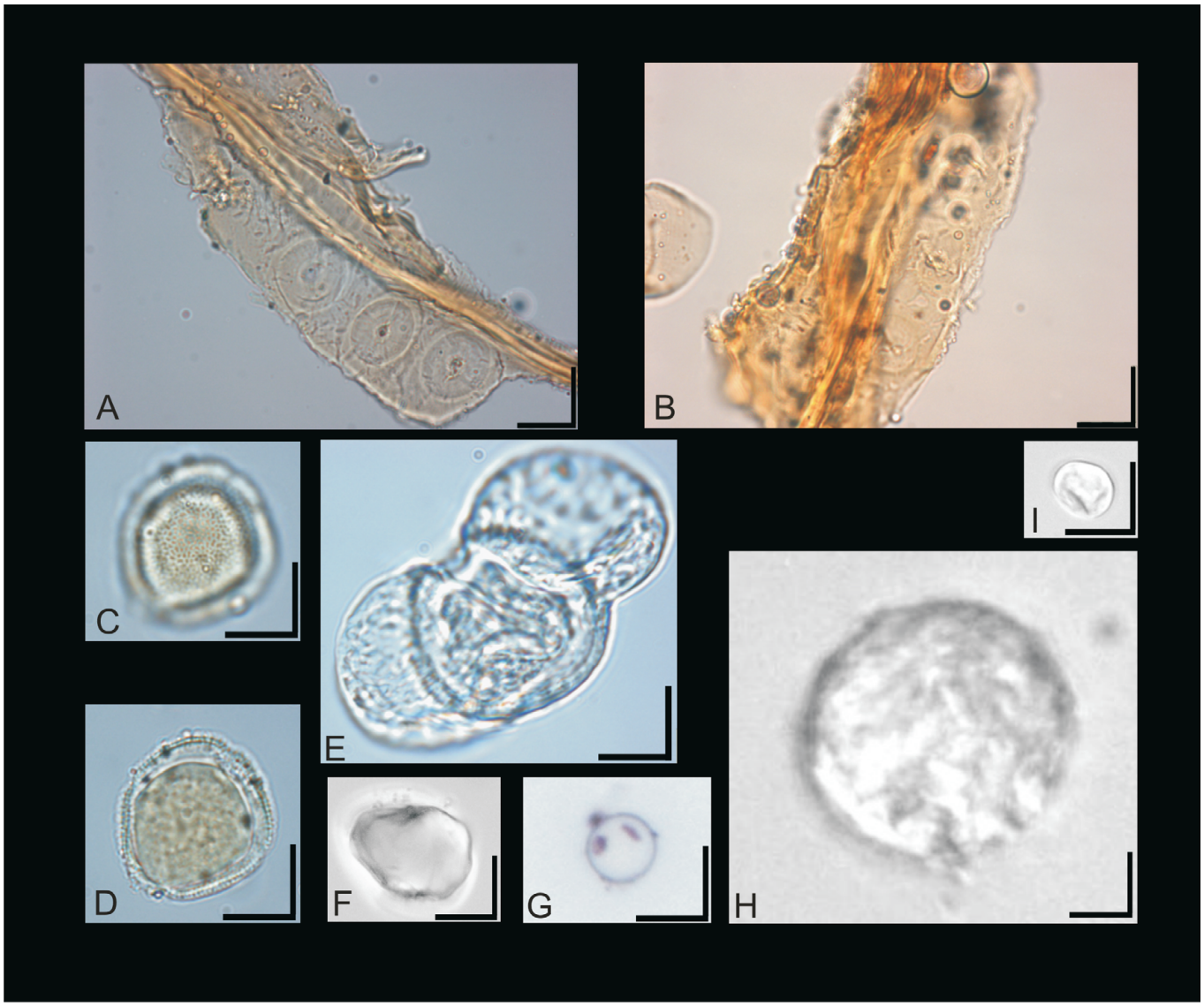

Figure 2. Microbotanical remains from the Malapa coprolite photographed under light microscope. **A, B**, cf. *Podocarpus* sp., tracheid with bordered pits on the radial wall. **C**, **D**, unidentified pollen grain (contaminant?). **E**, *Podocarpus* sp. pollen, bisaccate, length 52 μm. **F**, sub-orbicular irregular phytolith (fossil). **G**, modern *Podocarpus* leaf orbicular psilate phytolith. **H**, orbicular, rugulate fossil phytolith. **I**, orbicular, psilate fossil phytolith. (Scale bar on images A–E is 10 μm; images F–I is 2μm.)

undulating plains and low hills. The grassland is dominated by *Hyparrhenia hirta*, trees and shrubs such as *Rhus pyroides, Vangueria infausta* and *Anthospermum hispidulum* grow on rocky slopes. Soweto Highland Grassland appears in a broad band south of Krugersdorp. *Themeda triandra* is the most important member of the Poaceae; woody species include *Berkheya annectens, Ziziphus zeyheriana* and *Anthospermum* species (Mucina *et al.* 2006). At the precipitation-rich southern slopes of the Magaliesberg the Waterberg–Magaliesberg Summit Sourveld features few small trees and shrubs, e.g. *Englerophytum magalismontanum, Protea caffra* subsp. *caffra, Brachylaena rotundata,* as well as grassland. To the north of the grassland a narrow band of Gauteng Shale Mountain Bushveld appears where trees like *Acacia caffra, Dombeya rotundifolia, Celtis africana* and *Cussonia spicata* as well as a variety of Poaceae are common (Rutherford *et al.* 2006). Andesite Mountain Bushveld, forming small patches to the south of the site and a band north of the Gauteng Shale Mountain Bushveld, are characterized by *Acacia caffra, A. karroo, Celtis africana, Protea caffra* and grasses, e.g. *Themeda triandra.* The vegetation of the Gold Reef Mountain Bushveld, found on east–west trending ridges and close to Krugersdorp, consists of *Acacia* woodland. The herbaceous layer is dominated by Poaceae. The valley of the Magalies River and the region around Magaliesburg is dominated by Moot Plains Bushveld (Rutherford *et al.* 2006, Fig. 1). *Acacia nilotica, A. tortilis* subsp. *heteracantha, Rhus lancea* and *Buddleja saligna* grow on stony soils; grass is common in the herbaceous layer.

Northern Afromontane Forest is restricted to small patches in the mountain kloofs or small canyons (altitude: 1500–1900 m) of Magaliesberg to the north of the site and completely surrounded by Gold Reef Mountain Bushveld. Two patches border the Waterberg–Magaliesberg Summit Sourveld. In comparison the forest is species-poor: *Podocarpus latifolius, Olinia emarginata, Halleria lucida, Afrocarpus falcatus* and *Ilex mitis* are typical trees (Mucina & Geldenhuys 2006).

MATERIALS AND METHODS

A single, whitish coprolite of a rather undiagnostic, slightly flattened shape (29 mm × 21 mm × 11 mm; 7.71 g after cleaning, catalogue no. UW88-0905-B020) has been macerated in the palynology laboratory of the Bernard Price Institute for Palaeontological Research as a test for botanical remains. More coprolites from the Malapa site, which hopefully will be discovered in the future, will be analysed. The coprolite was first thoroughly cleaned with a brush, soap and distilled water to remove modern dust contamination and it was then weighed. To differentiate between ingested plant matter and external accumulation after expulsion of the faeces by the animal, the cleaned outer layer was dissolved in hydrochloric acid (10% HCl) for 2 minutes and the solution was retained for analysis. The outer layer dissolved in HCl had a thickness of 1–2 mm. The remaining inner core of the coprolite and the dissolved surface layers of the coprolite were processed separately for palynomorphs using a standard procedure which includes the addition of HCl, HF, KOH and heavy liquid separation in a saturated $ZnCl_2$ solution. Two *Lycopodium* spore tablets were added to the samples before processing.

A sub-sample of 1.83 g of the coprolite's inner core was set aside for phytolith processing. The sample was processed in 10% HCl to remove carbonates and 30% H_2O_2 to remove organic matter. The remaining residue was mounted onto one slide. There was insufficient outer surface material for phytolith processing and analysis. The pollen and phytolith slides were studied under a Zeiss Axiophot petrographic microscope and photographs taken with a digital camera at ×400 and ×1000 magnification.

RESULTS

The coprolite dissolved easily in HCl and hence was calcium carbonate-rich. Although not rich in plant remains some identifiable microbotanical remains were found and these are described below. Both the inner and outer layers of the coprolite were productive (Table 1); however, only the inner part of the coprolite was tested for phytoliths, a number of which were found and are described. Observed microfossils including wood, pollen and phytoliths are shown in Fig. 2.

Wood fragments

Fragments of tracheids and fibres of conifer and dicot woods respectively were visible in the sample from the outer layers of the coprolite but the dicot fragments are not diagnostic beyond this level of identification. However, there were two pieces of conifer tracheids with bordered pits arranged in a single vertical line along the length of the tracheid. The pits are well spaced, round in outline with a diameter of 20 μm and circular areole of 5 μm (Fig. 2A,B). Such tracheids are water-conducting tissues typically of conifers and the form and arrangement of the bordered pits are indicative of the family.

In order to identify the fragments of conifer wood that have very few features and are missing the key feature for identification, that of the cross-field pits, a survey of the southern hemisphere taxa was done (Phillips 1941; Greguss 1955; IAWA Committee 2004). Araucariaceae have 2–3 rows of pits, alternately arranged and in contact. The Cupressaceae and Podocarpaceae have uniseriate to biseriate and opposite, well-spaced bordered pits on the radial walls of the tracheids. The Pinaceae bordered pits are similar but the pits tend to be more crowded. Of these families only two are represented in southern Africa today with seven species. *Widdringtonia* (Cupressaceae) has three species and *Podocarpus* (Podocarpaceae) has four species (Germishuisen & Meyer 2003). *Widdringtonia* species have round, separate tracheid bordered pits that range in size from 8–20 μm. The pits in *Podocarpus* species have the same arrangement but tend to be larger, 20–35 μm in diameter. The fossil fragments have round, separate bordered pits that are 20 μm wide.

The three species of *Widdringtonia* (commonly called cedars) have disjunct distributions (Coates Palgrave 2002): *Widdringtonia cedarbergensis* Marsh is restricted to the Cederberg Mountains in the western Cape;

W. nodiflora (L.) Powrie occurs north of Zimbabwe, in eastern Zimbabwe, northern South Africa and inland along the eastern margin of the Cape and southern KwaZulu Natal; and *W. schwarzii* (Marloth.) Mast. occurs in the Eastern–Western Cape junction. The Podocarpaceae (yellowwoods) also have a disjunct distribution (Coates Palgrave 2002). *Podocarpus elongatus* (Ait.) L=Hérit. ex Pers. occurs in the western Cape, *Podocarpus* falcatus, or *Afrocarpus falcatus* (Thunb.) C.N. Page is more widespread, along the eastern side of the Cape, Natal and Mpumalanga. *Podocarpus henkelii* Stapf is restricted to KwaZulu Natal and *Podocarpus latifolius* (Thunb.) R.Br. ex Mirb. has a similar distribution to *P. falcatus* but also occurs in eastern Zimbabwe.

Based on the recorded distributions of these conifers none of them occurs naturally today in the Cradle area; so it likely that in the past at least one of the taxa was more widespread. To the north of the site are relict patches of Northern Afromontane Forest (Fig. 1) that includes *P. latifolius* and *P. (A.) falcatus.* Coates Palgrave (2002) notes that these conifers are not pioneers and most of these species grow to large trees in sheltered or protected areas (*W. cedarbergensis, W. nodifolia, W. schwarzii, A. falcatus, P. latifolius*). Most of the species also occur in moist montane or coastal forest or evergreen forest so it is very likely that the fossil trees did too. *P. falcatus,* for example, occurs at 1500–2400 m in East Africa but grows at lower altitudes in South Africa and it prefers an annual rainfall of (800–) 1200–1800(–2200) mm and a mean annual temperature of 13–20°C (Aerts 2008). *P. latifolius* prefers even higher rainfall (1000–2000 mm per annum; Okeyo 2008). Today the Cradle area (altitude 1300–1600m) has 650–750 mm summer rainfall per annum with temperatures varying between the recorded extremes of –12°C and 39°C with an average of 16°C (Bredenkamp & van Rooyen 1998). This is not very different from the preferred altitude and temperature range of *P. falcatus* or *P. latifolius* but the rainfall is much lower at the fossil site today.

Pollen

The sample from the core of the coprolite is barren with the exception of a few fragments of AOM (amorphous organic matter) and the sample from the outer layers of the coprolite is very poor in palynomorphs. One unidentified pollen grain features four apertures (colpi?) and a microreticulate sculpture. A clearly visible interior structure is reminiscent of cytoplasm, so it cannot be excluded that this pollen grain is a contaminant (Fig. 2C,D). Other evidence for contamination, for example pine pollen, is absent from the sample. A second pollen grain belongs to *Podocarpus* sp. (Fig. 2E). The well-preserved palynomorph has no obvious cell contents, is 52 μm wide and is vesiculate-bisaccate (see Erdtman, 1957). Although it seems rather unlikely that the *Podocarpus* pollen is a contaminant, we cannot exclude this possibility. Podocarp or yellowwood pollen is produced in abundance and they have an excellent dispersal mechanism because the air sacs give them some buoyancy. Consequently, yellowwood pollen is often overrepresented in pollen diagrams (Coetzee 1967). Since it is not possible to easily differentiate between the pollen of different *Podocarpus* species this was not attempted in the current study.

Phytoliths

Thirty one phytoliths were counted on the slide from the core of the coprolite. None of the morphotypes was distinctive to family level. Characteristic short-cell phytoliths from Poaceae (grasses) were absent. The majority of morphotypes (29) were spheres with nodulose, psilate or verrucate surfaces (Fig. 2F-I). Verrucate spheres have not been isolated in grasses (Piperno 2006); however, spherical morphotypes are most commonly observed in arboreal and herbaceous monocots and eudicots (Kindo *et al.* 1994; Kealhofer & Piperno 1998; Piperno 2006). A single unsegmented hair and various undiagnostic, irregularly shaped bodies were also observed. Comparing the fossil phytoliths with those from the modern reference collection housed at the Bernard Price Institute (Pereira 2009) we observed that psilate spheres in the size range 10 to 15 μm are also common in the leaves of *Podocarpus latifolius.* However, it should be noted that they are by no means exclusive to the species.

DISCUSSION

If we assume that the botanical material in the core of the coprolite represents plant material that was ingested by the animal then it was a browser, or a carnivore that ate a browser. The outer layer plant material is either ingested material or debris that adhered to the coprolite before preservation so it could indicate the local environment.

Both pollen and wood microbotanical remains in the coprolite indicate the presence of conifer trees. The phytolith morphotypes do not contradict this interpretation but indicate the presence of some woody species. The conifer is most likely a species of *Podocarpus/Afrocarpus.* All the living southern African species prefer higher rainfall than occurs in the area today. Such trees form a stable forest with medium light levels. It is not possible to determine the extent or height of the forest from these data. On the other hand it seems likely that Northern Afromontane Forests with *Podocarpus* also existed in the early Pleistocene, and were perhaps more widespread than today. Generally the genus *Podocarpus* must have been prominent in southern Africa around 2 Ma as its long distance-transported pollen occurs in marine sediments of this age off the Namibian coast (Dupont 2006). Out of a series of modern pollen surface samples from the 1980s in the Sterkfontein/Kromdraai area adjacent to Malapa, it only occurs rarely (0.4%) in one count from September 1988 (Scott 1995). Therefore it is remarkable that only one of the two pollen grains in the Malapa coprolite was a *Podocarpus.* Its apparent prominence in the study area might be a consequence of higher rainfall in the past and suppressed fire. Today the Afromontane Forest in the Magaliesberg is restricted to mountain kloofs. In strong summer rainfall regions forests can only grow if precipitation is greater than 725 mm. Today the distribution of Afromontane Forest is also limited by fire and is limited to areas protected from the wind (Mucina & Geldenhuys 2006). Therefore the borders to fire-prone ecosystems, e.g.

grassland and savannas, are naturally sharp. A more humid climate might have lead to the expansion of *Podocarpus* forest beyond Magaliesberg in the past. This trend has been noted from other Quaternary pollen archives from the same region in the Holocene (e.g. Scott & Vogel 1983) and in the Late Pleistocene where *Podocarpus* were quite prominent in certain periods before the last Glacial Maximum (Scott 1999). Apart from a slightly contaminated travertine sample from Kromdraai Member 3 (0.6%), it was only found in a very low concentration (0.4%) in a more reliable travertine sample from Sterkfontein Member 5 suggesting it was not a prominent part of the vegetation, which included Proteaceae at the time (Scott 1995).

The Pleistocene topography of the Malapa area was not static (Dirks *et al*. 2010). There may have been significant Karoo remnants remaining on top of the dolomite, the valleys in the area would have been less deep, the Magaliesberg was probably less pronounced and the overall altitude could have been lower, considering postulated rapid uplift in the late Pliocene (Partridge & Maud 2000). Direct comparisons with the current settings need some qualification and the past vegetation may well have been richer and more diverse.

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