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PALEOBIODIVERSITY AND LARGE MAMMAL ASSOCIATIONS DURING THE LATE PLIOCENE AND THE EARLY PLEISTOCENE IN SOUTH AFRICA

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ABSTRACT

We present a study of the evolution of large mammal associations during the Late Pliocene and the Early Pleistocene in South Africa. We show, based on factor analysis, the existence of at least three large mammal associations between 4.5 and 0.5 Ma with a large mammal turnover between 3.0 and 2.0 Ma. Furthermore, based on cluster analysis, a large mammal turnover between 2.61 and 2.4 is highlighted. Our results are consistent with the hypothesis of a faunal turnover around 2.5 Ma.

Keywords: mammals, Pliocene, Pleistocene, South Africa, biochronology, palaeoecology

RÉSUMÉ

PALÉOBIODIVERSITÉ ET ASSOCIATIONS DE GRANDS MAMMIFÈRES AU PLIOCÈNE SUPÉRIEUR ET PLÉISTOCÈNE INFÉRIEUR EN AFRIQUE DU SUD

Nous présentons une étude concernant l'évolution des associations de grands mammifères au Pliocène supérieur et Pléistocène inférieur en Afrique du Sud. Nous montrons, sur la base d'analyse factorielle, l'existence d'un minimum de trois associations de mammifère caractéristiques entre 4,5 et 0,5 Ma avec un renouvellement faunique entre 3,0 et 2,0 Ma. L'analyse phénétique met en évidence un renouvellement du cortège de grands mammifères entre 2,61 et 2,4 Ma. Nos résultats sont en accord avec l'hypothèse d'un renouvellement des grandes faunes aux alentours de 2,5 Ma.

Mots-clés : mammifères, Pliocène, Pléistocène, Afrique du Sud, biochronologie, paléoécologie

1 - INTRODUCTION

The transition between the Pliocene and the Pleistocene (2.58 Ma) is marked by the setting up of the glacial and interglacial cycle and the shift from warm-moist to cold-dry conditions (e.g. Zachos *et al*., 2001; DeMenocal, 2004, Maslin *et al*., 2015). This global climatic change resulted in an increase of arid environments and is often associated with a major faunal turnover (e.g. Coppens, 1975; Vrba, 1985, 1988, 1995; Behrensmeyer *et al*., 1997; Alemseged, 2003; deMenocal, 2004), and hominin evolution (e.g. Vrba, 1988, 1995; Potts, 1998; Bobe & Behrensmeyer, 2004; deMenocal, 2004; Behrensmeyer, 2006; Maslin & Christensen, 2007; Bonnefille, 2010; Levin, 2015; Maslin *et al*., 2015; Caley *et al*., 2018). Indeed, this period coincides with the emergence of two new hominin genera: *Homo* and *Paranthropus*. However, most of these relationships are based on the study of East African contexts (e.g. Potts, 1998; Bobe & Eck, 2001; Alemseged, 2003; deMenocal, 2004; Bobe, 2006; Trauth *et al*., 2009; Antón *et al*., 2014; Maslin *et al*., 2014). Despite the fact that previous comparisons between South and East African palaeontological records were made (Turner, 1988; Vrba, 1988; Turner & Wood, 1993a,b; Patterson *et al*., 2014), the geological context of South African caves has prohibited the use of absolute dating or geochemistry methods for a long time and the age of some deposits are still under debate (e.g. Berger *et al*., 2002; Clarke, 2002; Kramers *et al*., 2017; Stratford *et al*., 2017; Bruxelles *et al*., 2018). Thus, the comparison with the well chronological calibrated East African fossil record is challenging. However, the recent development of uranium-lead (U-Pb) and cosmogenic dating methods yielded absolute dates for speleothems and fossil enamel from South African deposits (e.g. Walker *et al*., 2006; Balter *et al*., 2008; de Ruiter *et al*., 2009; Granger *et al*., 2015; Pickering *et al*., 2018). Therefore, the South African faunas associated with hominin remains can now yield more accurate information about evolutionary patterns (e.g. Vrba, 1985, 1993; McKee, 1995), palaeoenvironments (e.g. Vrba, 1974a; Reed, 1997) or hominin evolution and subsistence behaviours (e.g. Brain, 1981; Pickering, 2006).

The goal of this paper is to explore the evolution of

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the large mammal palaeobiodiversity and associations during the Late Pliocene and Early Pleistocene in South Africa. Indeed, the evolution of diversity patterns of large mammal communities can provide significant information concerning the ecological context of hominin evolution (Turner & Wood, 1993b; Du & Alemseged, 2018). We apply cluster and factor analyses in order to test if a shift occurred in the large mammal associations. Our analyses provide a framework to better understand the evolution of ecological structure of large mammal communities during the Late Pliocene and Early Pleistocene in South Africa.

2 - MATERIAL AND METHODS

2.1 - FOSSIL DEPOSITS

Our analyses included 25 Plio-Pleistocene deposits from South Africa (tab. 1, fig. 1). In order to accommodate the disparity of geological dates (tab. 2) and the absence of stratigraphic sequences, we decided to pool deposits into eight 0.5 Ma standard time-units (STU). Moreover, we excluded Sterkfontein member 4 and Stw53 Infill as well as Gladysvale deposits from all the analyses because

Standard Time Unit	Deposits	Estimated ages (in million years)	Methods	References
-	Bolt's Farm Waypoint 160	4-5?	Biochronology	Sénégas & Avery (1998)
1	Jacovec Cavern	4.02	Cosmogenic (26Al/10Be)	Partridge et al. (2003); Kibii (2004)
2	Sterkfontein member 2 (STM2)	3.67 ± 0.16	Cosmogenic (26Al/10Be)	Berger et al. (2002); Granger et al. (2015)
3	Makapansgat member 2 (MKM2)	3.32-3.06	Palaeomagnetism	McFadden et al. (1979); Reed (1996)
3	Makapansgat member 3 (MKM3)	3.32-2.9	Palaeomagnetism	McFadden et al. (1979); Reed (1996)
3-4	Makapansgat member 4 (MKM4)	3.0-2.8	Palaeomagnetism	McFadden et al. (1979); Reed (1996)
-	Bolt's Farm Milo A	3.04-2.58?	Biochronology	Gommery et al. (2012b)
-	Bolt's Farm Aves Cave I	3.0-2.5?	Biochronology	Gommery et al. (2016)
4-5	Taung	2.8-2.4	Biochronology	McKee (1993)
-	STM4	2.95-1.95	U-Pb	Kibii (2004); Pickering et al. (2011)
-	STW53 Infill	2.6-1.49	Biochronology (2.6-2.0), ESR (1.66 ± 0.21), Palaeomagnetism (1.78-1.49 Ma)	Fauna (Pickering, 1999), ESR (Curnoe, 1999), Biochronology (Kuman & Clarke, 2000), Paleomagnetism (Herries & Shaw, 2011)
4-6	Drimolen MQ	2.664 ± 0.392-1.789 ± 0.104	U-Pb	Adams et al. (2016); Pickering et al. (2019)
4	Drimolen Makondo	? 2.61	Palaeomagnetism, ESR, U-Pb	Rovinsky et al. (2015) ; Herries et al. (2018)
5	Kromdraai member 2 (KM2)	> 2.2	Biochronology	Bruxelles et al. (2017); Fourvel et al. (2018)
5-6	Malapa	2.067 ± 0.161	U-Pb	Hartstone-Rose et al. (2013); Val et al. (2015); Kuhn et al. (2016); Pickering et al. (2019)
5-6	Sterkfontein member 5 Oldowan (ST5OL)	2.18 ± 0.21	Cosmogenic (26Al/10Be)	Pickering (1999); Granger et al. (2015)
-	Gladysvale	2.5-1.7	Biochronology	Berger (1993)
5-6	Haasgat Cave	2.3-1.95	Palaeomagnetism and Biochronology	Adams (2012a); Herries et al. (2014)
5-6	Swartkrans member 1 Lower Bank (SKLB)	2.24 ± 0.077-1.706 ± 0.069	U-Pb	Brain (1981); de Ruiter (2003); Pickering et al. (2019)
5-6	Swartkrans member 1 Hanging Remnant (SKHR)	2.248 ± 0.052-1.8 ± 0.005	U-Pb	Brain (1981); de Ruiter (2003); Pickering et al. (2019)
-	Minnaar's Cave	2.0?	Biochronology	Gommery et al. (2012a)
6	Kromdraai B (KB)	2.0-1.8	Biochronology	Brain (1981); Thackeray et al. (2002); Bruxelles et al. (2017)
6	Kromdraai A (KA)	1.8-1.6	Biochronology	Brain (1981); Pickford (2013); Bruxelles et al. (2017)
6	Gondolin 1 (GD1)	~1.78	Palaeomagnetism and Biochronology	Herries et al. (2006); Adams et al. (2007); Herries & Adams (2013)
6	Gondolin 2 (GD2)	~1.8	Palaeomagnetism and Biochronology	Herries et al. (2006); Adams et al. (2007); Herries & Adams (2013)
-	Wonderwerk 12-11	1.8-1.1	Palaeomagnetism	Chazan et al. (2012); Brink et al. (2016)
6-7	Motsetse	1.64-1.0	Biochronology	Berger & Lacruz (2003)
7	Cooper's	< 1.375	U-Pb	de Ruiter et al. (2009); O'Regan et al. (2013); Kuhn et al. (2017); O'Regan & Steininger (2017); Pickering et al. (2019)
7	Sterkfontein member 5 Acheulean (ST5AL)	1.3-1.1	Palaeomagnetism and ESR	Herries et al. (2010); Herries & Shaw (2011)
7	Swartkrans member 2 (SKM2)	1.36 ± 0.29	U-Pb	Brain (1981); de Ruiter (2003); Balter et al. (2008)
7-8	Cornelia	1.07-0.99	Palaeomagnetism	Brink et al. (2012)
8	Swartkrans member 3 (SKM3)	0.96 ± 0.09	Cosmogenic (26Al/10Be)	Brain (1981); de Ruiter (2003); Gibbon et al. (2014)
8	Elandsfontein	1.0-0.6	Biochronology	Klein et al. (2007)
-	Bolt's Farm X Cave	< 1.07-0.99?	Biochronology	Van Zyl et al. (2016)

Tab. 1: Main South African fossil deposits, with chronological frameworks and stand time unit used in our analyses.
We excluded STM4, STW53 Infill, Gladysvale, Bolt's Farm Waypoint 160, Bolt's Farm Mila A, Bolt's Farm Aves Cave I, Bolt's Farm X Cave, Minnaar's Cave and Wonderwerk 12-11 for all analyses (see text for more details).

Tab. 1 : Principaux dépôts fossilifères sud-africains, avec les données chronologiques et les unités standards de temps utilisés dans cette étude. Nous avons exclu STM4, STW53, Gladysvale, Bolt's Farm Waypoint 160, Bolt's Farm Mila A, Bolt's Farm Aves Cave I, Bolt's Farm X Cave, Minnaar's Cave et Wonderwerk 12-11 de toutes les analyses (voir texte pour plus de détails).

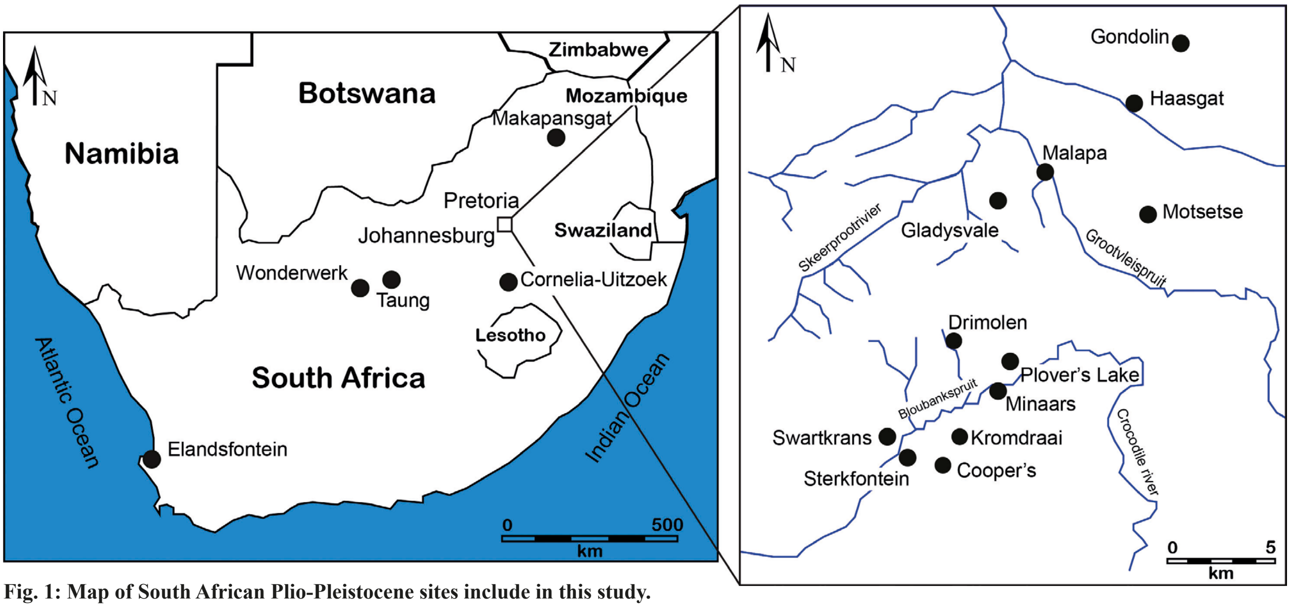

Fig. 1: Map of South African Plio-Pleistocene sites include in this study.
Fig. 1 : Carte des sites plio-pléistocènes sud-africains inclus dans cette étude.

Standard Time Units	Time Span (Million years)	Deposits	n deposits	Number of genera	Number of species
1	4.5-4.0	Jacovec Cavern	1	10	13
2	4.0-3.5	STM2	1	7	8
3	3.5-3.0	MKM2, MKM3, MKM4	3	29	35
4	3.0-2.5	Taung, MKM4, Drimolen MQ, Drimolen Makondo	4	28	35
5	2.5-2.0	Taung, Drimolen MQ, Haasgat, SKLB, KM2, ST5OL, SKHR, Malapa	8	38	59
6	2.0-1.5	KA, KB, SKLB, SKHR, Malapa, Drimolen MQ, GD1, GD2, ST5OL, Haasgat, Motsetse	11	35	59
7	1.5-1.0	Cooper's, ST5AL, SKM2, Motsetse, Cornelia-Uitzoek	5	44	61
8	1.0-0.5	SKM3, Cornelia-Uitzoek, Elandsfontein	3	43	60

Tab. 2: Summary of the composition of each Standard Time Unit (STU).
Tab. 2 : Résumé de la composition de chaque Unité de Temps Standard (UTS).

there is no agreement about their geological ages. The fossils deposits of Bolt's Farm were not considered here because we cannot be confident about their geological ages, the provenance of the material collected by Robert Broom or because they did not yield enough material for now (Gommery *et al*., 2014). Although the Minnaar's Cave has been recently localized, inventory issues, the uncertainty about material provenance and geological age lead us to exclude the site from all the analyses (Gommery *et al*., 2012a). Finally, the layers 11 and 12 of Wonderwerk are not considered because they yielded only two genera, *Eurygnathohippus* sp. and *Gazella* sp. (Brink *et al*., 2016).

2.2 - FAUNAL DATA

Based on literature, we recorded the large mammal fauna (greater than ~5 kg) of all the 25 fossil deposits in terms of presence and absence (tab. 3). We recorded 113 species within 63 genera of large mammals. All of them belong to 5 different mammalian orders (Primates, Carnivora, Cetartiodactyla, Perissodactyla, and Proboscidea) and 13 families. Following Turner and Wood (1993b), we included species identified as "cf." and "aff.". Furthermore, we took into account revised and synonymous taxa.

Our knowledge of palaeobiodiversity can be driven by palaeontological bias rather than true diversity (Durham, 1967; Raup, 1972; Lyman, 1994; Smith, 2001; Smith, 2005; Smith & McGowan, 2007; Lloyd, 2012). Moreover, multiple taphonomical agents could be involved in the accumulation processes of cave fossil assemblages (e.g. Brain, 1981; Pickering *et al*., 2004b; Hopley & Maslin, 2010; Bountalis & Kuhn, 2014; Denys & Patou-Mathis, 2014). For that reason, we decided to use the presence of species rather than its abundance. Indeed, it permits to reduce the taphonomical biases affecting the abundance of taxa (e.g. Behrensmeyer, 1991; Reed, 2008).

2.3 - CLUSTER ANALYSIS

In order to explore the similarity between fossil deposits, we applied cluster analysis on the presence – absence matrix at species level. We first produced a distance matrix by using the function *vegdist* from the

Order	Family	Tribe	Genus	Species	Jacovec Cavern	STM2	MKM2	MKM3	MKM4	STM4	Taung	STW53 Infill	Gladysvale	Haasgat Cave	SKLB	KA	KB	KM2	ST5OL	SKHR	Malapa	Drimolen Makondo	Drimolen MQ	GD1	GD2V	GD2	Motsetse	Cooper's	ST5AL	SKM2	Cornelia-Uitzoek	SKM3	Elands-fontein
Primate	Hominidae		Australopithecus	A. africanus	0	0	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Primate	Hominidae		Australopithecus	A. sediba	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Primate	Hominidae		Australopithecus	Australopithecus sp.	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Primate	Hominidae		Paranthropus	P. robustus	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	0	0	1	0	0	0	0	1	0	1	0	1	0
Primate	Hominidae		Homo	H. ergaster	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Primate	Hominidae		Homo	H. heidelbergensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Primate	Hominidae		Homo	Homo sp.	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0
Primate	Cercopithecidae		Cercopithecoides	C. williamsi	0	0	0	1	1	1	0	1	1	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
Primate	Cercopithecidae		Cercopithecoides	C. haasgati	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Primate	Cercopithecidae		Cercopithecoides	Cercopithecoides sp.	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0
Primate	Cercopithecidae		Papio	P. hamadryas robinsoni	0	0	1	0	0	1	0	0	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Primate	Cercopithecidae		Papio	P. hamadryas angusticeps	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Primate	Cercopithecidae		Papio	P. hamadryas	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0
Primate	Cercopithecidae		Papio	P. izodi	1	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Primate	Cercopithecidae		Papio	P. indens	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0
Primate	Cercopithecidae		Theropithecus	T. oswaldi	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1	0	1	1
Primate	Cercopithecidae		Theropithecus	T. darti	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Primate	Cercopithecidae		Cercocebus	Cercocebus sp.	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Primate	Cercopithecidae		Gorgopithecus	G. major	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Primate	Cercopithecidae		Gorgopithecus	Gorgopithecus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Primate	Cercopithecidae		Parapapio	P. jonesi	1	1	0	1	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Primate	Cercopithecidae		Parapapio	P. broomi	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Primate	Cercopithecidae		Parapapio	P. whitei	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Primate	Cercopithecidae		Parapapio	Parapapio sp.	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0
Carnivora	Canidae		Vulpes	V. chama	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1
Carnivora	Canidae		Vulpes	V. pulcher	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carnivora	Canidae		Vulpes	V. skinneri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Carnivora	Canidae		Vulpes	Vulpes sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0
Carnivora	Canidae		Lycaon	L. sekowei	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Carnivora	Canidae		Lycaon	L. pictus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Carnivora	Canidae		Lycaon	Lycaon sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carnivora	Canidae		Canis	C. mesomelas	1	0	0	1	1	1	1	1	0	0	1	1	0	1	0	1	0	0	0	0	1	1	1	1	1	1	0	1	1
Carnivora	Canidae		Canis	C. terblanchi	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carnivora	Canidae		Canis	C. brevirostris	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carnivora	Canidae		Canis	C. adustus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carnivora	Canidae		Canis	C. atrox	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carnivora	Canidae		Canis	Canis sp.	0	0	0	1	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carnivora	Felidae		Dinofelis	D. piveteaui	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0
Carnivora	Felidae		Dinofelis	D. barlowi	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0
Carnivora	Felidae		Dinofelis	D. aronoki	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Carnivora	Felidae		Dinofelis	Dinofelis sp.	0	0	1	1	1	0	0	0	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0	0
Carnivora	Felidae		Megantereon	M. whitei	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1
Carnivora	Felidae		Megantereon	M. cultridens	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Carnivora	Felidae		Megantereon	M. eurynodon	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carnivora	Felidae		Megantereon	Megantereon sp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carnivora	Felidae		Homotherium	H. crenatidens	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carnivora	Felidae		Homotherium	H. latidens	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carnivora	Felidae		Homotherium	Homotherium sp.	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Carnivora	Felidae		Panthera	P. pardus	1	1	0	1	0	1	1	0	1	0	1	0	1	1	0	1	1	0	1	0	0	0	0	1	0	1	0	1	1
Carnivora	Felidae		Panthera	P. leo	1	0	0	0	0	1	0	0	1	0	1	1	0	0	1	1	0	0	0	0	0	0	0	1	1	1	1	0	1
Carnivora	Felidae		Acynonix	A. jubatus	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0
Carnivora	Felidae		Panthera	Panthera sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Carnivora	Felidae		Caracal	C. caracal	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1
Carnivora	Felidae		Felis	F. serval	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carnivora	Felidae		Felis	Felis sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Carnivora	Hyaenidae		Crocuta	C. ultra	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Carnivora	Hyaenidae		Pachycrocuta	P. bellax	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carnivora	Hyaenidae		Pachycrocuta	P. brevirostris	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carnivora	Hyaenidae		Pachycrocuta	Pachycrocuta sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carnivora	Hyaenidae		Crocuta	C. crocuta	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	1	1	0	1	1

Order	Family	Tribe	Genus	Species	Jacovec Cavern	STM2	MKM2	MKM3	MKM4	STM4	Taung	STW53 Infill	Gladysvale	Haasgat Cave	SKLB	KA	KB	KM2	ST5OL	SKHR	Malapa	Drimolen Makondo	Drimolen MQ	GD1	GD2V	GD2	Motsetse	Cooper's	ST5AL	SKM2	Cornelia-Uitzoek	SKM3	Elands-fontein
Carnivora	Hyaenidae		Crocuta	Crocuta sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carnivora	Hyaenidae		Parahyaenna	P. brunnea	0	0	0	0	0	1	0	0	0	0	1	0	1	1	0	1	1	0	0	0	0	0	0	1	1	1	0	1	1
Carnivora	Hyaenidae		Hyaena	H. hyaena	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Carnivora	Hyaenidae		Hyaena	H. makapani	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carnivora	Hyaenidae		Chasmaporthetes	C. nitidula	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	1	0	1	0	1	0
Carnivora	Hyaenidae		Chasmaporthetes	C. silberbergi	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Carnivora	Hyaenidae		Chasmaporthetes	Chasmaporthetes sp.	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carnivora	Hyaenidae		Proteles	Proteles sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	0	1	0
Carnivora	Mustelidae		Aonyx	A. capensis	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1
Carnivora	Mustelidae		Mellivora	M. capensis	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Carnivora	Mustelidae		Mellivora	M. sivalensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Carnivora	Viverridae		Civettictis	C. civetta	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carnivora	Viverridae		Civettictis	C. braini	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artiodactyla	Bovidae	Alcelaphini	Megalotragus	Megalotragus sp.	0	0	0	1	0	1	0	0	1	1	1	1	0	1	0	1	1	0	1	0	0	0	0	1	0	1	0	1	0
Artiodactyla	Bovidae	Alcelaphini	Megalotragus	M. priscus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Artiodactyla	Bovidae	Alcelaphini	Megalotragus	M. eucornutus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Artiodactyla	Bovidae	Alcelaphini	Alcelaphus	A. buselaphus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artiodactyla	Bovidae	Alcelaphini	Alcelaphus	Alcelaphus sp.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artiodactyla	Bovidae	Alcelaphini	Connochaetes	C. taurinus	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Artiodactyla	Bovidae	Alcelaphini	Connochaetes	C. gnou	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Artiodactyla	Bovidae	Alcelaphini	Connochaetes	Connochaetes sp.	0	0	0	0	0	1	0	0	0	1	1	1	1	0	0	1	0	0	1	0	1	1	0	1	0	1	0	1	0
Artiodactyla	Bovidae	Alcelaphini	Damaliscus	D. lunatus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Artiodactyla	Bovidae	Alcelaphini	Damaliscus	D. dorcas	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artiodactyla	Bovidae	Alcelaphini	Damaliscus	D. niro	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Artiodactyla	Bovidae	Alcelaphini	Damaliscus	D. pygargus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artiodactyla	Bovidae	Alcelaphini	Damaliscus	D. gentryi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artiodactyla	Bovidae	Alcelaphini	Damaliscus	Damaliscus sp.	0	0	0	0	0	1	0	1	1	1	1	1	0	0	1	1	0	0	1	0	1	0	1	1	1	1	0	1	1
Artiodactyla	Bovidae	Alcelaphini	Parmularius	Parmularius sp.	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1
Artiodactyla	Bovidae	Alcelaphini	Numidocapra	N. arambourgi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Artiodactyla	Bovidae	Alcelaphini	Numidocapra	Numidocapra crassicornis	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artiodactyla	Bovidae	Ovicaprini	Makapania	M. broomi	1	0	0	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artiodactyla	Bovidae	Ovicaprini	Makapania	Makapania sp.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Artiodactyla	Bovidae	Antilopini	Antidorcas	A. marsupialis	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0
Artiodactyla	Bovidae	Antilopini	Antidorcas	A. recki	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	1	0	0	1	1	1	0	0	1	0	1	1	1	1
Artiodactyla	Bovidae	Antilopini	Antidorcas	A. bondi	0	0	0	0	0	1	0	0	1	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0
Artiodactyla	Bovidae	Antilopini	Antidorcas	A. australis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Artiodactyla	Bovidae	Antilopini	Antidorcas	Antidorcas sp.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	1
Artiodactyla	Bovidae	Antilopini	Gazella	G. vanhoepeni	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artiodactyla	Bovidae	Antilopini	Gazella	G. wellsi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artiodactyla	Bovidae	Antilopini	Gazella	G. gracilior	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artiodactyla	Bovidae	Antilopini	Gazella	Gazella sp.	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1
Artiodactyla	Bovidae	Aepycerotini	Aepyceros	A. melampus	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Artiodactyla	Bovidae	Aepycerotini	Aepyceros	A. helmoedi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Artiodactyla	Bovidae	Aepycerotini	Aepyceros	Aepyceros sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Artiodactyla	Bovidae	Neotragini	Ourebia	O. ourebi	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Artiodactyla	Bovidae	Neotragini	Raphicerus	R. campestris	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0
Artiodactyla	Bovidae	Neotragini	Raphicerus	R. melanotis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Artiodactyla	Bovidae	Neotragini	Raphicerus	Raphicerus sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	1	1	0	1	0	0
Artiodactyla	Bovidae	Bovini	Syncerus	S. caffer	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artiodactyla	Bovidae	Bovini	Syncerus	S. antiquus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Artiodactyla	Bovidae	Bovini	Syncerus	S. acoelotus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artiodactyla	Bovidae	Bovini	Syncerus	S. kohllarseni	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artiodactyla	Bovidae	Bovini	Syncerus	Syncerus sp.	1	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0
Artiodactyla	Bovidae	Bovini	Pelorovis	P. antiquus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Artiodactyla	Bovidae	Bovini	Pelorovis	Pelorovis sp.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Artiodactyla	Bovidae	Tragelaphini	Tragelaphus	T. oryx	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1
Artiodactyla	Bovidae	Tragelaphini	Tragelaphus	T. strepsiceros	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	1	1	0	0	0	1	0	0	1	0	1	0	1	1
Artiodactyla	Bovidae	Tragelaphini	Tragelaphus	T. scriptus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	0
Artiodactyla	Bovidae	Tragelaphini	Tragelaphus	T. angasi	0	0	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0
Artiodactyla	Bovidae	Tragelaphini	Tragelaphus	T. pricei	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Order	Family	Tribe	Genus	Species	Jacovec Cavern	STM2	MKM2	MKM3	MKM4	STM4	Taung	STW53 Infill	Gladysvale	Haasgat Cave	SKLB	KA	KB	KM2	ST5OL	SKHR	Malapa	Drimolen Makondo	Drimolen MQ	GD1	GD2V	GD2	Motsetse	Cooper's	ST5AL	SKM2	Cornelia-Uitzoek	SKM3	Elands-fontein
Artiodactyla	Bovidae	Tragelaphini	Tragelaphus	Tragelaphus sp.	0	0	0	1	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0
Artiodactyla	Bovidae	Hippotragini	Hippotragus	H. broomi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artiodactyla	Bovidae	Hippotragini	Hippotragus	H. equinus	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Artiodactyla	Bovidae	Hippotragini	Hippotragus	H. niger	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Artiodactyla	Bovidae	Hippotragini	Hippotragus	H. gigas	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1
Artiodactyla	Bovidae	Hippotragini	Hippotragus	H. angasi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artiodactyla	Bovidae	Hippotragini	Hippotragus	H. cookei	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artiodactyla	Bovidae	Hippotragini	Hippotragus	H. leucophaeus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Artiodactyla	Bovidae	Hippotragini	Hippotragus	Hippotragus sp.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0
Artiodactyla	Bovidae	Hippotragini	Kobus	K. leche	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Artiodactyla	Bovidae	Hippotragini	Kobus	K. ellipsiprymnus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artiodactyla	Bovidae	Hippotragini	Kobus	Kobus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artiodactyla	Bovidae	Hippotragini	Oryx	O. gazella	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Artiodactyla	Bovidae	Hippotragini	Wellsiana	W. torticornuta	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artiodactyla	Bovidae	Reduncini	Redunca	R. arundinum	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1
Artiodactyla	Bovidae	Reduncini	Redunca	R. fulvorufula	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0
Artiodactyla	Bovidae	Reduncini	Redunca	R. darti	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artiodactyla	Bovidae	Reduncini	Redunca	Redunca sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0
Artiodactyla	Bovidae	Peleini	Pelea	P. capreolus	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	1	0
Artiodactyla	Bovidae	Peleini	Pelea	Pelea sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Artiodactyla	Bovidae	Cephalophini	Oreotragus	O. oreotragus	0	0	0	1	0	0	1	0	1	0	1	0	0	0	0	1	0	0	0	1	1	0	1	0	0	1	0	1	0
Artiodactyla	Bovidae	Cephalophini	Oreotragus	O. major	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artiodactyla	Bovidae	Cephalophini	Oreotragus	Oreotragus sp.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Artiodactyla	Bovidae	Cephalophini	Cephalophus	Cephalophus sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artiodactyla	Bovidae	Cephalophini	Sylvicapra	S. grimmia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Artiodactyla	Giraffidae		Sivatherium	S. maurusium	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	1
Artiodactyla	Giraffidae		Giraffa	G. jumae	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artiodactyla	Suidae		Metridiochoerus	M. modestus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0
Artiodactyla	Suidae		Metridiochoerus	M. andrewsi	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	1	0	1	0	1	0	1	1
Artiodactyla	Suidae		Metridiochoerus	M. compactus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Artiodactyla	Suidae		Metridiochoerus	Metridiochoerus sp.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Artiodactyla	Suidae		Phacochoerus	P. antiquus	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artiodactyla	Suidae		Phacochoerus	P. aethiopicus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Artiodactyla	Suidae		Phacochoerus	Phacochoerus sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
Artiodactyla	Suidae		Phacochoerus	P. shawi	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artiodactyla	Suidae		Kolpochoerus	K. paiceae	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Artiodactyla	Suidae		Kolpochoerus	K. heseloni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Artiodactyla	Suidae		Potamochoerus	P. porcus	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artiodactyla	Suidae		Notochoerus	N. capensis	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artiodactyla	Suidae		Tapinochoerus	T. meadowsi	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artiodactyla	Hippopotamidae		Hippotamus	Hippopotamus sp.	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0
Artiodactyla	Hippopotamidae		Hippotamus	H. amphibius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Artiodactyla	Hippopotamidae		Hippotamus	H. gorgops	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Perissodactyla	Equidae		Equus	E. quagga	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	1
Perissodactyla	Equidae		Equus	E. capensis	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	1	0	1	1	1	1
Perissodactyla	Equidae		Equus	E. burchelli	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Perissodactyla	Equidae		Equus	Equus sp.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	1	1	1	0	0	1	0	0	0	0
Perissodactyla	Equidae		Hipparion	H. lybicum	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0
Perissodactyla	Equidae		Hipparion	H. steyleri	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Perissodactyla	Equidae		Hipparion	Hipparion sp.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Perissodactyla	Equidae		Eurygnathohippus	E. cornelianus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0
Perissodactyla	Rhinocerotidae		Ceratotherium	C. simum	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Perissodactyla	Rhinocerotidae		Diceros	D. bicornis	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Perissodactyla	Chalicotheridae		Ancylotherium	A. hennigi	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Proboscidea	Elephantidae		Elephas	E. recki	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Proboscidea	Elephantidae		Elephas	Elephas sp.	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Proboscidea	Elephantidae		Loxodonta	L. atlantica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

Tab. 3: Presence and absence of large mammal species in Late Pliocene and Early Pleistocene sites from South Africa.
*Tab. 3 : Présence et absence des espèces de grands mammifères des sites du Pliocène supérieur et du Pléistoc*ène inférieur d’Afrique du Sud.

vegan package in R (R Development Core Team, 2015), with the Jaccard Index method, which is based on the number of species shared by two samples and the number of species unique to each of them (e.g. Legendre & Legendre, 1997; Chao *et al*., 2004; Belmaker & Hovers, 2011). Then, we applied the *hclust* function on the distance matrix with the average method (UPGMA).

2.4 - FACTOR ANALYSIS

We performed factor analysis in order to identify characteristic associations of mammal taxa through time (Sepkoski, 1981; Figueirido *et al*., 2012; Morales et al., 2015). We first calculated the number of species by genera within each STU. Then, the *fa* function from the *psych* package in R software was applied. As recommended by Morales *et al*. (2015), we used the "varimax" rotation method to maximize the sum of variances of the square loadings. The number of factors was fixed at 3 according to the scree plot produced by the function *nScree* from the *nFactors* package. According to Sepkoski (1981), the scores of each variables (i.e. the number of species within genera) are measures of the relative importance or diversity of each taxon within the factor. Thus, genera with a score larger than or equal to 0.5 were selected, since they depict the main contribution to the taxonomic diversity within each factor (Sepkoski, 1981). These factors are interpreted as representing "great evolutionary faunas", which are defined as associations of taxa sharing time of origination, diversification and extinction (Figueirido *et al*, 2012).

3 – RESULTS

3.1 - CLUSTER ANALYSIS

The cluster analysis shows an interesting pattern (fig. 2). Indeed, most of the deposits were grouped by localities (Makapansgat, Gondolin, Swartkrans, Sterkfontein). The Jacovec Cavern (4.02 Ma) and Sterkfontein Member 2 (3.67 Ma), the two oldest deposits, are close to each other. Interestingly, Makapansgat member 3 (3.32-2.9 Ma) and 4 (3.0-2.8 Ma), which are grouped together, are also linked to Taung (2.8-2.4 Ma) when Makapansgat member 2 (3.32-3.06 Ma) is grouped with Drimolen Makondo (2.61 Ma). Haasgat, Drimolen MQ, Malapa and Kromdraai B, which are all three dated around 2.0 (tab. 1), showed similarity based on presence-absence data. Sterkfontein member 5 Oldowan (2.18 ± 0.21 Ma) and Acheulean (1.3-1.1 Ma) are grouped together, linked to Motsetse (1.64-1.0 Ma). Gondolin 1 (1.78 Ma) and 2 (1.8 Ma) are closed to each other. Our cluster analysis shows a group composed of Swartkrans member 1 to 3 (from 2.3 Ma for the member 1 to 0.96 Ma for member 3) which are close to Cooper's D (1.3 Ma), Elandsfontein (1.0-0.6 Ma), Kromdraai A (1.8-1.6 Ma) and member 2 (> 2.2 Ma), to a lesser extent. Finally, the Cornelia-Uitzoek (1.07-0.99 Ma) is isolated and seems to have a specific taxonomic composition.

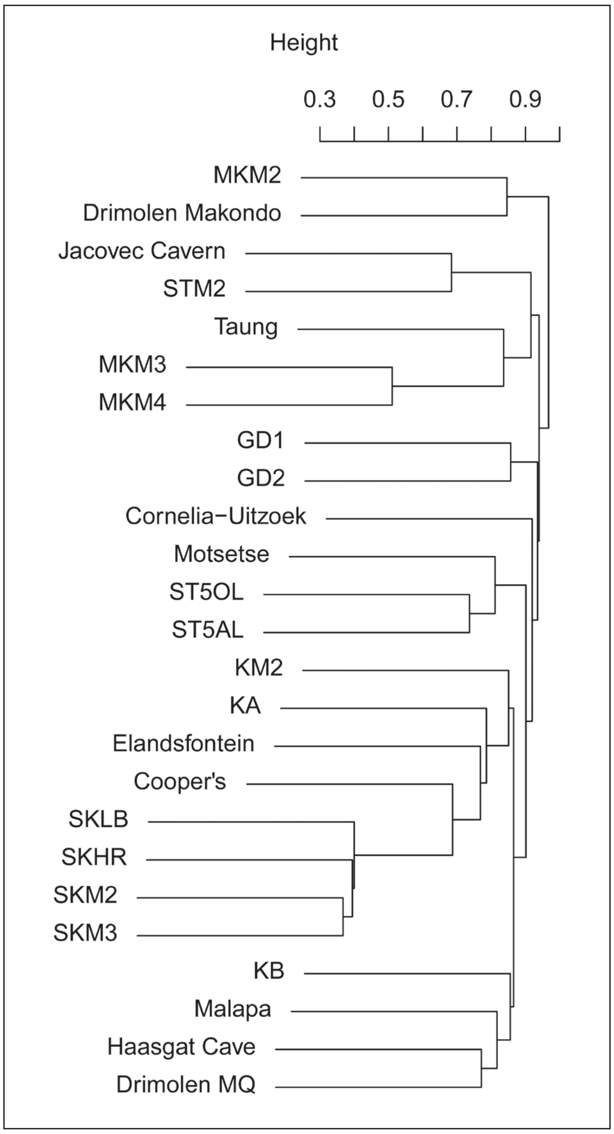

Fig. 2: UPGMA cluster analysis showing the similarity (Jaccard Index) of the deposits based on the presence-absence of species.

Fig. 2 : Résultat de l'analyse phénétique UPGMA montrant la similarité (indice de Jaccard) des dépôts selon la présence-absence des espèces.

3.2 - FACTOR ANALYSIS

Through the factor analysis, we could identify three characteristic large mammal associations (LMA) through the Late Pliocene and the Early Pleistocene in South Africa (fig. 3) that explain 68 % of the original variance. Each of these evolutionary faunas are composed of specific association of the most diverse genera (tab. 4). We should be cautious because the first two STU's are composed of only one deposit.

3.2.1 - Large Mammal Association I (STU 1-2)

This evolutionary fauna, covering the two first STU from 4.5 to 3.5 Ma and showing a peak of diversity between 4.0 and 3.5 Ma, seems to be characterized by a high diversity of carnivore taxa (tab. 4). Seven genera contribute to this LMA I (scores > 1). The most characteristic genus appears to be *Chasmaporthetes*. Indeed, it is represented by two species at that time,

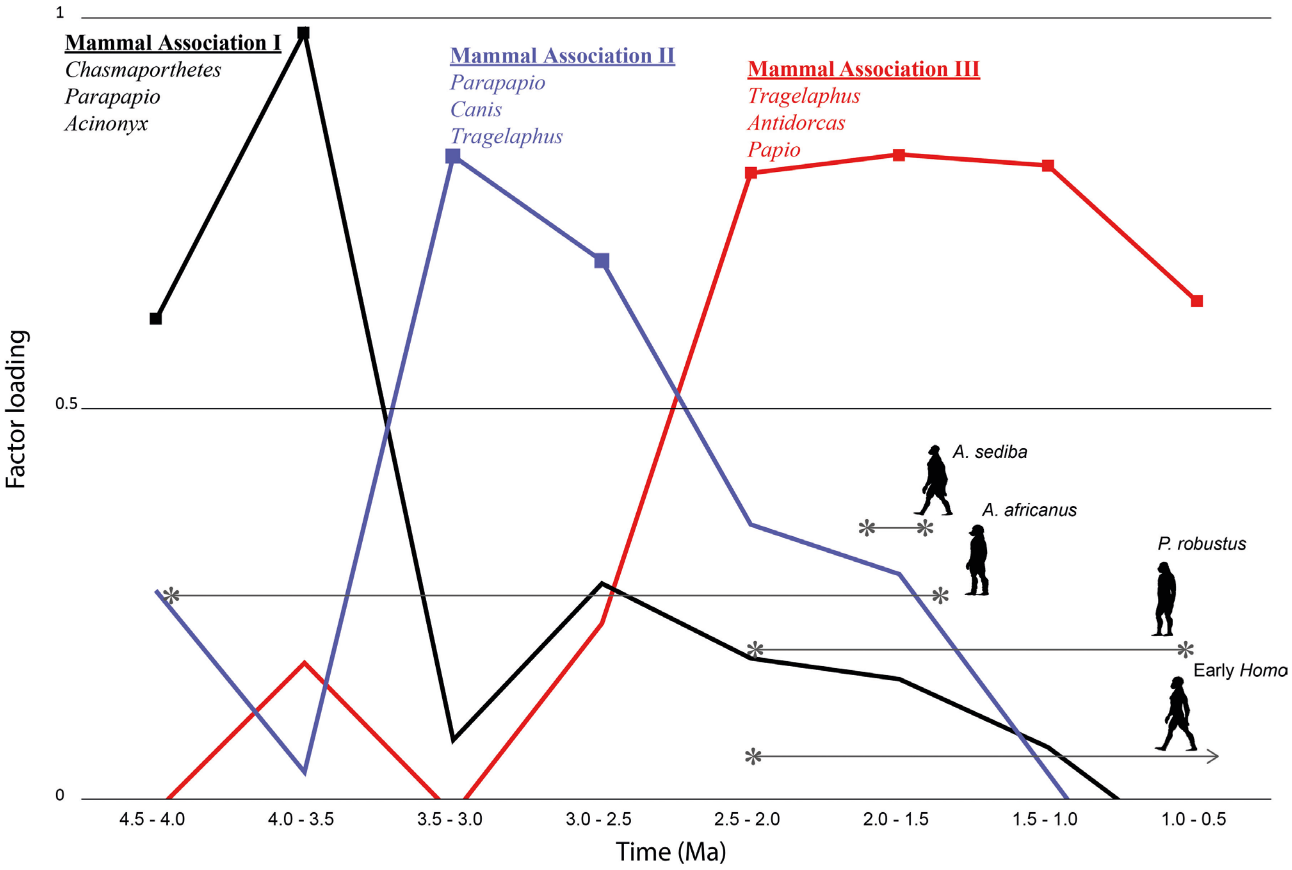

Fig. 3: Results from the factor analysis representing the succession of large mammal associations through time.

The associations are considered as representative of a time period when their factor loading exceed 0.5 (square marks). Only the three genera with the highest contribution of each associations are indicated (see figure 5 and the text for more details). We also indicate the time-span of each hominin taxa recognized during the Plio-Pleistocene in South Africa.

Fig. 3 : Résultats de l'analyse factorielle représentant la succession des associations de grands mammifères à travers les UTS. Les associations sont considérées comme représentatives de la période lorsque le coefficient factoriel est supérieur à 0,5 (carré). Seuls les trois genres contribuant le plus à chaque association sont indiqués (voir figure 5 ainsi que le texte pour plus de détails). Nous montrons également l'intervalle de temps de chaque taxon d'hominine présent au cours du Plio-Pléistocène en Afrique du Sud.

	Evolutionary faunas		
Scores	**LMA I**	**LMA II**	**LMA III**
> 2.0	*Chasmaporthetes*	*Parapapio*	*Tragelaphus*
	Parapapio	*Canis*	*Antidorcas*
	Acinonyx	*Tragelaphus*	*Papio*
	Panthera	–	–
	Dinofelis	–	–
	Megantereon	–	–
	–	–	–
> 1.0	*Papio*	*Redunca*	*Equus*
	–	*Gazella*	*Metridiochoerus*
	–	*Oreotragus*	*Megantereon*
	–	*Australopithecus*	*Connochaetes*
	–	*Cercopithecoides*	*Dinofelis*
	–	*Syncerus*	*Hippotragus*
	–	–	–
	–	–	–
> 0.5	–	*Makapania*	*Panthera*
	–	*Caracal*	*Damaliscus*
	–	*Vulpes*	*Redunca*
	–	*Notochoerus*	*Pachycrocuta*
	–	*Hyaena*	–
	–	*Papio*	–
	–	*Giraffa*	–
	–	*Theropithecus*	–
	–	*Phacochoerus*	–
	–	*Ceratotherium*	–
	–	*Crocuta*	–

Tab. 4: Summary of all genera with scores greater than 0.5 for each large mammal association identify by the factor analysis.

Tab. 4 : Résumé des genres avec des scores supérieurs à 0,5 pour chaque association de grands mammifères identifiée par l'analyse factorielle.

C. nitidula and *C. silberbergi*, which both occur at Jacovec Cavern and Sterkfontein Member 2 (Berger *et al.*, 2002; Kibii, 2004). The genus *Parapapio*, and more specifically the species *P. jonesi*, is known from both deposits, while *P. broomi* occurs only at Jacovec Cavern. The presence of *Acinonyx*, *Megantereon* and *Dinofelis* as major contributing taxa are more questionable. Indeed, only one species of each of these genera occur at both deposits. This could be a result of a general low diversity through the assemblages (tab. 2) and/or taphonomical biases (see Discussion). The LMA I declines immediately after 3.5 Ma but continues to maintain low factor loadings until after 1.0 Ma (fig. 3). This indicates the persistence of genera through the next two LMA, with a minor factor loading increase during the STU 4, which could be due (see below), to the important contribution of *Parapapio*.

3.2.2 - Large Mammal Association II (STU 3-4)

The second evolutionary fauna corresponds to the STU 3 and 4, from 3.5 to 2.5 Ma. It is characterised by the contribution of 20 genera (scores > 0.5). During that period of time, the pick of diversity of the genus *Parapapio* is the highest, specifically at Makapansgat, by the simultaneous presence of three different species, *P. jonesi*, *P. broomi* and *P. whitei*. Also, even if the genus *Canis* is already known at Jacovec Cavern (Kibii, 2004), the diversity increases during the LMA II, with the presence of three different species, *C. brevirostris*, *C. adustus* and the extant *C. mesomelas*. Finally, the genus *Tragelaphus*, which is absent from the two previous STU, is represent in this LMA by *T. pricei* and *T. angasi* at Makapansgat. The LMA II declines after the STU 3 and maintains low factor loadings until just after the STU 7. It means, like the LMA I, that there is a persistence of genera through the next evolutionary fauna.

3.2.3 - Large Mammal Association III (STU 5-8)

The LMA III is the longest in time evolutionary fauna identified by the factor analysis, covering the STU 5 to 8, between 2.5 to 0.5 Ma (fig. 3). It is characterized by a major contribution of *Tragelaphus* and *Antidorcas*. Indeed, even if *Tragelaphus* is already known before, it reaches his peak of diversity during the LMA III by the presence of four different species during that time, *T. oryx*, *T. strepsiceros*, *T. scriptus* and *T. angasi*. This is also the case for *Antidorcas*, with the presence of *A. recki*, *A. bondi* and *A. marsupialis* between the STU 5 and 8, and also *A. australis* during the STU 8. Moreover, the genus *Papio* becomes a major component of the association, by the presence of at least four different species and/or sub-species during the STU 5 and 6, *P. hamadryas robinsoni*, *P. hamadryas angusticeps*, *P. hamadryas* and *P. indens*. The genus *Metridiocheorus*, which appears during the STU 5, also contributes to this LMA. Even if the genus *Equus* is recognized during the STU 4 at Drimolen MQ (Adams *et al.*, 2016), it becomes more diversified after 2.5 Ma, by the presence of three different species, *E. quagga*, *E. capensis* and *E. burchelli*.

4 - DISCUSSION

The cluster analysis permitted to identify similar taxonomic composition between deposits based on species presence – absence. The Jacovec Cavern (4.02 Ma) and Sterkfontein Member 2 (3.67 Ma) are close, sharing a significant number of species, such as *Papio izodi*, *Parapapio jonesi*, *Panthera pardus*, *Chasmaporthetes nitidula* and *Chasmaporthetes silberbergi*. Kibii (2004), based on the composition of the faunal assemblage, suggests a mosaic of open and closed habitats for the Jacovec Cavern, which include riverine gallery forest, bushland and open environments. The same conclusions were obtained from the analysis of the Sterkfontein member 2 faunal assemblage (Pickering *et al.*, 2004). Our cluster analysis supports the similarity between the two assemblages.

One cluster is composed of Makapansgat members 3-4 and Taung. All the members of Makapansgat are comparable in terms of large mammal composition, notably by the presence of *Theropithecus darti*, *Cercocebus*, *Phacochoerus shawi* and *Gazella vanhoepeni*. However, Makapansgat member 2 is grouped with Drimolen Makondo, although they share only two taxa, *Dinofelis* sp. and *Cercopithecoides* sp. Even if the Drimolen Makondo (2.61 Ma) deposit could not provide useful information on palaeoecology until now, the results of our cluster analysis and the presence of *Chasmapothetes* ? *nitidula*, *Cercopithecoides* and *Dinofelis* sp. (Rovinsky *et al.*, 2015), indicates a possible similarity with the Makapansgat member 2 faunal assemblage composition and, by extension, palaeoecological reconstruction. Reed (1996, 1997, 1998) proposed an environmental reconstruction for Makapansgat members 2-4 from closed woodland to shrubland/bushland or edaphic grassland. Palaeoecological studies of the Taung (2.8-2.4 Ma) deposit indicate a woodland or forest environment (Williams & Patterson, 2010).

The Drimolen MQ (2.664 ± 0.392 - 1.789 ± 0.104 Ma) faunal assemblage has been interpreted as a mixed open-to-closed environments (Adams *et al.*, 2016). Our cluster analysis indicates a close similarity between the Haasgat (2.3-1.95 Ma) and Drimolen MQ assemblages, sharing taxa such as *Cercopithecoides williamsi*, *Dinofelis* sp., *Megalotragus* sp., *Connochaetes* sp., *Damaliscus* sp., *Tragelaphus* sp., *Oreotragus* sp. and *Equus quagga*. Moreover, the position of Malapa (2.067 ± 0.161 Ma) and Kromdraai B (2.0-1.8 Ma), close to the Drimolen MQ-Haasgat cluster, could indicate a similar non-specific palaeoenvironment as it has been suggested for Drimolen MQ.

The Sterkfontein member 5 Oldowan (2.18 ± 0.21 Ma) and Acheulean (1.3-1.1 Ma) faunal assemblages point out a more drier and open environments, but with still a moist and cover component, than older deposits (Kuman & Clarke, 2000), with shared taxa such as *Antidorcas* sp., *Equus* sp. and *Damaliscus* sp. In contrast to Kuman and Clarke' study, we do not consider *Panthera leo*, which is present in both assemblages, as a grassland species since it can occur in open habitat (less than 20 % canopy cover) to mixed habitat (approximately 20 % canopy cover) (Lewis, 1997). No palaeoenvironmental interpretation has been provided until now for the Motsetse (1.64-1.0 Ma) assemblage. However, according to our cluster analysis, it seems that Motsetse is similar to Sterkfontein member 5 Oldowan and Acheulean.

All the taxa (*Antidorcas recki*, *Redunca* sp., *O. oreotragus* and *Equus* sp.) recognized at Gondolin 1 (1.78 Ma) are present at Gondolin 2 (1.8 Ma), which are close to each other. According to his taphonomical analysis, Adams (2012b) identified the leopard (*Panthera pardus* or leopard-like felids) as the main accumulator of GD 2 and then postulated that the habitat surrounding Gondolin site should support this predator as well as their preys. Based on this assumption, Gondolin faunal assemblage indicates a dominance of open to wooded grassland with patches of rocky hillsides combined with seasonal to continuous water in valley floors.

It is not surprising to observe a resemblance between the faunal assemblages of all Swartkrans members (from 2.3 Ma for the member 1 to 0.96 Ma for member 3).

Indeed, they have a lot of taxa in common (de Ruiter, 2003) with a dominance of grassland component. However, taxa such as *Hippopotamus* (members 1-3), *Elephas* (members 1 and 3), *Sivatherium* (member 2), *Kobus* cf. *leche* (member 2 and 3) or the *Redunca* cf. *arundinum* (member 1) suggest the presence of a permanent source of water and an extensive woodlands surrounding the site. The majority of the Cooper's D (< 1.375 Ma) faunal assemblage, which seems similar to Swartkrans according to our cluster analysis, has been interpreted as indicative of grassland environment with wooded component and a permanent water source (de Ruiter *et al*., 2009). The Elandsfontein (1.0-0.6 Ma) faunal assemblage indicates a more humid habitat, samples an interval of great vegetational productivity causes by an increase of moisture according to Klein *et al*. (2007). Our cluster analysis shows that the Kromdraai A assemblage (1.8-1.6 Ma) is close to Elandsfontein and by extension to Cooper's D and Swartkrans. This illustrates a similar faunal composition between these sites.

Finally, the Cornelia-Uitzoek (1.07-0.99 Ma) seems to be the most specific faunal assemblage compared to other deposits. Indeed, it has yielded a unique combination of taxa such as *Aepyceros helmoedi*, *Megalotragus eucornutus*, *Metridiocheorus compactus*, *Kolpochoerus heseloni*, *Hippopotamus gorgops* or *Eyrygnathohippus cornelianus* (Brink *et al*., 2012).

The most interesting result of the cluster analysis was probably the distinction between two clusters. The first one is composed of all the deposits older than 2.4 Ma if the age interval of Taung is confirmed. The second one includes all the assemblages younger than 2.6 Ma, which corresponds to the lower limit of the Drimolen MQ deposit. Based on this observation, it seems that the cluster analysis supports the hypothesis of a faunal turnover between 2.61 and 2.4 Ma in South Africa. The only exception is the group formed by Makapansgat member 2 and Drimolen Makondo. Subsequent analyses will be necessary in order to test our interpretation. The factor analysis allows us to identify three characteristic associations of large mammal fauna between 4.5 and 0.5 Ma in South Africa (tab. 4, fig. 3 & 4).

Only Carnivores (*Chasmaportethes*, *Acinonyx*, *Panthera*, *Dinofelis* and *Megantereon*) and Primates (*Parapapio* and *Papio*) taxa have the highest scores (> 2) within the LMA I (from 4.5 to 3.5 Ma). However, we should be cautious about the interpretation of this result. Indeed, as we mentioned before, this evolutionary fauna covers the two first STU which are both composed of only one deposit, the Jacovec Cavern (STU 1) and the Sterkfontein member 2 (STU 2). According to Kibii (2004), the Jacovec Cavern primate assemblage corresponds to a leopard refuse assemblage. The Sterkfontein member 2 was interpreted as a death-trap characterized by the presence of several carnivore species (Pickering *et al*., 2004). Thus, the pattern observed through the LMA I could be due to taphonomical biases in these two deposits rather than representing a palaeobiodiversity signal.

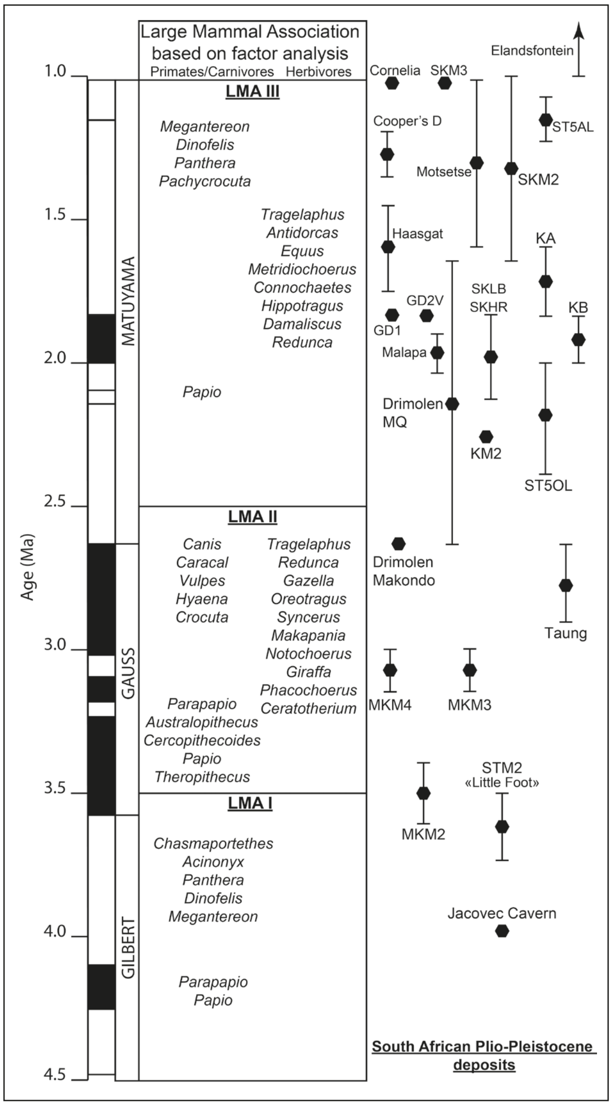

Fig. 4: Detailed composition of each large mammal associations in terms of characteristic genera (scores > 0.5) resulting from the factor analysis.

The geomagnetic polarity and South African Plio-Pleistocene deposits are also shown.

Fig. 4 : Composition détaillée de chaque association de grands mammifères en termes de genres caractéristiques (scores > 0.5) résultant de l'analyse factorielle. La polarité du champ magnétique terrestre et les dépôts plio-pléistocènes sud-africains sont également montrés.

The second LMA (from 3.5 to 2.5 Ma) is mainly composed of a mixed-environment signal by the presence of both woodland and grassland adapted taxa such as *Tragelaphus*, *Oreotragus*, *Cercopithecoides*, *Syncerus*, *Notochoerus* and *Giraffa* for the first category and *Parapapio*, *Gazella*, *Theropithecus*, *Phacochoerus* and *Ceratotherium* for the second.

If we look at the composition of the LMA III, we notice the presence of *Antidorcas, Tragelaphus*, *Metridiochoerus*, *Equus*, *Connochaetes*, *Hippotragus*, *Damaliscus*, *Redunca*, *Raphicerus and Cercopithecoides*. Although most of them refer to open-grassland adapted taxa (Alcelaphini, Antilopini, *Metridiochoerus* and *Equus*), wetland genera (Reduncini and Hippotragini) and woodland (*Tragelaphus*, *Raphicerus* and *Cercopithecoides*) tribes are also present. The LMA III, which differs from previous LMA, could be a response of South African large mammals to a climatic shift around 2.5 Ma.

If we look more closely at the large mammal associations, the **Primate** association is marked by the presence of *Parapapio* and *Papio* as high scoring taxa during the LMA I, follow by *Parapapio*, *Cercopithecoides, Papio* and *Theropithecus* in the LMA II. Then, the Primate association of the LMA III is only composed of *Papio*. Thus, Primates seem to be more diverse between 3.5 and 2.5 Ma. Also, after 2.5 Ma, we observe a decrease of the diversity inside the *Cercopithecoides* when the genus *Papio* become a more important component of the Primate association. This could indicate an opening of the environment.

As for the **carnivores** it was noticed, that the genus *Canis* migrated from Eurasia and first appeared in Africa ca. 2.5 Ma, and that this taxon is a good indicator of the environment opening (Turner, 1995). However, in South Africa, we highlight the presence of this genus since at least at 4.0 Ma in Jacovec Cavern (Kibii, 2004), but also at 3.0 Ma in Makapansgat member 3 and member 4 (Reed, 1996). This can be consistent with the hypothesis of a long and gradual opening of the environment since 4 Ma (Reed, 1997). As pointed by Turner (1995), the success of felids (and notably pantherines) shows the changing to open landscape but their emergence in the fossil record are not correlated to any particular climate event. Moreover, we can notice that scores of machairodonts decrease between LMA I and III. It is also emphasized by the progressive decline of the LMA I through time, especially after the STU 7 (1.5-1.0 Ma). This is consistent with the extinction of machairodont species after 1.5 Ma (Turner, 1988, 1990), which is linked to the opening of the landscape, thus making the prey more difficult to catch (Turner, 1990). Concerning the hyaenids, the *Pachycrocuta* genus seems to have occupied a wide variety of environments (Turner, 1990). Its presence in the LMA III, even if it is relatively minor (score > 0.5), supports the hypothesis of a mixed wooded-open habitat during that time. As it was recognized before, South African caves display a high diversity of carnivore taxa, notably because most of the deposits have been interpreted as carnivore dens (Brain, 1981; Cruz-Uribe, 1991; Pickering, 2002). This could explain the huge frequency of carnivore genera as characteristics of large mammal associations through time, especially for the first LMA as it was mentioned before.

Bovids are recognized to be representative of their environments and have therefore long been used in palaeoecology (Vrba, 1974a,b, 1975; Greenacre and Vrba, 1984; Alemseged, 2003). The first association (LMA I) does not display score larger than 0.5 for any bovid genera. However, we can notice that the second LMA is marked by more "wet-closed" adapted genera such as *Tragelaphus*, *Oreotragus*, *Syncerus* and *Redunca* but with *Gazella* as grassland adapted genus. After 2.5 Ma, during the LMA III, we observe that the bovid composition is more characterized by a mix of open environment and "wet-closed" adapted species such as *Antidorcas, Connochaetes* and *Damaliscus* for the first category and *Tragelaphus*, *Redunca* and *Hippotragus* for the second.

As for the **Suids**, the presence of *Notochoerus* and *Phacochoerus* in the LMA II (score > 0.5) suggests the presence of some open area in the environment (Harris & Cerling, 2002). During the LMA III, the rise of *Metriodiochoerus* genus (score > 1) which is more adapted to abrasive diet, tends to indicate the opening of the landscape (Harris & Cerling, 2002).

Therefore, we can identify a more woodland adapted fauna before 2.5 Ma (*Parapapio*, *Tragelaphus*, *Syncerus*, *Oreotragus,* and *Cercopithecoides*) followed by a more pronounced 'open-grassland' type of habitat with the indication of wooded components and the presence of a permanent water source. Indeed, grassland taxa are represented by the presence of *Antidorcas*, *Metridiochoerus*, *Equus*, *Connochaetes* and *Damaliscus* although *Tragelaphus*, *Raphicerus*, *Hippotragus* and *Redunca* are more representative of the humid-closed type of habitat.

The identification of a "mosaic" habitat after 2.5 Ma requires additional comments. According to Reynolds *et al*. (2015), the concept of a heterogeneous landscapes is poorly defined and suffers from the lack of focus on temporal and spatial scale. Moreover, Hopley and Maslin (2010) introduced to concept of "climate-averaging" which is defined as the "amalgamation of individuals living under one or more climatic states within a single faunal deposit". This is a crucial statement which highlights the artificial increase of biodiversity of broad range ecomorphologies and diets within the same faunal assemblage. It results from a poor definition of the duration of bone accumulation. In order to resolve this problem, Hopley and Maslin (2010) proposed to compare palaeoclimatic data set which is independent of faunal assemblages.

Based on this statement, it has been previously observed that the proportion of C4 grasses seems to drastically increase at about 1.7 Ma in South Africa (Luyt & Lee-Thorp, 2003; Hopley *et al*., 2007), and reflecting drier environmental conditions and a more open habitat after that time. Our factor analysis, supported by the cluster analysis, place this shift between the STU 4 and 5 (3.0 and 2.0 Ma) by the presence of *Equus*, and more Alcelaphini-Antilopini bovid composition as well as large terrestrial primates and *Metridiochoerus* as characteristic of the third large mammal association after 2.5 Ma.

5 - CONCLUSION

Our results confirm that a shift occurred in term of variability of biodiversity and large mammal associations during the Late Pliocene and Early Pleistocene. More interestingly, our results allow us to support the hypothesis of a faunal turnover identify between at least 2.61 and 2.4 Ma based on the cluster analysis. Based on the factor analysis, three evolutionary fauna could be identified between 4.5 and 0.5 Ma in South Africa. The first one, between 4.5 and 3.5 Ma, is characterized by high contribution of carnivore genera, probably driven by taphonomical biases. It is followed by faunal assemblages, between 3.5 and 2.5 Ma, which indicate a mosaic of open and closed environments. Finally, the third evolutionary fauna assemblage, between 2.5 and 0.5 Ma, corresponds to a “mosaic” type of habitat, a mixed of ‘open-grassland’ and woodland components with the presence of a permanent water source.

The concept of “mosaic” habitat remains loosely defined and could be a consequence of the lack of focus on temporal and spatial scale (Reynolds *et al*., 2015). Therefore, future investigation is necessary in order to identify the probable climate-averaging of South African Late Pliocene and Early Pleistocene deposits. That should yield an improved framework for a better understanding of the evolutionary dynamics which driven large mammal communities during the Late Pliocene and Early Pleistocene and through the Plio-Pleistocene transition in South Africa.

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