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Fossil Bovidae from the Hominini-bearing site of Cooper's D (Bloubank Valley, South Africa): implications for *Paranthropus robustus* Broom, 1938 and early *Homo* Linnaeus, 1758 habitat preferences

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ABSTRACT

The Cooper's D deposit has been dated by U-Pb at a maximum age of 1.37 Ma \pm 0.113 and has yielded seven Hominini remains, six of them are attributed to the Southern African endemic species *Paranthropus robustus* Broom, 1938. However, the taxonomic composition of the faunal assemblage recovered at this site, especially ruminants, remains poorly understood. This paper updates the pre-

KEY WORDS
Bovid,
paleoecology,
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South Africa.

vious palaeontological and biochronological works and provides the first taxonomic description and paleoecological analysis of the whole bovid material from Cooper's D. We propose a minimum age of 1.0 Ma for the Cooper's D bone accumulation. Thus, we conclude that the assemblage accumulated between 1.375 ± 0.113 and 1.0 Ma based on the complementary results obtained from radiometric dates and biochronology. The paleoecological analysis suggests that Cooper's D is likewise dominated by grassland with sparse covered habitat and probable water sources in the vicinity. Finally, we show a strong statistically significant negative correlation between the presence of grassland-adapted bovid species and *P. robustus*. This result indicates that *P. robustus* was more likely to be an eurytopic species and dietary generalist than an exclusive grazer.

RÉSUMÉ

Bovidés fossiles du site à Hominini de Cooper's D (vallée de Bloubank, Afrique du Sud) : implications pour les préférences d'habitat de Paranthropus robustus Broom, 1938 et des premiers représentants du genre Homo Linnaeus, 1758.

Le gisement Cooper's D a été daté par U-Pb à un âge maximum de $1,37 \text{ Ma} \pm 0,113$ et a livré sept restes d'Hominini, dont six sont attribués à l'espèce endémique d'Afrique australe, *Paranthropus robustus* Broom, 1938. Cependant, la composition taxinomique de l'assemblage faunique retrouvé sur ce site, en particulier les ruminants, reste mal connue. Cet article met à jour les résultats des travaux paléontologiques et biochronologiques précédents et fournit la première description taxinomique et analyse paléoécologique de l'ensemble du matériel de bovidé de Cooper's D. Nous proposons un âge minimum de 1,0 Ma pour l'accumulation osseuse de Cooper's D. Ainsi, nous concluons que l'assemblage s'est accumulé entre $1,375 \pm 0,113$ et 1,0 Ma sur la base des résultats complémentaires obtenus à partir des dates radiométriques et de la biochronologie. L'analyse paléoécologique suggère un environnement dominé par des prairies, avec un habitat couvert clairsemé et des sources d'eau permanentes à proximité. Enfin, nous montrons une forte corrélation négative, statistiquement significative entre la présence d'espèces de bovidés adaptées aux prairies et *P. robustus*. Ce résultat indique que *P. robustus* était plus susceptible d'être une espèce eurytopique qu'un végétarien spécialisé.

MOTS CLÉS
Bovidés,
paléoécologie,
gisement Cooper's,
Pléistocène inférieur,
Afrique du Sud.

INTRODUCTION

Cooper's Cave is located in the UNESCO Sterkfontein, Swartkrans, Kromdraai and Environs World Heritage Site in South Africa (Fig. 1). It is situated 1.5 km northeast of the Sterkfontein Caves and 1 km southwest of Kromdraai (Berger *et al.* 2003; de Ruiter *et al.* 2009). The site contains three distinct localities: Cooper's A, B, and D (de Ruiter *et al.* 2009). For this study, we focus on the decalcified sediments from Cooper's D deposit which have yielded abundant and diverse fauna (e.g. Berger *et al.* 2003; de Ruiter *et al.* 2009).

The Cooper's D deposit has been dated by U-Pb to 1.526 ± 0.088 Ma for the basal speleothem and *c.* 1.4 Ma for the flowstone situated in the middle of the deposit sequence (de Ruiter *et al.* 2009). However, more recent U-Pb dating of the basal flowstone suggests an age of 1.375 ± 0.113 Ma (Pickering *et al.* 2019), indicating that the deposit is younger than 1.4 Ma.

The first preliminary estimation of faunal diversity at Cooper's D was given by Berger and collaborators (Berger *et al.* 2003) and pointed out that the fauna is surprisingly diverse with an abundance of suids and canids, corresponding to the assemblages from Swartkrans and Kromdraai A. Previous palaeontological analysis highlighted a high diversity of carnivore taxa (Hartstone-Rose *et al.* 2007; Kuhn *et al.* 2017) and the presence of the first well identified modern cheetah in Africa (O'Regan & Steininger 2017). It is also the earli-

est site of the Bloubank Valley to preserve the African civet, *Civettictis cf. civetta* (Schreber, 1776) (O'Regan *et al.* 2013). The faunal assemblage is also characterized by an abundance of *Theropithecus* I. Geoffroy, 1843 fossils (Folinsbee & Reisz 2013; DeSilva *et al.* 2013; Val *et al.* 2014).

Subsequently, the first taphonomical analysis of the Cooper's D faunal assemblage suggested that the hyaenid – mostly the brown hyena (*Parahyaena brunnea* (Thunberg, 1820)) – was the main accumulator agent for the faunal assemblage (de Ruiter *et al.* 2009). This is corroborated by the presence of coprolites attributed to *Parahyaena brunnea*, but a new taphonomical analysis of the primate assemblage identified both leopards and brown hyenas as bone accumulator agents of the Cooper's D faunal assemblage (Val *et al.* 2014).

Despite the diversity of mammal species, the majority correspond to ungulate taxa indicative of grassland environments, such as Antilopini, Alcelaphini, *Equus* Linnaeus, 1758, and *Metridiochoerus andrewsi* Hopwood, 1926, which in some cases could represent the last appearance of these taxa in Africa (de Ruiter *et al.* 2009). However, the presence of Cercopithecidae, Giraffidae, Bovini and Tragelaphini pointed out the wooded component of the environment (de Ruiter *et al.* 2009). Here, we provide the first description of the bovid material from Cooper's D based on the analysis of the entire bovid assemblage derived from the decalcified materials excavation from 2001 to present.

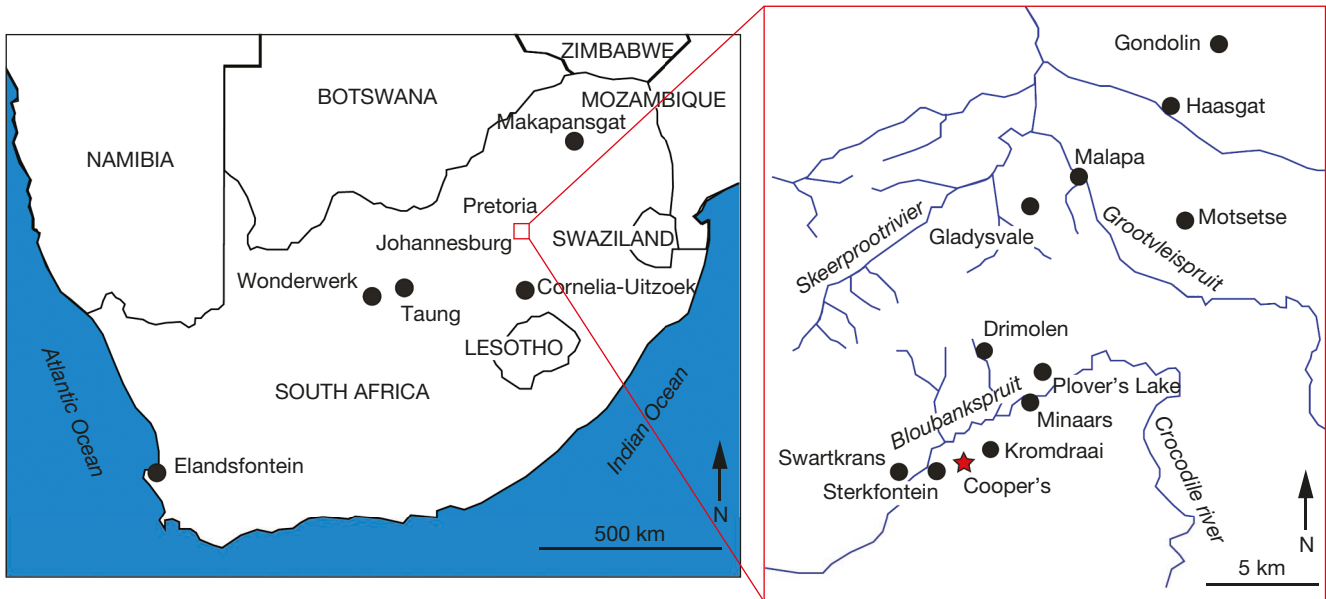


FIG. 1. — Location of Cooper's Cave site and other Early Pleistocene Hominini-bearing deposits in South Africa.

MATERIAL AND METHODS

FAUNAL ANALYSIS

Fossil identifications were made by using modern bovid collections housed at the Evolutionary Studies Institute (ESI), University of the Witwatersrand and the Ditsong National Museum of Natural History in Pretoria. Furthermore, the bovid material from Cooper's D was compared to collections from Sterkfontein, Swartkrans, and Kromdraai housed in the Ditsong National Museum of Natural History in Pretoria and at the Evolutionary Studies Institute at the University of the Witwatersrand.

We calculated the minimum number of individuals by combination (MNIc), which represents the most represented lateralized anatomical element in the assemblage for a given species, considering the age estimation in the count (Lyman 1994), for each taxon identified at least at the genus level. Specimens without confident identification (i.e., unidentified molars) were not taking into account for the calculation.

Specimens are measured using digital calipers and all the measurements are provided in millimeters. Horn core measurements (anteroposterior and transverse diameters) are taken at the base. For comparisons with other Pleistocene South African bovid assemblages, all tooth measurements are taken at the occlusal surface following Vrba (1974). The nomenclature used in this paper follows the International Code of Zoological Nomenclature, as well as Bengtson 1988. The dental nomenclature used for material descriptions follows Gentry (2010) and Bärmann & Rössner (2011).

ABBREVIATIONS

APD	anteroposterior diameter;
BL	buccolingual diameter;
CH	crown height;
ESI	evolutionary studies institute;
MD	mesiodistal diameter;
MNI	minimum number of individuals;

MNIc	minimum number of individuals by combination;
NISP	number of identified specimens;
TD	transverse diameter.

Deposits and estimated ages

Drimolen MNQ	Drimolen Main Quarry (2.04-1.95 Ma);
KB	Kromdraai B (2.0-1.8 Ma);
KM2	Kromdraai Member 2 (>2.2 Ma);
SKM2	Swartkrans Member 2 (1.36 ± 0.29 Ma);
SKM3	Swartkrans Member 3 (0.96 ± 0.09 Ma);
SKHR	Swartkrans Member 1 Hanging Remnant (2.3-1.795 Ma);
SKLB	Swartkrans Member 1 Lower Bank (2.317-1.637 Ma);
ST5OL	Sterkfontein Member 5 East Oldowan (2.18 ± 0.21 Ma).

TAPHONOMICAL CONSIDERATIONS

As we already mentioned, all the material analyzed in this study is coming from decalcified sediments. Decalcification process as the particularity to complicate the accumulation history of an assemblage by separating sediments and fossils from their original place of deposition (Brain 1981). Moreover, decalcification can also affect skeletal element distribution by the disappearance of the less dense and compact bones (de Ruiter *et al.* 2008).

At Cooper's D, the decalcified sediment is comprised between fossiliferous breccias and dolomitic walls which permits to assume that its deposition is the result from erosion of the hard breccias (Berger *et al.* 2003; de Ruiter *et al.* 2009). It has been shown that the accumulation corresponds to a deposition slope (de Ruiter *et al.* 2009), which several species used to visit the cave entrance, particularly carnivores.

Based on the study of modern carnivore kill data, it has been shown that carnivore accumulated assemblages are representative of their surrounding habitats which makes South African cave accumulations suitable for paleoecological

TABLE 1. — Bovid assemblages from *Paranthropus robustus* Broom, 1938 and early *Homo* Linnaeus, 1758 sites used in this study. Hominini are quantified in MNI (taken from de Ruiter *et al.* 2008). The Simpson's index is calculated for each assemblage after bovid data in the Table 2.

Deposits	Sedimentary context	Taphonomical context	Estimated age (Ma)	<i>Homo</i> sp.	<i>P. robustus</i>	Simpson's index (D)	References
SKLB	Decalcified	Carnivore/Hominini accumulation	2.317-1.637	1	9	0.4791	(Brain 1981; de Ruiter 2003; Pickering <i>et al.</i> 2008, 2019)
KM2	Decalcified	Carnivore accumulation	>2.2	1	16	0.5357	(Braga <i>et al.</i> 2017; Fourvel <i>et al.</i> 2018)
ST5OL	Decalcified	Carnivore	2.18 ± 0.21	0	2	0.5777	(Brain 1981; Pickering 1999; Kuman & Clarke 2000; Granger <i>et al.</i> 2015)
KB	Calcified	Carnivore	2.0-1.8	0	6	0.2747	(Bruxelles <i>et al.</i> 2017; Fourvel <i>et al.</i> 2018)
SKHR	Calcified	Carnivore/Hominini accumulation	2.3-1.795	1	58	0.4596	(Brain 1981; de Ruiter 2003; Pickering <i>et al.</i> 2008; Pickering <i>et al.</i> 2019)
DMQ	Calcified/ Decalcified	–	2.04-1.95	4	44	0.2988	(Adams <i>et al.</i> 2016; Herries <i>et al.</i> 2020)
Cooper's D	Decalcified	Carnivore accumulation	1.3-1.0	0	2	0.2532	This study
SKM2	Decalcified	Carnivore/Hominini accumulation	1.36 ± 0.29	2	8	0.3001	(Brain 1981; de Ruiter 2003; Balter <i>et al.</i> 2008; Pickering <i>et al.</i> 2008)
SKM3	Decalcified	Carnivore/Hominini accumulation	0.96 ± 0.09	0	6	0.3835	(Brain 1981; de Ruiter 2003; Pickering <i>et al.</i> 2008; Gibbon <i>et al.</i> 2014)

TABLE 2. — MNI of bovid taxa and their assignment to each ecovvariable used in this study for *Paranthropus robustus* Broom, 1938 and early *Homo* Linnaeus, 1758 South African sites. Data from de Ruiter *et al.* (2009, 2012).

Deposits	SKLB	KM2	ST5OL	SKHR	Drimolen	MQ	Cooper's D	SKM2	SKM3	KB	Diet	Habitat	Water
Alcelaphini Brooke, 1876	44	6	25	112	19	31	76	73	5	Grazer	Grass	Water dependent	
Antilopini Gray, 1821	21	0	3	52	19	26	27	47	6	Mixed feeders	Grass	Water independent	
<i>Tragelaphus oryx</i> (Pallas, 1766)	0	1	2	0	0	1	1	2	1	Mixed feeders	Woodland	Partially water dependent	
<i>Tragelaphus strepsiceros</i> (Pallas, 1766)	0	0	0	7	0	1	6	2	0	Browser	Woodland	Partially water dependent	
<i>Tragelaphus scriptus</i> (Pallas, 1766)	0	0	0	0	0	0	4	0	0	Browser	Closed wet	Water dependent	
<i>Reduncini</i> Knottnerus- Meyer, 1907	0	0	0	1	3	9	1	1	1	Grazer	Closed wet	Water dependent	
<i>Bovini</i> Gray, 1821	2	0	0	2	0	3	3	3	1	Grazer	Woodland	Water dependent	
<i>Hippotragini</i> Brooke, 1876	0	0	0	3	0	3	9	5	0	Grazer	Closed wet	Water dependent	
<i>Neotragini</i> Sclater & Thomas, 1894	1	1	2	1	1	3	10	4	0	Browser	Woodland	Water independent	
<i>Cephalophini</i> Blyth, 1863	1	0	1	1	9	1	3	1	0	Fruit plus	Woodland	Water independent	
<i>Peleini</i> Gray, 1872	1	0	0	3	0	4	10	2	0	Mixed feeders	Grass	Water independent	
Total	70	8	33	182	51	82	150	140	14	–	–	–	

reconstructions (de Ruiter *et al.* 2008). Thus, we studied only cranio-dental material (mandibles, teeth and horn-cores) which is less affected by carnivore action, usually better preserved than post-cranial remains, and is then susceptible to similar taphonomical agents and processes (Alemseged 2003). Therefore, it is more suitable for paleoecological studies and interpretations. We assume that the combined use of isotaphonomic assemblages and cranio-dental remains for

identifications allow us to minimize the effect of taphonomical biases on our paleoecological interpretations.

PALEOECOLOGICAL ANALYSIS

Paleobiodiversity

With regard to palaeoecology, several evenness indices have been used as tools for measuring African mammal palaeobiodiversity (e.g. Turner & Wood 1993; Geraads 1994; Patterson *et al.*

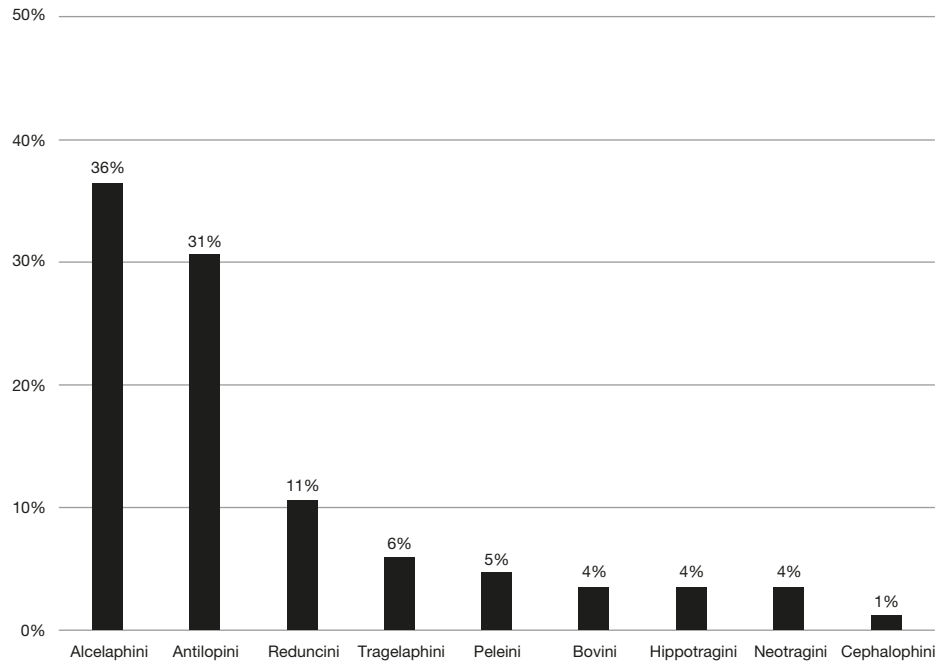


Fig. 2. — Distribution of the MNI per bovid tribes from Cooper's D.

2014; Hanon *et al.* 2019). According to Faith & Du (2018), Simpson (1949) index, which represents the probability that two individuals selected at random from the assemblage belong to the same species (Magurran 1988), appears to be the best index compared to the Shannon and Smith and Wilson ones. Furthermore, Magurran (2004) states that Simpson's index is one of the most robust and significant diversity indices. We applied an unbiased estimate of the Simpson's index which is calculated as follows (Magurran 1988; Hammer *et al.* 2001; Faith & Du 2018):

$$D = \sum \frac{n_i(n_i - 1)}{N(N - 1)}$$

D = Simpson's index;

n_i = MNI for species i ;

N = total MNI for the assemblage.

D represents the uniformity of the assemblage in terms of species. If the D is close to 0, the assemblage is highly diverse, while a of 1 indicates a monospecific assemblage. The Simpson's index was calculated using PAST 3.22 software (Hammer *et al.* 2001).

Taxonomic composition

In order to characterize the Cooper's D bovid paleoecology, we studied taxonomic abundance and presence-absence of taxa. Also, our results are compared with a compilation of the bovid list of all other *Paranthropus robustus* Broom, 1938 and early *Homo* Linnaeus, 1758 sites of South Africa ($n = 8$; Tables 1; 2). It has long been showed that bovid taxonomic data are suitable for reconstructing paleoenvironment (Greenacre & Vrba 1984; Alemseged 2003).

As a first approach, we studied the associations of bovid using the method of de Ruiter *et al.* (2012) and de Ruiter

et al. (2008), in terms of abundance data at tribe level. For the Tragelaphini, we have distinguished the species (*Tragelaphus oryx* (Pallas, 1766), *Tragelaphus scriptus* (Pallas, 1766), *Tragelaphus strepsiceros* (Pallas, 1766)), because they have different ecological preferences. Then, we assigned to each taxon (tribes and Tragelaphini species) a diet category, a preferred habitat and a water requirement. These three parameters called "ecovari-ables" (de Ruiter *et al.* 2012) are composed of different classes:

Diet category. Grazer, browser, fruit or mixed.

Habitat. Wooded savannah, open or humid savannah.

Water requirement. Dependent, independent or partially dependent.

We then apply a series of correspondence analyses to observe the distribution of assemblages according to ecovariables. The relationships between ecovariables have been analyzed through a Spearman's correlation test. All correspondence analyzes were performed by using the software R 3.5.2 using the extensions "ca", "fac toextra", "vegan" and "FactoMineR". All univariate statistical tests were conducted using PAST 3.22 software (Hammer *et al.* 2001).

RESULTS

SYSTEMATIC NOTES

We have identified 5558 remains belonging to the Bovidae family (Table 3): 2330 cranio-dental and 3228 post-cranial. Based on the cranio-dental remains, a minimum of 112 individuals were identified. The complete assemblage includes nine bovid tribes, nine genera and at least 11 bovid species.

TABLE 3. — Bovid material recovered from Cooper's D with the NISP and estimates of MNI.

Tribes	Taxa	Bovid size class	NISP	MNI
Alcelaphini Brooke, 1876	<i>Megalotragus</i> sp.	IV	11	4
	<i>Connochaetes</i> sp.	III	60	7
	<i>Damaliscus</i> sp.	–	30	7
	Medium sized Alcelaphines	III	270	13
Antilopini Gray, 1821	<i>Antidorcas marsupialis</i> (Zimmermann, 1780)	II	50	11
	<i>Antidorcas</i> cf. <i>recki</i> (Schwarz, 1932)	II	45	8
	Antilopini indet.	II	82	7
Hippotragini Sundevall, 1845	<i>Hippotragus</i> sp.	III	13	3
Tragelaphini Blyth, 1863	<i>Tragelaphus</i> cf. <i>strepsiceros</i> (Pallas, 1766)	III	1	1
	<i>Tragelaphus</i> cf. <i>oryx</i> (Pallas, 1766)	IV	4	1
	<i>Tragelaphus</i> sp.	–	15	2
	<i>Tragelaphini</i> indet.	–	8	1
Reduncini Knottnerus- Meyer, 1907	<i>Redunca</i> sp.	II	2	1
	<i>Reduncini</i> indet.	–	37	8
Peleini Gray, 1872	<i>Pelea</i> sp.	II	10	4
Neotragini Sclater & Thomas, 1894	<i>Neotragini</i> indet.	I	26	3
Cephalophini Gray, 1871	<i>Cephalophini</i> indet.	–	7	1
Bovini Gray, 1821	<i>Syncerus</i> sp.	IV	3	2
	<i>Bovini</i> indet.	–	1	1
Indeterminate	Indeterminate	Small	739	8
		Medium	1709	11
		Large	747	8
		–	1688	–
Total		–	5558	112

The springbok, which is today the most abundant antelope species in South Africa, is the best-represented bovid at Cooper's D. At the tribe level, we notice that Alcelaphini (MNI = 31) and Antilopini (MNI = 26) dominate the assemblage (Fig. 2). The high diversity of these two tribes during the Pleistocene (Gentry 1990), coupled with their important morphological similarities, does not always allow specific identification from isolated teeth. As a result, their MNI could be undoubtedly underestimated.

Class MAMMALIA Linnaeus, 1758
 Order ARTIODACTYLA Owen, 1848
 Family BOVIDAE Gray, 1821
 Tribe TRAGELAPHINI Blyth, 1863
 Genus *Tragelaphus* Blainville, 1816

Tragelaphus cf. *strepsiceros* (Pallas, 1766)

Molars attributed to *Tragelaphus* are characterized by a caprine-like shape, such as a simple occlusal and central cavity outlines. Ribs and styles are not well developed. The basal pillar is absent from upper molars but small on the lower ones.

The goat-fold is absent on lower molars. Premolars are large and characterized by the paraconid-metaconid fusion. The teeth are not hypsodont. Unfortunately, no horn-cores have been found. The specimen CD 5399, a lower second molar, is similar in size to the common Swartkrans kudu (*T. strepsiceros*) (Table 4).

Tragelaphus cf. *oryx* (Pallas, 1766)

Three molars, especially CD 5410, are attributed to kudu and could belong to the eland, *T. oryx* (Fig. 3). The eland was recognized at Cooper's D by (Berger *et al.* 2003), but not by de Ruiter *et al.* (2009). The paucity of these remains is consistent with other Early Pleistocene assemblages in South Africa such as Sterkfontein Member 4, Swartkrans Members 1-3 or Kromdraai, where this animal is usually represented by only a few isolated teeth (Brain 1981).

Tribe BOVINI Gray, 1821
 Genus *Syncerus* Hodgson, 1847

Syncerus sp.

An upper first molar (CD 11062) is characterized by a general quadrangular shape, a constricted medial lobe, a well-defined basal pillar and ribs particularly rounded on the lateral side. Also, the outline of the central cavities is complex. This specimen is smaller than the tooth from Langebaanweg attributed to the species *Simatherium demissum* Gentry, 1980 (L45001, MD = 33.7 mm) (Gentry 1980) and from Olduvai, allocated to the species *Pelorovis oldowayensis* Reck, 1928 (HWK EE - T28 - L41, MD = 31.5 mm; BL = 29.4 mm) (Bibi *et al.* 2018). According to (Gentry & Gentry 1978), the genus *Syncerus* is characterized by medium-sized molars with an entostyle (basal pillar) and central pits with a less complex design in the genus *Bos* Linnaeus, 1758. Concerning the upper molars, the jugal pillars (metacone and paracone) are less pronounced than in the genus *Bos*. The genus *Pelorovis* Reck, 1928 is distinguished by small entostyle molars and simple central pits (Gentry & Gentry 1978). Finally, Gentry (2011) indicates that the species *Simatherium kobllarseni* Dietrich, 1941 has less derivative characters than the modern species *S. caffer* (Sparman, 1779) such as limited hypsodonty, a less developed metacone and paracone, and small to medium entostyle. Referring to these identification keys, we consider that the characters of the CD 11062 molar are close to those of *Syncerus* but without making assumption about the species.

Tribe CEPHALOPHINI Gray, 1871

Cephalophini gen. et sp. indet.

According to Gentry (2010), representatives of the Cephalophini tribe have brachyodont teeth with a basal pillar on

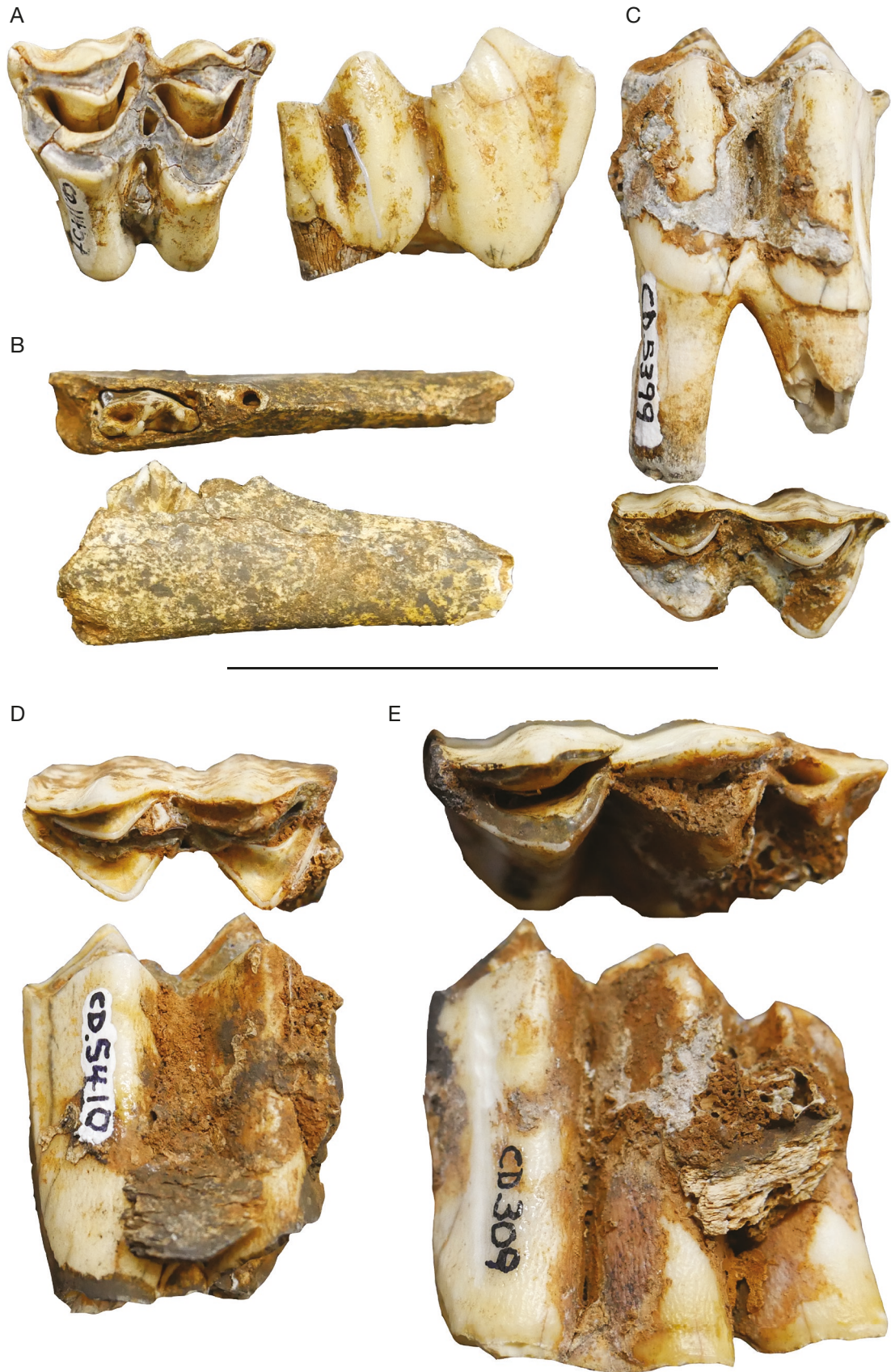


FIG. 3. — Isolated teeth attributed to the genus *Tragelaphus* Blainville, 1816 from Cooper's D: **A**, right dp4 (CD 11457); **B**, right mandible fragment (CD 5289); **C**, left M2 (5399); **D**, left M2 (CD 5410); **E**, left M3 (CD 309). Scale bar: 5 cm.

TABLE 4. — Lower second molar dimensions of modern and fossil Greater Kudu and Eland. Comparison data from Vrba (1974) and Berger & Lacruz (2003).

Samples	Taxa	no.	Measures	Mean (mm)	Min.	Max.	s.d.
Modern	<i>Tragelaphus strepsiceros</i> (Pallas, 1766)	12	Mesiodistal	24.3	22.3	26.7	1.2
		12	Buccolingual	17.1	13.1	14.7	1.2
Modern	<i>Tragelaphus oryx</i> (Pallas, 1766)	6	Mesiodistal	27.5	25.2	28.4	1.2
		6	Buccolingual	17.4	15.4	16.3	0.8

		Specimens		Dimensions (mm)
Gladysvale	<i>Tragelaphus strepsiceros</i> (Pallas, 1766)	MT 1955	Mesiodistal	25.8
			Buccolingual	13.2
Cooper's	<i>Tragelaphus cf. strepsiceros</i>	CD 5399	Mesiodistal	26.89
			Buccolingual	13.03
Swartkrans	<i>Tragelaphus cf. scriptus</i> (or <i>pricei</i> ?)	SK 3114	Mesiodistal	13.5
			Buccolingual	6
	<i>Tragelaphus cf. scriptus</i> (or <i>pricei</i> ?)	SK 14205	Mesiodistal	11.4
			Buccolingual	7.5
	<i>Tragelaphus cf. strepsiceros</i>	SK 3110	Mesiodistal	26
			Buccolingual	14.5

the upper and lower molars, rounded lobes and little or no development of styles and stylides. Only one specimen from Cooper's D, an unworn upper molar, has these characteristics and could therefore be attributed to that tribe.

Tribe NEOTRAGINI Sclater & Thomas, 1894

Neotragini gen. et sp. indet.

Two horn-cores are short and not very divergent, with a small uncompressed cross-section that is straight or slightly curved forward and are therefore been attributed to the Neotragini tribe. The teeth are characterized by having no basal pillar, straight lobes, a disappearance of central cavities early in wear, the presence of small styles and ribs rarely vertical (Gentry & Gentry 1978). According to Faith (2011), it is not possible to discriminate the two species of *Raphicerus* Hamilton Smith, 1827 (*R. campestris* (Thunberg, 1811) and *R. melanotis* (Thunberg, 1811)) based on dental criteria. It is, moreover, difficult to differentiate representatives of the genus *Raphicerus* from those of the genera *Oreotragus* (A. Smith, 1834), *Ourebia* Laurillard, 1842 and *Madoqua* (Ogilby, 1837). In keeping with a conservative approach, we attributed all of this material to the Neotragini tribe, without genus or species identification.

Tribe ANTILOPINI Brook in Wallace, 1876
Genus *Antidorcas* Sundevall, 1847

Antidorcas marsupialis (Zimmermann, 1780)

The extant springbok *Antidorcas marsupialis* is only represented at Cooper's D by isolated teeth (Fig. 4) and one fragmentary left mandible. They are indistinguishable from the extant form, sharing a strong development of styles on upper molars, straight cavities on lower molars, and a well-developed hypoconulid on lower third molars (Gentry & Gentry 1978). The material includes 50 remains corresponding to at least 11 individuals.

Antidorcas cf. recki
(Schwarz, 1932)

The two horn-cores CD 3111 and CD 8268 are similar to the *Antidorcas recki* material from other Plio-Pleistocene sites (Fig. 5). They display a mediolateral compression, a strong backward curvature, and a lack of divergence or torsion (Gentry & Gentry 1978). The comparison of *A. recki* horn-corn measurements, with other extinct and extant *Antidorcas* species, shows that Cooper's material fits comfortably within the *A. recki* size range from both East and South Africa (Fig. 6).

The teeth are similar to *A. marsupialis* but undoubtedly smaller (Figs 4; 7). For the dentition, we follow E. S. Vrba (Vrba 1973, 1974), who showed that M2 dimensions, and especially mesio-distal diameters, allow to separate *A. recki* from *A. australis* (Hendey, 1968) and *A. marsupialis* at Kromdraai A. We identified at least eight individuals (two juveniles, four adults and two old individuals).

Tribe PELEINI Gray, 1872
Genus *Pelea* Gray, 1851

Pelea sp.

Traits such as, the general "Antilopini" type shape, very pronounced development of mesostyles on the upper molars, a tendency to develop parastylids on the lower molars, a central fossa wide open, and teeth smaller than the species of the Antilopini tribe (Vrba 1974) permit to allocate this material to the genus *Pelea*.

Vrba (1974), in her study on Swartkrans bovid material, noted that the early representatives of the genus *Pelea* from the Member 1 are identical to the present form, while those of Member 2 and Kromdraai A are larger in size. She concluded that all the specimens from Swartkrans and Kromdraai A should be allocated to the same species which was on average larger than the present species.

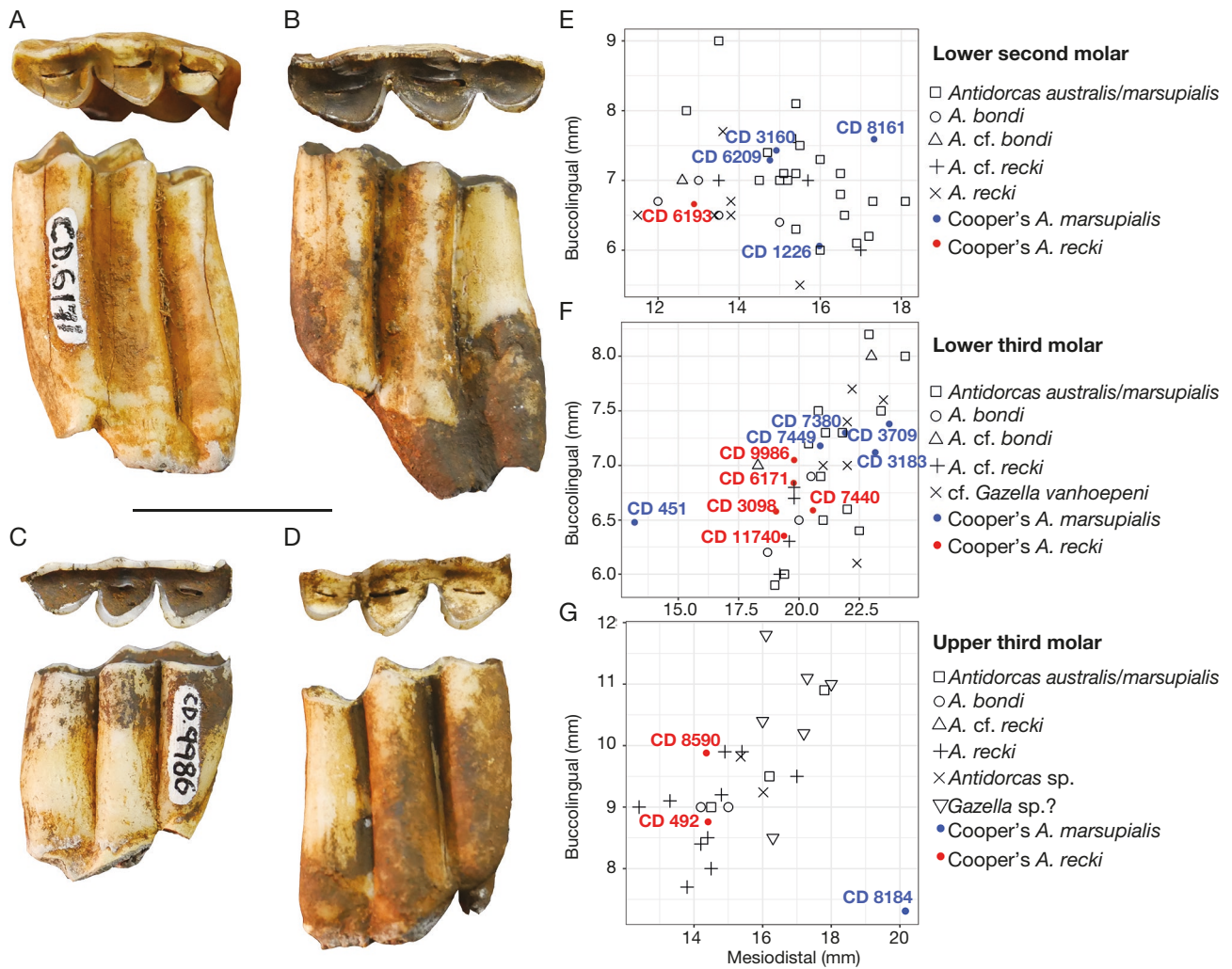


FIG. 4. — Specimens attributed to the genus *Antidorcas* Sundevall, 1847 from Cooper's D in occlusal and buccal view: **A, B**, left M3 (CD 6171 and CD 7380); **C, D**, right M3 (CD 9986 and CD 8184). Bivariate plot comparing mesiodistal and buccolingual diameters of lower second molars (**E**), lower (**F**) and upper (**G**) third molars from different African Antilopini. Comparison data from Vrba (1973, 1974) and Adams (2018). Scale bar: 2 cm.

Tribe REDUNCINI Knottnerus-Meyer, 1907
Genus *Redunca* C. H. Smith, 1827

Redunca sp.

We observe on this material the presence of a basal pillar (ectostylid and entostyl), a curvature of the central fossae with an occlusal enamel pattern simpler than the modern form and the constriction of the lobes, on the lingual side for the upper molars and vestibular surface for the lower molars. These specimens share close morphological features with the reedbeek, *Redunca fulvorufula* (Afzelius, 1815). However, the reedbeek is uncommon within the Early Pleistocene of South Africa. To our knowledge, the only site of the Cradle of Humankind having yielded remains attributed to the taxon *R. cf. fulvorufula* is Drimolen Main Quarry (Adams *et al.* 2016) and are represented by only horn-cores specimens. The mountain kob is definitely attested during the Middle Pleistocene at the Gladysvale

External Deposits (Lacruz *et al.* 2002). The lack of cranio-dental comparative material does not permit to go beyond the genus identification.

The Reduncini tribe is also represented by one fragmentary horn core (CD 3120), a fragmentary left mandible (CD 330) and an upper right molar (CD 17213) without genera or species identification.

Tribe HIPPOTRAGINI Sundevall, 1845
Genus *Hippotragus* Sundevall, 1845

Hippotragus sp.

Molars are characterized by a boödont occlusal morphology, the presence of a basal pillar and vertical ribs between the styles or stylids. These features allow us to attribute this material to the genus *Hippotragus* (Gentry, 2010) but without making any assumptions about the species identification.

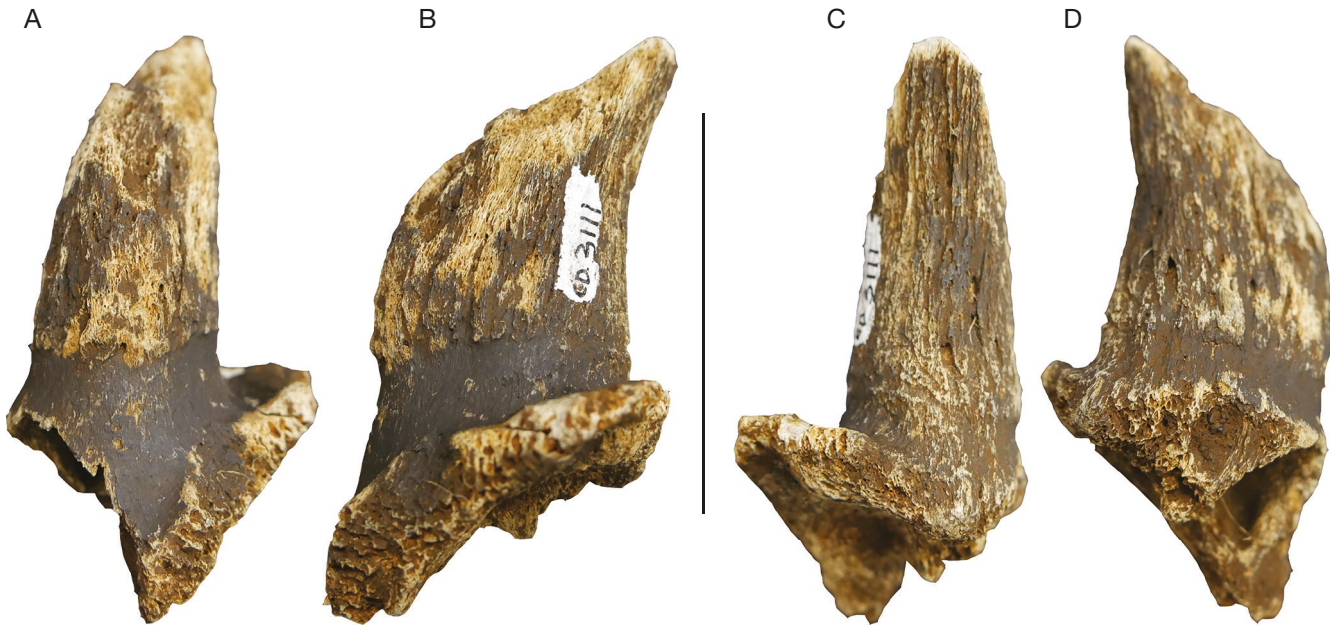


FIG. 5. — Right horn-core fragment attributed to the genus *Antidorcas* Sundevall, 1847 (CD 3111) from Cooper's D: **A**, anterior; **B**, medial; **C**, posterior; **D**, lateral view. Scale bar: 5 cm.

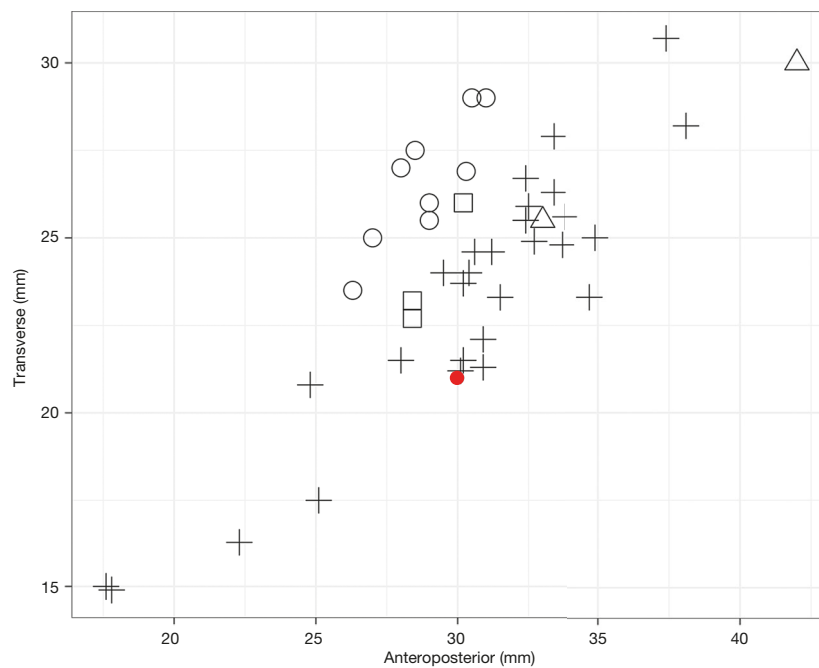


FIG. 6. — Bivariate plot comparing anteroposterior and transverse diameters of horn-cores of different African Antilopini. Comparison data from Vrba (1973, 1974) and Gentry & Gentry (1978). Symbols: □, *Antidorcas australis* (Hendey, 1968); ○, *A. bondi* (Cooke & Wells, 1951); △, *A. cf. recki* (Schwarz, 1932); +, *A. recki*; ●, CD3111.

Tribe ALCELAPHINI Brooke, 1876
Genus *Connochaetes* Lichtenstein, 1814

Connochaetes sp.

Nowadays, there are two different species of wildebeest in South Africa, the blue wildebeest (*Connochaetes taurinus* (Burchell, 1823)) and the black wildebeest (*Connochaetes gnou* (Zimmer-

mann, 1780)). The first is larger than the second. However, it seems that the size difference was less marked during the Pleistocene (Brink 1993). According to (Lacruz *et al.* 2002), it is difficult to differentiate the two species based on isolated teeth. For this reason, all material is attributed to the genus *Connochaetes* without specific identification. If we consider that this material corresponds to a homogeneous sample, seven individuals (three juveniles and four adults) are identified.



FIG. 7. — Mandible specimens attributed to the species *Antidorcas recki* (Schwarz, 1932) from Cooper's D: **A**, right mandible fragment (CD 24079) with preserved P3-M3; **B**, right mandible fragment (CD 8672) with preserved P4-M2. Scale bar: 2 cm.

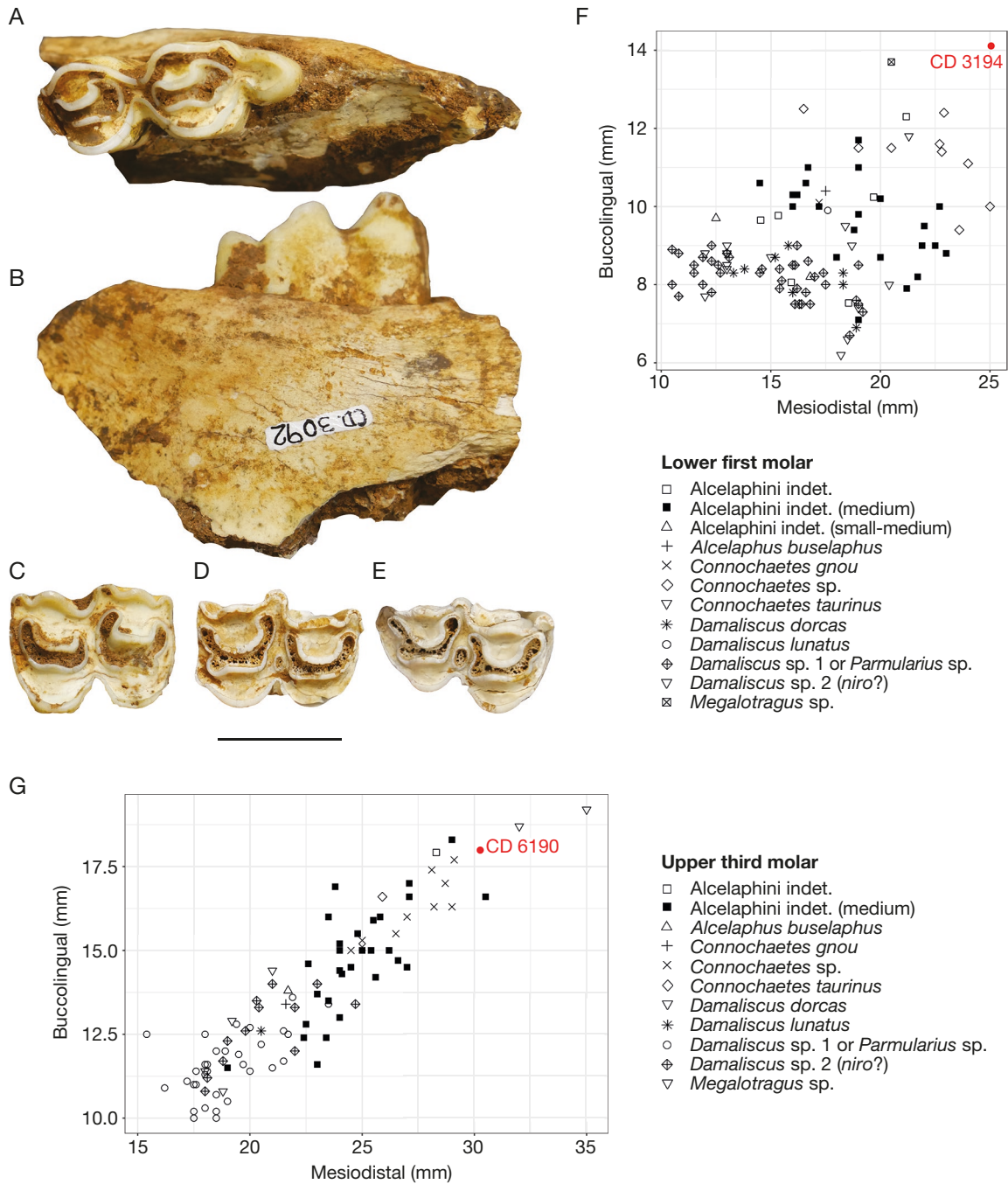


FIG. 8. — Specimens attributed to the genus *Megalotragus* van Hoepen, 1932 from Cooper’s D: **A, B**, left mandible fragment (CD 3092) in occlusal (**A**) and lingual view (**B**); **C**, left M2 (CD 3689); **D**, right M3 (CD 6190); **E**, right M1 (CD 6187); **F**, bivariate plot comparing mesiodistal and buccolingual diameters of lower first molars from different African Alcelaphini; **G**, bivariate plot comparing mesiodistal and buccolingual diameters of upper third molars from different African Alcelaphini. Comparison data from Adams (2018). Scale bar: 2 cm.

Genus *Damaliscus* Sclater & Thomas, 1894

Damaliscus sp.

Berger *et al.* (2003) mention the presence of *Damaliscus* cf. *dorcas* (Pallas, 1766) at Cooper’s D. After a re-examination of the material, and following de Ruiter *et al.* (2009), we attribute all these remains to the genus *Damaliscus* without

specific identification. Indeed, it is likely that several species of *Damaliscus* Sclater & Thomas, 1894 could be represented at Cooper’s D. Surprisingly, some dental specimens (CD 3699, CD 1928, CD 8182 and CD 15624) are similar, in terms of shape and size, to the extant *Damaliscus lunatus* Burchell, 1823, the tsessebe, which is typically found in younger deposits than those of Cooper’s D. This species is present in the Member 3 of Swarokrans (Vrba 1974, 1997) around 0.96 ± 0.09



FIG. 9. — Specimens attributed to the tribe Alcelaphini from Cooper's D: **A, B**, left mandible fragment (CD 9127B) in occlusal (**A**) and lingual view (**B**); **C**, left M3 (CD 3103); **D, E**, left M2 (CD 3096) in occlusal (**D**) and buccal view (**E**). Scale bar: 2 cm.

(Gibbon *et al.* 2014) among the medium sized alcelaphine dental material. Klein & Cruz-Urbe (1991) also report the presence of a *D. aff. lunatus* at Elandsfontein (*c.* 1.0-0.6 Ma) based on complete horn-cores and isolated teeth. However, the material was subsequently attributed to *Beatragus* by Vrba (1997). CD 10637, CD 7499 and CD 3101 are similar to the extant *D. dorcas*, the blesbok. Gentry (2010) noted the presence of *D. dorcas* during the Late Pleistocene of South Africa, but it could also be present in older Middle Stone Age deposits at Florisbad (Brink 1987). Additionally, the species seems to be present around 1.36 ± 0.29 Ma in Swartkrans Member 2 (Vrba 1974, 1997; Balter *et al.* 2008). *Damaliscus dorcas* could be much older since the *D. cf. dorcas* horn-cores from Kromdraai A (Vrba 1974) are now dated around 1.8-1.6 Ma (Braga *et al.* 2017). Following de Ruiter *et al.* (2009), we identified at least seven individuals: three juveniles, three adults and one old individual.

Genus *Megalotragus* van Hoepen, 1932

Megalotragus sp.

We attributed eleven specimens to the giant alcelaphin genus *Megalotragus* (Fig. 8). According to Gentry & Gentry (1978), the genus *Megalotragus* is characterized among other Alcelaphini by its large teeth and a simpler occlusal morphology of the molars. The teeth identified at Cooper's D have a simple occlusal pattern and larger in size than *Connochaetes*, such as CD 6190 and CD 3194 (Fig. 8). The type species *Megalotragus priscus* Broom, 1909, is usually recognized in the Cape Province, based on dental remains (Gentry 2010). It is one of the larger body mass species that became extinct at the end of the Pleistocene, around 12 000 BP (Klein 1974). We have identified a minimum of four individual (one juvenile, one subadult, one adult and an old individual).

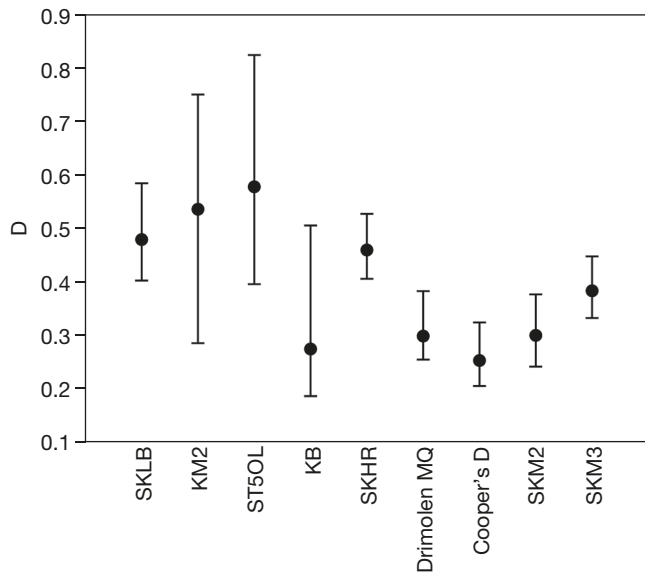


FIG. 10. — Unbiased Simpson index (D) obtain from bovid assemblages of *Paranthropus* Broom, 1938 and early *Homo* Linnaeus, 1758 South African sites. Data from Table 2.

Medium-sized Alcelaphini gen. et sp. indet.

A total of 269 remains, mainly isolated teeth or fragments of dental enamel, have been attributed to the Alcelaphini tribe based on the roundness of the lobes, the development of the pillars, the absence of entostyle, ectostylid and protostylid (basal pillars and caprine fold), according to the criteria of Gentry & Gentry (1978) (Fig. 9). This material could represent a minimum of thirteen individuals.

PALAEOECOLOGICAL ANALYSIS

Paleobiodiversity

With regards to bovid paleobiodiversity, we observe that Cooper's D (D = 0.2532) has one of the most diverse bovid assemblage compare to other *Paranthropus* Broom, 1938 and early *Homo* sites (Fig. 10; Table 1). It seems that neither the sedimentary nor the taphonomical context influenced the diversity of the assemblages (Table 1). However, the most diverse bovid assemblages are coming from youngest deposits. Indeed, all the assemblages with a Simpson's index mean lower than 0.4 are dated as younger as 2.0 Ma, except for Drimolen Main Quarry, for which the time averaging is too important.

Taxonomic composition

In order to test the ecological preferences of *P. robustus* and early *Homo*, we compared the distribution of Bovidae according to four ecological variables (diet, habitat and water requirement) from all sites that yielded *P. robustus* and early *Homo* remains. Given the number of deposits and variables, we first exploited the data using correspondence analyses (Fig. 11). We can first extract the following observations.

Diet category. The correspondence analysis applied on diet categories shows a partitioning along the first axis explained

mostly by the fruit plus diet category notably because Drimolen MNQ is the only site to has yielded an important Cephalophini material. We observe that Cooper's D is one of the closest assemblages to the Grass category. Kromdraai Member 2 seems to provide more Browser taxa than other deposits while Drimolen Main Quarry, which is characterized by the dominance of the Cephalophini tribe, is closest to the fruit plus category. More interestingly, it seems that Hominini, which are here inserted as supplementary points, are close to the fruit plus category.

Habitat. Concerning the habitat preference categories, we observe that almost all the deposits are grouped together near the grassland category although Swartkrans Member 2, Kromdraai B and Cooper's D seem to include more woodland adapted taxa and Drimolen Main Quarry and Kromdraai Member 2 preserve more wet adapted species. Hominini are positioning along the second axis far away from the grassland and woodland categories. However, they tend to be aligned with the wet category. This trend is more pronounced for the *Homo* genus.

Water requirements. Finally, the water requirements variable indicate that Cooper's D like Drimolen MQ is close to the water independent category. The partially water dependent category is an outlier although Kromdraai Member 2 seems to be close to this category, but only two rare taxa are representative of this category. The position of Hominini is aligned with the partially water dependent category along the second axis and opposed to the water dependent category.

Hominini habitat associations. In order to confirm the correlation between Hominini and ecovariables, we performed Spearman's correlation. We found a strong, statistically significant negative correlation between the proportion of *Paranthropus robustus* individuals and grassland adapted bovid species ($r_s = -0.8$; p -value = 0.01). This is consistent with previous negative correlation obtained by de Ruiter *et al.* (2008, 2012) between *P. robustus* individuals and different grassland adapted taxa such as primates, equids and suids. However, none other statistically significant correlation between Hominini and palaeohabitats, neither positive nor negative, has been obtained.

DISCUSSION

MINIMUM AGE ESTIMATE OF COOPER'S D

The basal flowstone below the calcified bone breccia has been recently dated by U-Pb to 1.375 ± 0.113 Ma (Pickering *et al.* 2019) which provides only a maximum age for the whole sequence. Our study has updated the list of large mammals at the Cooper's D site. It differs somewhat from the two previously published lists (Berger *et al.* 2003; de Ruiter *et al.* 2009). Four bovid taxa are no longer included in the updated list, as we have doubts about their identification: *Raphicercus* sp., *Tragelaphus* cf. *scriptus*, *Simatherium kohllarseni* and *Damalis-*

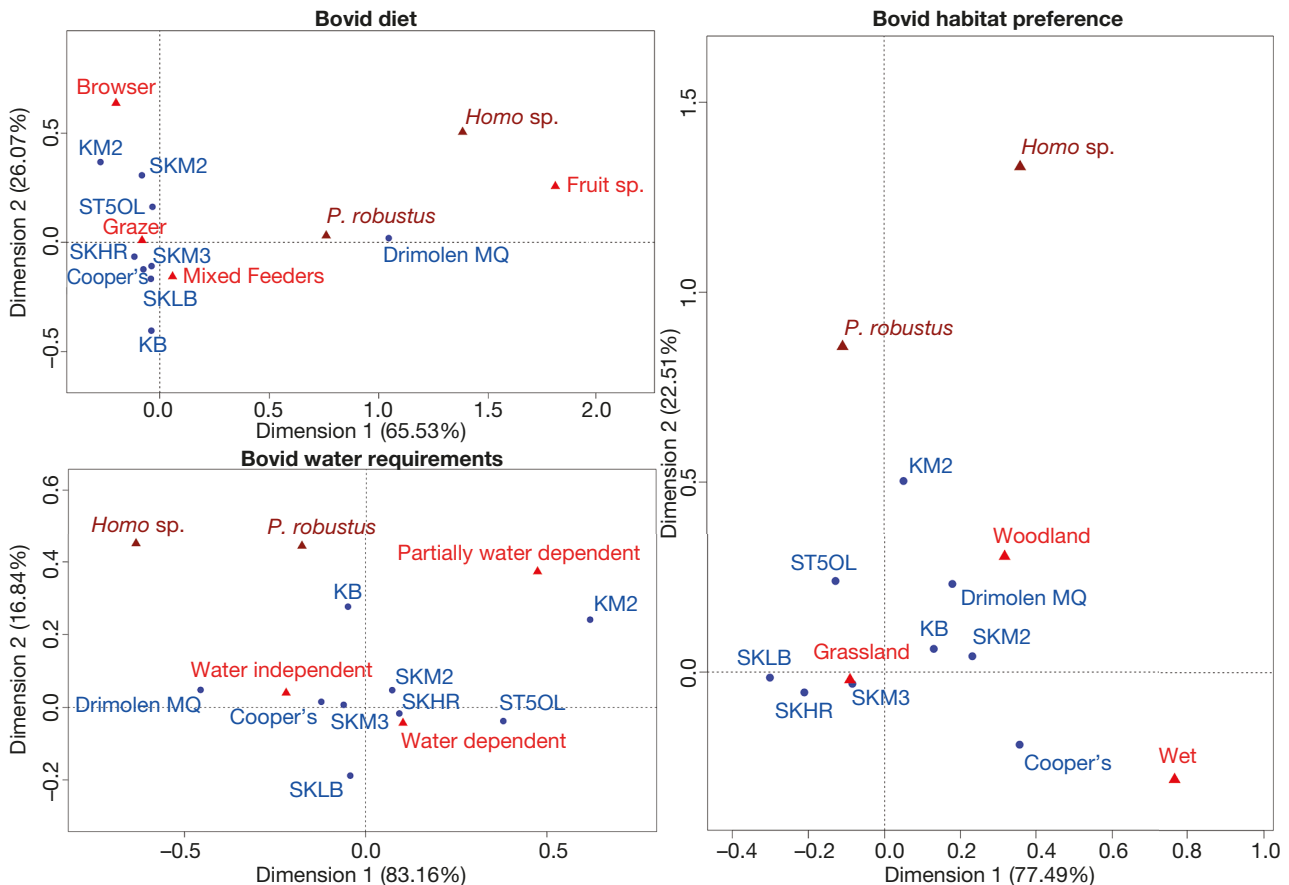


FIG. 11. — Correspondence analyses of the three different ecovariates (diet, habitat and water requirements) derived from the bovid assemblages used in this study (Table 2).

cus cf. *dorcas*. Most of the bovid taxa do not provide useful information for interpreting the age of the deposit. Indeed, all of them are preserved in older deposits. However, *A. recki* disappeared from the South African fossil record around 1.0–0.6 Ma at Elandsfontein (Klein *et al.* 2007) and *Megalotragus* became extinct during the Late Pleistocene (Faith 2014).

Taking into account the complete faunal list (Hartstone-Rose *et al.* 2007; Folinsbee & Reisz 2013; DeSilva *et al.* 2013; O’Regan *et al.* 2013; O’Regan & Steininger 2017; Kuhn *et al.* 2017; Badenhorst & Steininger 2019), the assemblage of large mammals consists of both extinct (*Paranthropus robustus*, *Theropithecus oswaldi* Andrews, 1916, *Lycaon sekowei* Hartstone-Rose, Werdelin, de Ruiter, Berger & Churchill, 2010, *Dinofelis aronoki* Werdelin & Lewis 2001, *Megantereon whitei* Broom, 1937, *Chasmaporthetes nitidula* Geraads, 1997, *Crocota ultra* Ewer, 1954, *Megalotragus* sp., *Antidorcas recki*, *Sivatherium maurusium* Pomel, 1893, *Metridiochoerus modestus* (van Hoepen & van Hoepen, 1932), *Metridiochoerus andrewsi*, *Equus capensis* Broom, 1909 and *Eurygnathohippus cornelianus* van Hoepen, 1930) and modern taxa (*Lupulella mesomelas* (Schreber, 1775), *Lycaon pictus* (Temminck, 1820), *Vulpes chama* (A. Smith, 1833), *Panthera leo* (Linnaeus, 1758), *Panthera pardus* (Linnaeus, 1758), *Caracal caracal* (Schreber, 1776), *Felis lybica* Forster, 1780, *Felis silvestris* Schreber, 1777, *Acinonyx jubatus* Brookes, 1828, *Crocota*

crocuta (Erxleben, 1777), *Parahyaena brunnea* (Thunberg, 1820), *Proteles cristata* (Sparrman, 1783), *Antidorcas marsupialis* (Zimmermann, 1780), *Redunca fulvorufula* (Afzelius, 1815) and *Orycteropus afer* (Pallas, 1766)).

Among these taxa, some species are very old, such as *Chasmaporthetes nitidula* which is known from 4 Ma in Jacovec Cavern (4.02 ± 0.27 – 3.76 ± 0.26 Ma; Fig. 12) (Kuhn *et al.* 2017). Some species, such as *Metridiochoerus modestus* and *Sivatherium maurusium*, appeared more recently in South Africa at Swartkrans Member 2 (de Ruiter 2003), dated around 1.4 Ma (Balter *et al.* 2008) or 1.7 Ma (Pickering *et al.* 2011). However, the temporal range of *M. modestus* is established between 2.21 and 0.7 Ma from Member G of the Shungura Formation (Werdelin & Sanders 2010). Moreover, *S. maurusium* is also known from the “E” Quarry at Langebaanweg, estimated around 5.2 Ma (Werdelin & Sanders 2010; Roberts *et al.* 2011). All the modern taxa are known from older sites such as Kromdraai, Swartkrans Members 1–3, Gondolin, members of Sterkfontein and Drimolen in the region and do not allow us to give an age to the assemblage. Furthermore, by looking at the extinction dates of fossil species, we note that they all disappeared from the fossil record around 1 Ma (Fig. 12), except for *Megalotragus*. Swartkrans Member 3 (0.96 ± 0.09 Ma) contains the last occurrence of the hyena species *Crocota ultra* and *Chasmaporthetes nitidula*

in South Africa (de Ruiter 2003; Werdelin & Peigné 2010; Kuhn *et al.* 2017). The giant baboon *Theropithecus oswaldi*, the sabre-toothed cat *Megantereon whitei*, the antelope *Antidorcas recki* and the warthog *Metridiochoerus andrewsi* are recognized up to 1.0–0.6 Ma at Elandsfontein (Klein *et al.* 2007). The horse *Eurygnathohippus cornelianus* and the warthog *Metridiochoerus modestus* are no longer known after 1.07–0.99 Ma at Cornelia-Uitzoek (Brink *et al.* 2012). Finally, we can notice the absence of the plain's zebra *Equus burchelli*, which appeared after 1 Ma (Badenhorst & Steininger 2019).

The biochronological data therefore indicate that the accumulation of this assemblage most likely occurred between 2.0 and 1.0 Ma. Based on the complementary results obtained from radiometric dating method (U-Pb) and biochronology, we estimate that the Cooper's D bone assemblage accumulated between 1.375 ± 0.113 and 1.0 Ma.

USING BOVIDS FOR RECONSTRUCTING PALEOENVIRONMENTS

It was previously argued that the Cooper's assemblage represents one of the grassiest local environments in the Sterkfontein Valley (de Ruiter *et al.* 2008). The current analysis confirms that Alcelaphini and Antilopini are the most abundant taxa in the Cooper's D assemblage (Fig. 2). It was demonstrated that among Bovid tribes, Alcelaphini and Antilopini have been shown to be good markers of open and arid environments among all Bovidae tribes (Vrba 1974; Bobe & Eck 2001; Alemseged 2003; Bobe & Behrensmeier 2004; Bobe 2006). Vrba (1974) used the ratio (Alcelaphini + Antilopini)/MNI_{bovids} as a measure of the openness of the habitat. At Cooper's D, this ratio is relatively low (70% of identified taxa) compared with other South African sites. This suggests that open landscapes were not as common around the cave during the time of the bone accumulation. This result is consistent with the dominance of large body-sized bovid at Cooper's D ($n = 54\%$ of size class III or larger). According to Vrba (1974), the presence of large body-sized bovid is indicative of a "closed" environment.

The study of Cooper's D's paleocommunity of Bovidae allowed us to highlight the important diversity of species adapted to the consumption of grasses and mixed foods (leaves + grasses). The category of species dependent on the permanent presence of water predominates in terms of diversity, followed by species which are independent of the permanent presence of a water source. Finally, the assemblage is largely dominated by large and medium-sized species, which are dependent on grassy savannah environments. These results permit to nuance those obtained from the study of the fauna as a whole (de Ruiter *et al.* 2009). In fact, a two-component environment emerges: on the one hand, a predominantly open environment, largely represented by grassy savannah; on the other hand, a few humid wooded areas punctuating the savannah landscape, probably on the surrounding of a permanent water point. Of course, Cooper's D may represent a variety of palaeohabitats resulting from both time and climate-averaging, a bias already identified in several south African fossil sites (O'Regan & Reynolds 2009; Hopley & Maslin 2010).

EARLY *HOMO* AND *PARANTHROPUS ROBUSTUS* HABITAT PREFERENCES

In a recent publication, Pickering *et al.* (2019) indicate that south African caves are more likely to preserve during dry phases, when the caves are open. On the contrary, major wet periods are indicated in karst by the formation of speleothems (e.g. stalagmites, stalactites, stalagmitic floors) when the caves were closed. Thus, Pickering *et al.* (2019) suggest that since the accumulation of bones occurs mainly during arid periods, the fossil record is biased, as are our interpretations concerning the palaeoecology of Hominini, by an over-representation of taxa adapted to the open-dry environment.

Because bone accumulation is likely to be restricted to drier intervals, Pickering *et al.* (2019) argue that the view of Hominini paleoecology is biased. Then, they conclude that Hominini time-range (such as *Paranthropus* and *Homo*), which are found during dry periods, unequivocally straddle wet periods, indicating either that these species were ecological generalists or that they left the Cradle of Humankind landscape during the wet periods only to return at a later, drier time.

Our results indicate that the abundance of Hominini is similar to the relative representation of bovid with more fruit-based diet, wet environment and partially water dependent species. This observation is consistent with the Hominini diet reconstitution by isotopic analysis undergone by Lüdecke *et al.* (2018), who noted that "*P. robustus* probably also lived in a woodland environment and had a similarly mixed diet. [...] *P. robustus* maintained a C3 dominated diet in the wetter and more mesic environments of southern Africa".

We found a statistically significant correlation between bovid grassland adapted taxa and the presence of *P. robustus*. Thus, this species has occupied environments close to those inhabited by bovids such as the kudu (*Tragelaphus strepsiceros*, large, partially water dependent, occupying wooded or shrubby areas, consuming leaves), the bushbuck (*Tragelaphus scriptus*, small bovids occupying rocky wooded or shrubby areas, partially dependent and consuming leaves) or the klipspringer (Cephalophini of the genus *Oreotragus*, small in size, partially dependent on water sources and integrating more of fruit in his diet).

Thereby, it appears that *Paranthropus* and early *Homo* lived in a wide range of environments, from closed/wet to a grassland landscape. This supports previous isotopic analysis conducted on bovids and on *P. robustus* remains as well (Lee-Thorp *et al.* 1994, 2000, 2010; Sponheimer *et al.* 2006; Brophy 2011; Steininger 2011; Ungar & Sponheimer 2011; Balter *et al.* 2012; Lüdecke *et al.* 2018). Our study also supports precedent conclusions obtained by de Ruiter *et al.* (2008, 2012) using a similar approach on different taxa such as primates, equids and suids.

CONCLUSION

We provide the first taxonomic and paleoecological analysis of the Cooper's D bovid assemblage with the first biochronological interpretations. Our study permits to propose

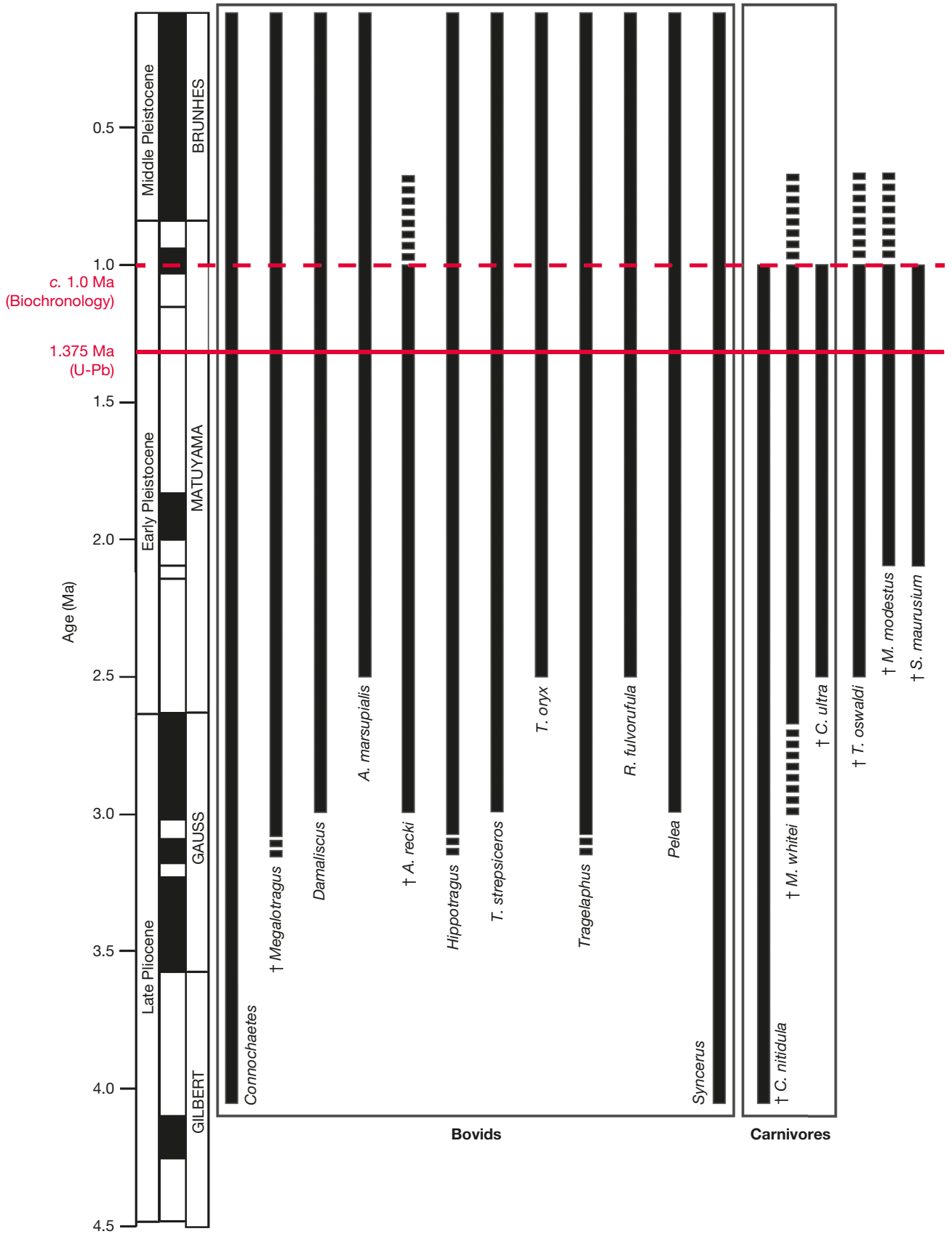


Fig. 12. — Time range of selected large mammal present at Cooper's D.

a minimum age for the Cooper's D bone accumulation, estimated to be around 1.0 Ma. Thus, we conclude that the assemblage accumulated between 1.375 ± 0.113 and 1.0 Ma based on the complementary results obtained from radiometric dates and biochronology.

Previous analyses tend to show that the Cooper's assemblage represents one of the grassiest local palaeoenvironments during the Early Pleistocene in the Sterkfontein Valley (de Ruiter *et al.* 2008). The current analysis confirms that Alcelaphini and Antilopini are the most abundant taxa in the Cooper's D assemblage but in a relative low proportion compared to other South African Hominini-bearing caves. This suggests that Cooper's D is likewise dominated by grassland with the presence of sparse covered habitat and a probable water source in the vicinity. Moreover, we showed a strong statistically significant negative correlation between the presence of grassland adapted bovid species and *P. robustus*. This result indicates that *P. robustus* was more likely to be an eurytopic species and dietary generalist.

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