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New fossil Bovidae (Mammalia: Artiodactyla) from Kromdraai Unit P, South Africa and their implication for biochronology and hominin palaeoecology

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ABSTRACT

Kromdraai is a Plio-Pleistocene site located in the Cradle of Humankind (Gauteng Province, South Africa). It has produced diverse and abundant faunal assemblages and key hominin specimens like the holotype of *Paranthropus robustus* and early *Homo*. We provide the first taxonomic study of the Bovidae Family from the hominin-bearing Unit P at Kromdraai and discuss its potential to unravel its paleoecological context. We describe the presence of an unknown medium-sized buffalo (*Syncerus* sp.) that could be closely related to *S. acoelotus*. The bovid assemblage from Kromdraai Unit P combines older Plio-Pleistocene (*Gazella gracilior*, *Makapania broomi*, *Numidocapra* cf. *porrocornutus*) and younger Pleistocene taxa (*Tragelaphus strepsiceros*, *Oreotragus oreotragus*, *Raphicerus campestris*, *Damaliscus lunatus*). Overall, these bovid species indicate a grassland-dominated environment for Unit P. Comparisons with other Plio-Pleistocene South African sites indicate that *Australopithecus* was associated with woodland and closed-wet environment-adapted taxa, whereas *Homo* was found in association with bovid species adapted to open and dry environments. In contrast, the assemblages associated with *Paranthropus* show an extensive range of environmental adaptation among the bovids. The biochronology indicates that Kromdraai Unit P accumulated between 2.9 and 1.8 Ma. If Kromdraai Unit P were to be confirmed to date to the older end of this scale, it would provide the earliest appearance of *Paranthropus robustus*, *Numidocapra*, and *Damaliscus* in southern Africa.

1. Introduction

Bovidae is often the most abundant large mammal family found in Quaternary archaeological and palaeontological sites in Africa. Due to their ecological diversity, bovids represent one of the best choices for reconstructing past environments through the study of fauna. Moreover, many bovid species are the preferred prey of large carnivores and hominins (Brain, 1981; Hayward and Kerley, 2005; Hayward, 2006; Matt W. Hayward et al., 2006; M. W. Hayward et al., 2006; Périquet et al., 2015). Therefore, bovids are a good proxy for reconstructing the taphonomic history of a deposit as well as carnivore and hominin behaviours. Despite their importance in the fossil record, bovids are relatively understudied in South Africa, especially from a taxonomic point of view. Since the work undergone by Wells and Cooke (1956), Wells (1965), Vrba (1971, 1973, 1973, 1974, 1975, 1977, 1978, 1987), Klein and Cruz-Uribe (1991), Watson and Plug (1995), Brink (1993, 1999, 2005) and later Brink and Stynder (2009), Brophy et al. (2016) and Adams et al. (2016), Adams (2018), many fossiliferous deposits from South Africa (e.g., Motsetse, Matjhabeng, Gladysvale, Bolt's Farm, Wonderwerk) have yielded more bovid assemblages that would benefit

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from deeper taxonomic investigation (Berger, 1993; Lacruz et al., 2002; Berger and Lacruz, 2003; de Ruiter et al., 2010; Badenhorst et al., 2011; Brink et al., 2016; van Zyl et al., 2016).

The Kromdraai archaeological site is located in the UNESCO World Heritage Site known as the "Cradle of Humankind", Gauteng Province, South Africa (Fig. 1). It corresponds to an unroofed dolomitic cave chamber filled with both calcified and decalcified fossiliferous sedimentary deposits (Braga and Thackeray, 2016; Braga et al., 2017, 2022b). Kromdraai is particularly known for having yielded the holotype of *Paranthropus robustus* (Broom, 1938).

Fieldwork carried out at Kromdraai by Vrba (1981) resulted in the establishment of the initial stratigraphic sequence at this site. For further information on the successive phases of excavations at Kromdraai, refer to Braga et al. (2013, 2017, 2022b) and Braga and Thackeray (2016). The ongoing phase of systematic excavation at Kromdraai was initiated in 2002 under the auspices of the Kromdraai Research Project (KRP) (Braga and Thackeray, 2016; Braga et al., 2013, 2017). The fieldwork conducted by the KRP revealed that fossil-rich sediments at Kromdraai extended further north and east than previously recognized by Brain (1958, 1981) or Vrba (1977). Consequently, the Kromdraai A (KA) and Kromdraai B (KB) infillings were integrated into a singular, revised stratigraphic sequence (Bruxelles et al., 2016; Braga et al., 2017, 2022b). The oldest part of the Kromdraai revised stratigraphic sequence - Units O and P - is represented in the central part of the excavation (Braga and Grine, 2024: Fig. 1). Unit P is considered to be equivalent to the decalcified deposits that were designated as 'Member 2' and considered as 'sterile' by Vrba (1981)(see also Partridge, 1982; Bruxelles et al., 2016). There is also a large stalagmite, the base of which formed on an unconformity separating Unit O from Unit P above (Braga et al., 2022b). The younger sediments that have been designated Units Q-R

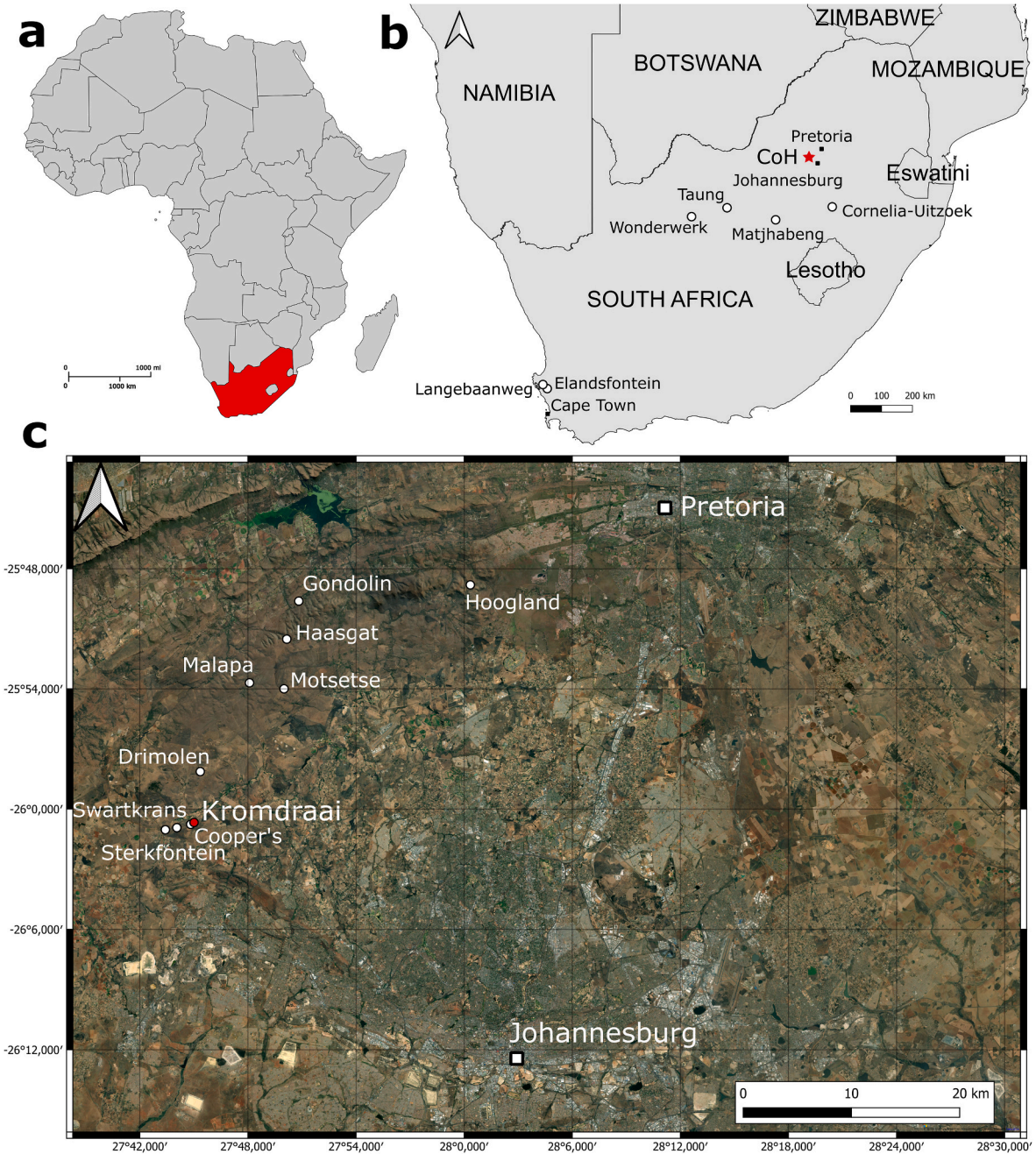


Fig. 1. Map of southern Africa with a focus on the Cradle of Humankind (CoH) and the location of the Kromdraai site.

(previously referred to as 'Member 3') are separated from the underlying Unit P by another unconformity and another flowstone that was recognized and illustrated by Vrba (1981). The youngest part of the Kromdraai stratigraphic sequence - Units X-Z - is represented only at the periphery of the site, on its eastern, northern and western ends. This latter end was previously designated 'KA'. As already emphasized by Braga et al. (2013, 2017, 2022b), the KB fauna and hominins recovered before 2002 cannot be treated as a temporally homogeneous sample, and cannot serve to provide any biochronological estimates and palaeoenvironmental reconstructions.

Even though the geochronological context of Kromdraai is not fully resolved, one of the flowstones in its sequence records the Olduvai subchron (1.78–1.95 Ma) (Thackeray et al., 2002). The stratigraphically older (i.e., underlying) Units QR and P were deposited prior to the Olduvai subchron and contained *P. robustus* specimens (Braga et al., 2013, 2021, 2022b, 2023; Braga and Grine, 2024). The hominin and faunal assemblages from Kromdraai Unit P predate previous KA or KB assemblages, including the holotype of *P. robustus*, TM 1517, and other specimens recovered before 2014.

Since 2014, the KRP collected more than 6000 fossil remains (Braga et al., 2022b) representing mammals (Fourvel, 2018; Fourvel et al., 2018; Fourvel and Frerebeau, 2022; Fourvel and Thackeray, 2022), including hominins (Braga et al., 2021, 2022a, 2023; Harper et al., 2022; Braga and Grine, 2024), and birds (Pavia, 2019, 2020), most of them deriving from Unit P (Braga and Thackeray, 2016; Braga et al., 2017, 2022b; Ngoloyi et al., 2020). The Kromdraai Unit P is characterized by an abundant and rich large mammal (Fourvel et al., 2018: Table 2) and avian (Pavia, 2020: Table 1) faunas. At least 51 cranial and postcranial hominin remains were recovered from Unit P, most of them attributed to *P. robustus* (Braga et al., 2017, 2021, 2022a, 2023; Braga and Grine, 2024).

In this paper, we propose the first taxonomic study of the bovid fossil remains from the hominin-bearing Kromdraai Unit P. Based on bovid faunal evidence, we explore the palaeoecological context of the deposit as well as the biochronological framework in which the assemblage was accumulated.

2. Material and methods

This study comprises 565 bovid cranio-dental specimens recovered from Kromdraai Unit P between 2014 and 2022 (Braga and Thackeray, 2016; Braga et al., 2017, 2022b). We used the prefix 'KW' adopted by the Kromdraai Research Project since 2016 (Braga and Thackeray, 2016) for all the new specimens recovered at Kromdraai recovered under the ongoing Kromdraai hominin site excavation permit (ID:3035, 3176 and 3888) issued to J. Braga in collaboration with B. Zipfel and F. Thackeray.

All the specimens are housed at the Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg. We used the modern comparative collection and the fossil collections from Makapansgat, Kromdraai (A and B), Sterkfontein and Swartkrans housed at the Evolutionary Studies Institute and the Ditsong Museum in Pretoria. The catalogue of the specimens included in this study is provided in the **Supplementary_Material_S1**.

Table 1
Bovid classification used in this study. Extinct genera are indicated by '†'. Adapted from Marcot (2007), Hassanin et al. (2012), Bibi (2013), Bärmann et al. (2013) and Bärmann and Schikora (2014).

Subfamily	Tribe	Genera
Bovinae	Boselaphini	*Boselaphus, Tetracerus, Miotragocerus*†
	Tragelaphini	*Tragelaphus, Taurotragus*
	Bovini	*Syncerus, Bubalus, Bison, Bos, Simatherium*†, *Pelorovis*†, *Ugandax*†
Antilopinae	Cephalophini	*Cephalophus, Philantomba, Sylvicapra*
	Neotragini	*Neotragus*
	Oreotragini	*Oreotragus*
	Antilopini	*Antidorcas, Antilope, Gazella, Ourebia, Raphicerus, Saiga, Eudorcas, Nanger, Litocranius, Procapra, Dorcatragus, Madoqua*
	Aepycerotini	*Aepyceros*
	Reduncini	*Kobus, Redunca, Pelea*
	Hippotragini	*Hippotragus, Oryx, Addax, Wellsiana*†
	Alcelaphini	*Alcelaphus, Connochaetes, Damaliscus, Beatragus, Megalotragus*†, *Parmularius*†, *Numidocapra*†, *Damalacra*†
	Caprini	*Makapania*†, *'Bos'*, *Ovis, Capra, Pantholops, Ovibos, Capricornis, Naemorhedus, Ammotragus, Arabitragus, Rupicapra, Budorcas, Oreamnos, Pseudois, Hemitragus*

2.1. Faunal analysis

Each individual specimen was recorded separately in the catalogue with its accession specimen number, provenance (Unit), skeletal element, side, taxonomic identification, age and size class estimation. The bovid size class system used in this paper follows Brain (1981).

All measurements were taken with a digital calliper and recorded in millimetres, unless stated otherwise. The horn-core measurements were taken at the base of the horn, just above the pedicel. Tooth measurements were taken at the occlusal surface, following Vrba (1974). The zoological nomenclature follows the International Code of Zoological Nomenclature as well as Bengtson (1988). The anatomical descriptions follow the nomenclature provided by Gentry (1978, 1992, 2010) and Bärmann and Rössner (2011).

The bovid classification followed in this study is provided in Table 1.

To quantify the bovid faunal assemblage, we used the Number of Identified Specimens (NISP) and the Minimum Number of Individuals (MNI). We applied MNI by combination (cMNI) which corresponds to the most represented anatomical element for a given species by taking into account the side, age, sex and size of the specimens (Lyman, 1994).

Regarding the palaeoecological analysis, we analysed both bovid taxonomic abundance and presence-absence data of Kromdraai Unit P.

To explore the bovid taxonomic abundance and composition at these sites, we applied the method pioneered by Reed (1996, 1998) and subsequently developed by de Ruiter et al. (2008, 2012) and Hanon et al. (2022). The method consists of assigning each taxon habitat preference, diet category and water requirement. These parameters are referred below to as "ecovariables" (de Ruiter et al., 2012) and are composed as follows.

Habitat: closed and wet, woodland, grassland or mixed.
Diet: fruit-leaves, fresh grass, browser, grazer, mixed-feeder.
Water requirement: dependent, independent or partially dependent on the presence of a permanent water source.

The ecovariables are assigned based on isotopic analyses, micro and mesowear data, as well as uniformitarianism (Reed, 1996). The description and assignment of each ecovariable to each taxon are provided in Table 2.

After assigning the taxon to the three ecovariables, we applied a 'Multiple Correspondence Analysis' (MCA) to observe the distribution of the assemblage for each ecovariable. MCA was also performed on the bovid abundance (in MNI) per bovid tribe. MCA were carried out in PAST software (Hammer et al., 2001)

Finally, we explored the presence-absence data of bovid taxa by applying a UPGMA cluster analysis using the Jaccard similarity index (Belmaker and Hovers, 2011).

The full datasets are provided in Supplementary Material S2-4 and were compared with other South African Plio-Pleistocene sites (Table 3).

Institutional abbreviations – ESI: Evolutionary Studies Institute, University of Witwatersrand, Johannesburg; **DNMNH**: Ditsong National Museum of Natural History, Pretoria.

Deposit abbreviations – **CD** = Cooper's D; **DMQ** = Drimolen Main Quarry; **MAL** = Malapa; **MKM3** = Makapansgat Member 3; **MKM4** =

Table 2
Description and assignment of each ecovariables to the bovid taxa. Derived from Reed (1996, 1998).

Ecovariable	Variables	Description	Taxa
Habitat	Grassland	Open savannas are dominated by grasses and herbs with scattered groups of trees and shrubs.	*Antidorcas*, *Raphicerus*, *Connochaetes*, *Damaliscus*, *Pelea*, *R. fulvorufula*, *Hippotragus*
	Woodland	Landscape with more than 20% of tree cover. It differs from forest by being composed of trees that are more branched than columnar, deciduous, and ranging from eight to 20 m in height.	Tragelaphini, *Oreotragus*
	Mixed	Comprise species adapted to mixed environments, from grassland to woodland, as well as closed and wet environments.	*Alcelaphus*, *Syncerus*, *Sylvicapra*, *Hippotragus*
	Closed/Wet	Forest environment is composed of columnar trees with complex closed canopies and high humidity.	Cephalophini, *Kobus*, *R. arundinum*
Diet	Grass	Grasses	Alcelaphini, Hippotragini
	Fresh grass	Floodplain, edaphic and wetland grasses	*Kobus*, *R. arundinum*
	Fruit plus	Fruit with leaves or insects	Cephalophini, Neotragini
	Browsers	Leaves	Tragelaphini, Cephalophini, *Raphicerus*, *Gazella*
	Mixed-feeders	Mixed leaves and grasses	*Antidorcas*, *Syncerus*
Water requirements	Dependent		*Connochaetes*, *Hippotragus*, Bovini, Reduncini
	Independent		Cephalophini, Antilopini, *Alcelaphus*
	Partially dependent		*Tragelaphus*, *Damaliscus*

Table 3
Comparative bovid assemblages were used in this study.

Site	Deposit	Sedimentary context	Age	Hominins	References
Cooper's	Cooper's D	D	1.5–1.0 Ma	P	(de Ruiter et al., 2009; Pickering et al., 2019; Hanon et al., 2022)
Drimolen	Main Quarry	C/D	2.0–1.95 Ma	P/H	(Adams et al., 2016; Herries et al., 2020)
Kromdraai	Unit P	D	>2.2 Ma	P	(Fourvel et al., 2018); This study
Malapa	Malapa	C/D	2.0–1.8 Ma	A	(Berger et al., 2010; Dirks et al., 2010; Val et al., 2015; Brophy et al., 2016)
Makapansgat	Member 3	C	2.9–2.6 Ma	A	(Wells and Cooke, 1956; McFadden et al., 1979; Reed, 1996; Partridge, 2000; Herries et al., 2009)
	Member 4	C	3.0–2.6 Ma	A	(Wells and Cooke, 1956; McFadden et al., 1979; Reed, 1996; Partridge, 2000; Herries et al., 2009)
	Member 5	C	2.4–0.8 Ma	–	(Wells and Cooke, 1956; McFadden et al., 1979; Reed, 1996; Partridge, 2000)
Motsetse	Motsetse	D	1.6–1.0 Ma	–	Berger and Lacruz (2003)
Sterkfontein	Member 2	C/D	3.7 ± 0.2 Ma	A	(Pickering et al., 2004a; Granger et al., 2015)
	Member 4	C	3.5 ± 0.2–3.4 ± 0.1 Ma	A	(Pickering et al., 2004b; Kibii, 2007; Pickering and Kramers, 2010; Granger et al., 2022)
	Member 5 East Oldowan	D	2.2 ± 0.2 Ma	P	(Pickering, 1999; Granger et al., 2015)
	Member 5 West Acheulean	D	1.3–1.1 Ma	H	(Pickering, 1999; Herries and Shaw, 2011)
Swartkrans	Hanging Remnant	C	2.3–1.8 Ma	P/H	(Brain, 1993; Kuman et al., 2021)
	Lower Bank	D	2.2 ± 0.1 Ma	P/H	(Brain, 1993; Kuman et al., 2021)
	Member 2	D	1.4 ± 0.3 Ma	P/H	(Brain, 1993; Balter et al., 2008)
	Member 3	D	1.0 ± 0.1 Ma	P	(Brain, 1993; Gibbon et al., 2014)

Abbreviations. **C** = calcified, **D** = decalcified, **P** = *Paranthropus*, **H** = *Homo* sp., **A** = *Australopithecus*.

Makapansgat Member 4; **MKM5** = Makapansgat Mermber 5; **MOT** = Motsetse; **SKHR** = Swartkrans Member 1 Hanging Remnant; **SKLB** = Swartkrans Member 1 Lower Bank; **SKM2** = Swartkrans Member 2; **SKM3** = Swartkrans Member 3; **ST5AL** = Sterkfontein Member 5 West Acheulean; **ST5OL** = Swterkfontein Member 5 East Oldowan; **STM2** = Sterkfontein Member 2; **STM4** = Sterkfontein Member 4.

Anatomical abbreviations – A = *Australopithecus*; **Aepy** = Aepycerotini; **Alce** = Alcelaphini; **Anti** = Antilopini; **APD** = anteroposterior diameter; **B** = browser; **BL** = buccolingual diameter; **Bose** = Boselaphini; **Cal** = calcified; **Ceph** = Cephalophini; **CH** = crown height; **CI** = compression index of the horn-core (anteroposterior diameter:transverse diameter); **C/W** = closed/wet; **Dec** = decalcified; **DEP** = dependent; **dm** = decidual molar; **dp** = decidual premolar; **e** = the letter "e" after a number indicates an estimated measure when the specimen is not complete preserved; **FG** = fresh grass; **FL** = fruit and leaves; **Grass** = grassland; **G** = grazer; **H** = *Homo* sp.; **hc** = horn-core; **HI** = hypsodonty index; **Hippo** = Hippotragini; **IND** = independent; **L** = left; **Lr** = labial ribs; **lw** = labial walls; **M** = molar; **MD** = mesiodistal length; **MF** = mixed feeder; **MNI** = minimum number of individuals; **ms** = metastyle; **Mx** = mixed habitat; **NISP** = number of identified specimens; **Or** = orbital ridge; **P** = premolar; **Pa** = *Paranthropus*; **PART** = partially dependent; **poc** = pseudo-occipital crest; **R** = right; **Red** = Reduncini; **rs** = rugose surface; **sf** = supraorbital foramen; **TD** = transverse diameter; **tr** = temporal ridge; **Trage** = Tragelaphini; **W** = woodland.

3. Systematic palaeontology

Order ARTIODACTYLA Owen, 1841.
Family BOVIDAE Gray, 1821.
Subfamily BOVINAE Gray, 1821.
Tribe Bovini Gray, 1821.
Genus *Syncerus* Hodgson, 1847.
Syncerus sp.
(Fig. 2)

Material examined – KW 9463, frontal with horn-core bases. **NISP** = 1; **MNI** = 1.

Description – KW 9463 is a partial frontal bone with two horn-core bases, part of the occipital bone and the upper part of the right orbit. The

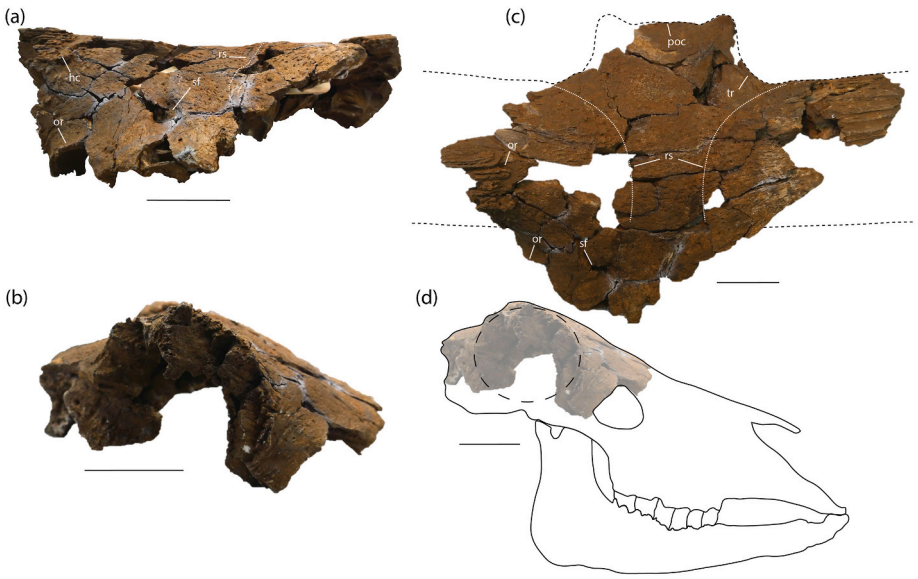


Fig. 2. *Syncerus* sp. from Kromdraai Unit P. The frontlet KW 9463 is in (a) anterior, (b) lateral and (c) dorsal view. (d) Proposed cranial reconstitution from right lateral view. Scales = 5 cm.

skull is low and wide, that of a medium-size bovine. The horn-cores emerge transversally, just above the back of the orbits, as the upper ridge of the orbital line corresponds to the middle point of the horn-core. The horns very slightly go upward and backward. There are deep vascular grooves on the cores. The roof of the frontal bone is almost strictly horizontal and transverse between the horn bases and not elevated. A rugose surface is present on the frontals between the horns but lacks large basal bosses, as in *S. caffer*. The cross-section is most likely to be a rounded triangle with little or no compression. Transverse ridges, as well as keels, appear to be absent, but we don't have access to complete horn-cores. The lower and upper surfaces of the left horn-core are separated by a shallow line with keel tendency. The upper surface is rounded, while the lower one is flat. The braincase is small relative to the size of the specimen. The orbits are projected laterally. The supra-orbital foramina are wide and close to each other. Internal sinuses are well developed in the frontal and the base of the horn-cores. The temporal line is very marked but almost exclusively restricted to the back of the horn-cores as they are inserted closely to the orbit line.

Discussion – The Bovini are often present in Plio-Pleistocene South African deposits, although they usually represent a small portion of the bovid assemblage. According to Gentry (2010), there are at least four genera recognized so far in the South African fossil record: *Syncerus* Hodgson, 1847, *Simatherium* Dietrich, 1941, *Pelorovis* Reck, 1928 and *Ugandax* Cooke and Coryndon, 1970.

The extinct species *Ugandax demissum* (Gentry, 1980) is only recognized at Langebaanweg 'E' Quarry, Zanclean (5.3–5.1 Ma). It has short horn-cores that emerge uprightly, divergent at the base and then slightly converge while curved backwards, which drastically differs from KW 9463. The horn-cores have a tendency of triangular cross-section and a strong anterior keel and remains of the posterolateral keel (Gentry, 1980, 2010). Gentry and Gentry (1978) and Vrba (1987) have proposed that *Ugandax* should be regarded as the ancestor of *Syncerus*.

At least three different *Syncerus* species are recognized in the South African fossil record: *Syncerus acoelotus* Gentry and Gentry (1978), *Syncerus antiquus* (Duvernoy, 1851) and *S. caffer*. *Syncerus acoelotus* has horn-cores emerging transversally, curved backward, a triangular cross-section with anterior, upper and lower surfaces. There is a keeled tendency between the anterior and upper surfaces with a cross-section that is almost triangular. Three dentitions from Makapansgat Member 5 have been attributed to *S. acoelotus* (Reed, 1996), and it could also be present at Taung Type Site (McKee, 1993). The species *Syncerus antiquus* corresponds to a very large buffalo with longer horns and more posterior curvature than other *Syncerus* species.

Simatherium kohllarseni (Dietrich, 1941) is a large bovine with horn-cores inserted behind the orbits, well inclined backward in lateral view, not transverse like in KW 9463. This species has been tentatively identified at Makapansgat Member 3 and 4 (Reed, 1996). Several authors have proposed that Simatherium should be regarded as the ancestral form of *Pelorovis*. *Pelorovis* species have horn-cores slightly compressed dorso-ventrally and forwardly curved from their close insertions, not like in KW 9463. One left P_4 from Swartkrans Member 2 has been tentatively attributed to *Pelorovis* sp. (de Ruiter, 2003). This taxon has also been reported at Gladysvale External Deposit (Berger, 1993) but without description.

The specimen KW 9463 looks similar to a modern *S. caffer* except that it lacks the diagnostic massive basal bosses between the horn-cores, like *S. acoelotus* (Gentry and Gentry, 1978; Gentry, 1985). The species *S. acoelotus* is originally known from middle to upper Bed II (1.66–1.15 Ma) and possibly Beds III (1.15–0.8 Ma) and IV (0.93–0.5 Ma) at Olduvai, Tanzania (Gentry and Gentry, 1978; Gentry, 2010). A *S.* ?*acoelotus* is known from the Shungura Formation Member B, C and G in the Omo Valley, Ethiopia (Gentry, 1985), therefore known from 3.4 to 1.95 Ma (Barr, 2015). The sub-species from Member C is of smaller size (Gentry, 1985, 2010).

KW 9463 is significantly smaller than an adult extant buffalo, and nothing in the morphology of the specimen indicates that it belongs to a juvenile individual. In general, KW 9463 is close to *S. acoelotus* (e.g. moderate size, horn-cores emerging transversely, horn-cores internally hollowed near the bases, extension of the hollowing in the frontals, frontals with rugose surface but no basal bosses; Table 4). In this respect, KW 9463 could be similar to OF 68.196, from Olduvai Beds III-IV, which has been attributed to a female *S. acoelotus* (Gentry and Gentry, 1978).

Interestingly, dental material from Swartkrans Member 1, Kromdraai A and Sterkfontein Member 4 (Type Site) has been tentatively assigned to *S.* cf. *acoelotus* (Vrba, 1974). This material differs from *S. caffer* by being undoubtedly larger and simpler in its occlusal surface enamel pattern. As already stated by Vrba (1974: 59), this bovine material "belong to one or more *Syncerus* species, probably evolving into *S. caffer*". Because no dental material attributed to bovine has been yet discovered at Kromdraai Unit P, it is for now impossible to state the conspecific nature of KW 9463 and specimens from the other sites.

The KW 9463 specimen from Kromdraai Unit P could be closely

Table 4
Measurements (in mm) of the specimen KW 9463 compared with extinct *S. acoelotus*. Comparative data from Gentry and Gentry (1978), Hadjouis (pers. communication).

Measurements	KW 9463	*S. acoelotus* (OF 68.196)	*S. acoelotus* (OF 068/ 5811)	*S. antiquus complexus* (Allo.61.281)
Antero-posterior diameter of horn-core	100e	109e	137	134.5
Dorso-ventral diameter of hon-core	82e	73e	110	88
Width between lateral edges of supra-orbital foramina	70e	135	125	–
Maximum width of the supra-orbital foramina	9	–	–	–
Maximum length of the supra-orbital foramina	25	–	–	–
Minimum width between temporal lines	ca 108	–	–	–

related to the specimen Allo.61.281 from the 'Phacochères' deposit, Algeria, described by Hadjouis (2002) as *S. antiquus complexus*. Hadjouis (2002) noted that *S. a. complexus* is larger than modern buffalo, which is not the case for the KW 9463 (Table 4).

More material would be necessary to confirm the affinities of KW 9463 with other Pleistocene bovine material.

Tribe Tragelaphini Blyth, 1863.

Genus *Tragelaphus* de Blainville, 1816.

Tragelaphus strepsiceros (Pallas, 1766)

Material examined – KW 6986, RM^1; KW 50001, LM^3. **NISP** = 2; **MNI** = 2.

Description – KW 50001 is mesodont, in early wear, corresponding to a juvenile/sub-adult individual. The styles are particularly well developed, and the ribs, although discrete in some sort, are visible. The lingual lobes are pointed, and the occlusal enamel outline is simple. KW 6986 is an unworn right M^1 and belongs to a young juvenile individual. It displays the same morphological features as KW 50001.

These dental specimens from both units are morphologically indistinguishable from the living greater kudu *T. strepsiceros*. They are both juveniles but do not fit with each other.

Tragelaphus sp.

Material examined – KW 10181, KW 10179, RM^3; KW 10180, RM^2. **NISP** = 3; **MNI** = 1.

Description – KW 10181 and KW 10179 refit and represent the same right upper third molar (**MD** = 32.3; **BL** = 25.14; **CH** = 42). They are also attributed to the same individual as KW 10180, a right upper second molar (**MD** = 37.4; **BL** = 24.29; **CH** = 39.17). These teeth are slightly worn. The teeth are mesodont, with the presence of well-developed labial styles. The ribs between the styles are discrete. The metastyle on the third upper molar is not well-developed. There is no basal pilar, and the occlusal outline is extremely simple (without developed enamel folds around the central cavities). The lobes are slightly pointed, and a slight rugosity is visible on the labial surface.

Discussion – This material is morphologically close to *Tragelaphus* but generally simpler (e.g., no development of the metastyle on the M^3), more hypsodont, less pointed lobes and a rough labial surface on the lobes. Moreover, the teeth are bigger than the living *Tragelaphus* and *Taurotragus* species that we have studied but are similar in size with the large *Tragelaphus* cf. *strepsiceros* from Swartkrans (Vrba, 1974, Table 5).

Tragelaphini indet.

Material examined – KW 10680, horn-core; KW 9762, R mandibular condyle; KW 10524, LP_4; KW 9651, upper molar. **NISP** = 4.

Description – KW 10680 is characterised by a strong mediolateral compression, almost flat, associated with significant torsion. The specimen is 149 mm long, preserving only the tip of the horn. The original horn-core could have been at least twice as longer. The important compression creates two opposite keels and leads to a 'spatula' shape of the tip. Vascular grooves are visible along the horn-core but remain relatively shallow.

KW 9762 is a right mandibular condyle belonging to a juvenile individual based on the porous articular surface of the bone. The general shape and size allow for this specimen to be attributed to the Tragelaphini tribe but without possible further identification. The same statement can be made for KW 10524, an unworn left P_4 that is morphologically similar to the living greater kudu *T. strepsiceros* but is much larger (**MD** = 21.2 mm; **BL** = 10.8 mm).

Subfamily ANTILOPINAE Gray, 1821.

Tribe Oreotragini (Pilgrim, 1939)

Genus *Oreotragus* Smith, 1834.

Oreotragus oreotragus (Zimmermann, 1783)

Material examined – KW 6960, KW 7417, horn-cores. **NISP** = 2; **MNI** = 1.

Description – KW 6960 and KW 7417 are both tiny spiky horn-cores that preserve the tip and most of the horn. They have an elliptical cross-section associated with vascular grooves. They are both much similar to M476, a frontlet from Makapansgat that has been previously attributed to an extinct species of large klipspringer, *Oreotragus major* Wells, 1951; Wells and Cooke (1956). However, subsequent investigation has challenged the validity of this species (Watson and Plug, 1995), the authors arguing that there are not enough morphological differences between *O. major* and the extant *O. oreotragus* to support the hypothesis of two different species. Although we agree with that statement, the specimen M476 exhibits an interesting morphology compared with the modern klipspringer, notably by its robust morphology, shorter horn-cores, no pedicels and shallower inter-frontal suture and supra-orbital foramina. This material could benefit from an amended description in the future.

Tribe Cephalophini Gray, 1871.

Genus *Sylvicapra* Ogilby, 1936.

Sylvicapra sp.

Material examined – KW 7892, incomplete horn-core; KW 10509, L maxilla with P^{2-3}. **NISP** = 2; **MNI** = 1.

Description – KW 7892 is characterized by the presence of deep vascular grooves and a slight anterior curvature. The horn is also well-compressed medio-laterally. In its general morphology, it is similar to the living common duiker *Sylvicapra grimmia* (Linnaeus, 1758).

Table 5
Measurements of *Tragelaphus* sp. dental material from Kromdraai Unit P compared with *T.* cf. *strepsiceros* from Swartkrans Member 1. Comparative data from Vrba (1974).

Site	Specimen	Taxon	Element	Side	BL	MD	CH
Kromdraai Unit P	KW 10181	*Tragelaphus* sp.	M3/	R	32.3	25.14	42
	KW 10180	*Tragelaphus* sp.	M2/	R	37.4	24.29	39.17
	KW 10179	*Tragelaphus* sp.	M3/	R			
Swartkrans Member 1	SK 3000	*T.* cf. *strepsiceros*	M3/		34	22	
	SK 2095	*T.* cf. *strepsiceros*	M3/		36	26	
	SK 2681	*T.* cf. *strepsiceros*	M2/		26.5	20	

However, as we cannot measure its total length, the base and pedicel, we cannot confirm its specific identification. KW 10509 is a fragment of a left maxilla preserving the P^2 and P^3. It is at an advanced stage of wear, but it is very similar in its morphology with the living common duiker, although slightly bigger than the available comparative material at the ESI.

Cephalophini indet.

Material examined – KW 9112, LP_2; KW 9508, upper L molar; KW 10983a, upper molar; KW 10987, incomplete L maxillary; KW 10425, incomplete horn-core. **NISP** = 5.

Description – KW 9508, KW 10983a and KW 10987 are morphologically closest to the living klipspringer *O. oreotragus*, but as they are badly preserved, it is impossible to be confident about any generic or specific identification. KW 10425 is a tip fragment of a horn-core. The cross-section is ovoid, mediolaterally compressed, with a slight curvature forward. It is about the same size as KW 7892 assigned to *Sylvicapra* sp. but much more robust at the tip and without deep vascular grooves. We attributed the KW 10425 to the Cephalophini tribe.

Tribe Antilopini Gray, 1821.

Genus *Gazella* de Blainville, 1816.

Gazella gracilior Wells and Cooke, 1956.

(Figs. 3 and 4)

Material examined – KW 10075, frontal bones preserving L horn-core; KW 8123, KW 9722A, L horn-cores; KW 8849, KW 10668, R horn-core; KW 8769, R and L M^{2-3}; KW 10912, RM^2; KW 8532, upper molar; KW 9776 incomplete L mandible preserving P_3 – M_3. **NISP** = 9; **MNI** = 3.

Description – KW 10075 is a partial skull preserving the left horn-core (Fig. 3). The horn-core shows a slight medio-lateral compression (**APD** = 20.8 mm; **TD** = 18.5 mm). The lateral side of the horn is flattened while the medial side is more convex. Vascular grooves are well-defined on the posterior and postero-lateral sides of the horn. The horn is inserted just above the back of the orbit and slightly diverges from base to tip. The horn curves gently backwards and is inclined in lateral view. There is no elevation of the frontals between the horns. The supra-orbital pits are deep and triangular in shape around the supra-orbital foramina. There is a lack of frontal sinuses. The three isolated horn-cores gently curve backward in the lateral view with a rounded cross-section. However, these specimens do not possess frontal sinuses and we can observe on KW 9722A and KW 10668 that the orbital rim is as high as the frontal bone between the two horn-cores. These are typical gazelle characters. They also have a flattened lateral surface, which leads to a slight post-eromedial swelling on KW 9722A. On both KW 9722A and KW 10668, the supraorbital foramen is situated just below the medial edge of the horn-core. There is no torsion and almost no divergence between the horns.

KW 9776 is a left hemi-mandible lacking part of the diastema as well as the mandibular branch and condyle. However, the tooth row is almost complete, preserving from the P_3 to the M_3 but missing the P_2. The mandibular corpus is thin and long, which differs from the *Antidorcas* Sundevall, 1846. The tooth row (**L** = 74e mm) is longer than in *Antidorcas* and much more similar to what we observed in *Aepyceros* Sundevall, 1846. The labial lobes are pointed and angular, more than in *Antidorcas*, associated with a well-developed parastylid. There is no basal pillar, and the lingual walls are wavier than the general convex form of *Antidorcas*. By direct comparison, KW 9776 is undistinguishable from the *Gazella vanhoepeni* (Wells and Cooke, 1956) mandibular specimens (M521, M502 and M38) from Makapansgat Member 3 (Figs. 4 and 5).

The KW 8769 set of upper molar teeth, as well as KW 8532 and KW 10912, also exhibit *Gazella* characters more than *Antidorcas*, such as the simpler outline occlusal pattern, the extremely pointed lingual lobes, the labial ribs between the styles that are developed in the upper part of the tooth but progressively disappear to have a more concave form of the wall in the lower part.

Discussion – Two species of *Gazella* have been recognized from the Plio-Pleistocene of southern Africa. *Gazella vanhoepeni* and *G. gracilior* have both been identified at Makapansgat by Wells and Cooke (1956). Subsequently, Vrba (1973) suggested that *G. gracilior* could be *Antidorcas* sp. However, Gentry and Gentry (1978) argued that *G. gracilior* was in fact the female of *G. vanhoepeni*. Reed (1996) maintained the distinction between the two species and argued that the differences were too important to be explained only by sexual dimorphism. After seeing the original Makapansgat material, it is unlikely that both taxa were, in



Fig. 3. *Gazella gracilior*. (a) Partial frontlet of a male from Kromdraai Unit P (KW 10075); (b) holotype of *G. gracilior* from MKM3 (M773); (c) R horn-core of a female from Kromdraai Unit P (KW 10668); (d) L horn-core of a female from Kromdraai Unit P (KW 9722a); (e) R horn-core of a male from Kromdraai Unit P (KW 8849); (f) R mandible from Kromdraai Unit P (KW 9776). Scales = 5 cm.

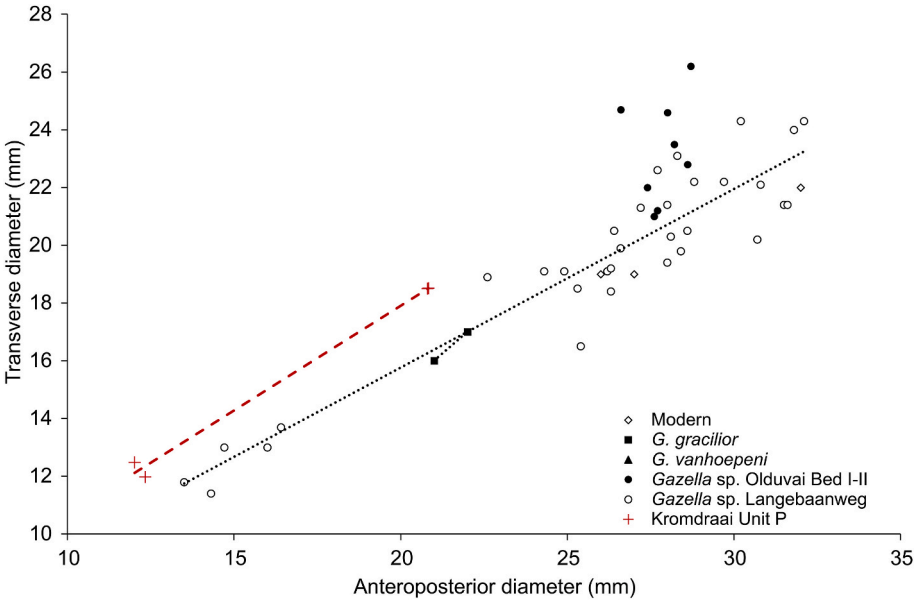


Fig. 4. Horn-core dimensions of extant and extinct *Gazella* compared with the specimens from Kromdraai Unit P. The overall distribution and linear regression of Kromdraai specimens indicates a close similarity with *G. gracilior* from Makapansgat and *Gazella* sp. from Langebaanweg. Comparative data from Wells and Cooke (1956), Gentry and Gentry (1978), and Gentry (1980).



Fig. 5. *Antidorcas* from Kromdraai Unit P. *A. recki*: (a) R horn-core of a male in lateral and anterior view (KW 9995). *Antidorcas* sp.: (b) L horn-core in anterior and lateral view (KW 11161); (c) R horn-core in anterior and lateral view (KW 10704); (d) R horn-core in lateral and anterior view (KW 9611); (e) partial occipital bone (KW 10410). Scales = 5 cm.

fact, females and males of the same species.

Horn-core specimens from Kromdraai are not conspecific with *G. vanhoepeni*. The former are too small (Fig. 5) and do not show the strong mediolateral compression as well as the distinct backward curvature that we see in *G. vanhoepeni*. After a direct comparison with the holotype specimen of *G. gracilior* (M 773), and other specimens attributed to that species from Makapansgat Member 3, the Kromdraai specimens are almost indistinguishable from *G. gracilior* but differ from *G. vanhoepeni* from Makapansgat. The *Gazella* sp. from Olduvai Bed I-II probably represents a different species than *G. gracilior* from Kromdraai and Makapansgat.

Genus *Antidorcas* Sundevall, 1846.

Antidorcas recki (Schwarcz, 1932)
(Figs. 5 and 6)

Material examined – KW 6930A, L horn-cores with part of the frontal; KW 7633, KW 9995, R horn-core with part of the frontal; KW 6629, KW 11161, L horn-cores; KW 6530, KW 6638, KW 6699, KW 6930B, KW 7900, KW 8984, KW 9710, KW 9867, KW 10090, horn-core fragments; KW 6939, R mandible with $P_{2\text{-}4}$ and M_3. **NISP** = 15; **MNI** = 5.

Description – In total, 14 horn-cores have been attributed to the extinct species *A. recki* (Fig. 6). Among these specimens, it is possible to distinguish two morphological groups (Fig. 7). The first group is composed of short and robust horn-cores, mediolaterally compressed, without any torsion and with almost no distal divergence. The horns

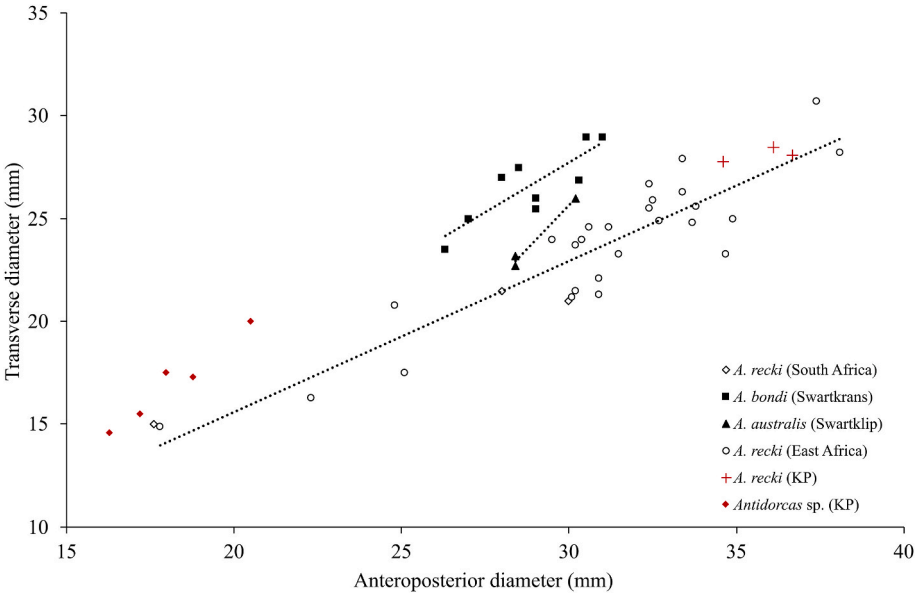


Fig. 6. Horn-core dimensions of extinct *Antidorcas* species compared with the specimens from Kromdraai Unit P. The overall distribution and linear regression indicate a close similarity between Kromdraai Unit P specimens and *A. recki*. Comparative data from Vrba (1973, 1974), Gentry and Gentry (1978), and Hanon et al. (2022).

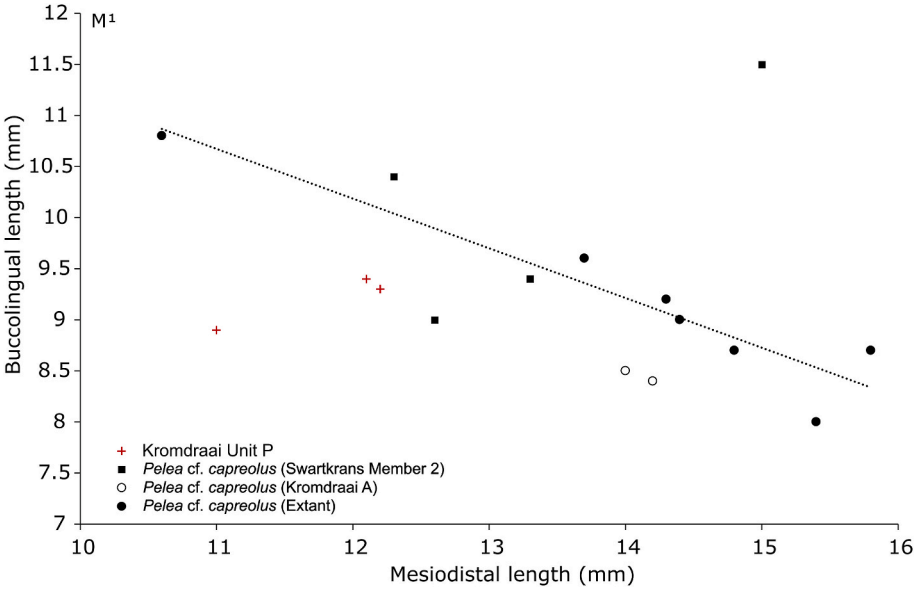


Fig. 7. Comparison of the M^1 dimensions between Kromdraai Unit P, *P.* cf. *capreolus* from KA and Swartkrans and the extant *P. capreolus*. Comparative data from Vrba (1974).

strongly curve backward just above the pedicel and the sinuses extend within the frontal and the base of the pedicel. The second group is composed of smaller and less robust horn-cores. The horns slightly curved backward inserted more uprightly than in *Antidorcas marsupialis* Zimmermann, 1780. The horns are almost parallel at the base and then slightly diverge distally. The postcornual fossa is shallow. They do not show signs of torsion except in a few specimens (cf. KW 11161 below). The cross-section is rounded with a slight swelling at the base. It is argued here that the morphological differences between the two groups represent sexual dimorphism. Specimens from the first group belonging to males and those of the second group are females.

KW 11161 exhibits a morphology with mixed *Gazella* and *Antidorcas* characters. It is a frontal bone preserving the horn-core and the upper ridge of the orbit. Among the *Gazella* characters, we observe a deep triangular supraorbital pit around the foramen, very limited frontal sinuses, a slight divergence of the horn, a deep vascular groove on the medio-lateral side of the horn, and the horn curved gently backwards in lateral view. However, the upper ridge of the orbit is slightly below the frontal line, the postcornual fossa is shallow, and the horn-core has a slight heteronymous torsion, characters unique to *Antidorcas*. Based on the rounded cross-section and the gracile morphology of KW 11161, it most likely belongs to a female antelope. Interestingly, this specimen is larger than any female *Antidorcas* specimens used for comparison. Moreover, it exhibits unusual characteristics, such as a flattened medial surface and a slight posteromedial swelling at the base of the horn.

KW 6939 is a right mandible fragment preserving the $P_{2\text{-}4}$ and M_3. The specimen is similar to *A. marsupialis* but smaller. The teeth are not as hypsodont as observed in *Antidorcas bondi* (Cooke and Wells, 1951). The

M_3 is less wide than in *Gazella*, and the lingual wall is slightly convex. As noted by Vrba (1973: 299), "the presence of the P_2 serves as a good indicator to attribute this specimen to *A. recki*". Indeed, *A. recki* is similar to *A. bondi* in this respect but less hypsodont. The P_2 is generally absent in *A. marsupialis* and *Antidorcas australis* (Hendey and Hendey, 1968).

Discussion – The genus *Antidorcas* is confined to southern Africa today. Schwarcz (1932) identified the presence of an extinct antelope at Olduvai named *Adenota recki* and then *Phenacotragus recki* (Schwarcz, 1937). Subsequently, the genus *Phenacotragus* has been synonymized with *Antidorcas* (Gentry, 1966; Gentry and Gentry, 1978). The species is characterized by the retention of the second lower premolar (P_2) and has more concave labial walls behind their more prominent mesostyles on upper molars (Klein and Cruz-Uribe, 1991; de Ruiter, 2003). According to Klein and Cruz-Uribe (1991), *A. recki* should be regarded as an extinct subspecies of *A. marsupialis* and was probably its ancestral form. This is a plausible hypothesis considering the atrophy or absence of P_2 in *A. marsupialis*, which is believed to be an advanced grazing adaptation (Gentry, 1966). All the specimens from Kromdraai Unit P fall into the range of *A. recki* known from other Early Pleistocene sites from both East and South Africa (Figs. 6 and 7). The *A. recki* assemblage from Kromdraai Unit P comprises at least 5 individuals.

Antidorcas sp.

(Fig. 5)

Material examined – KW 7444, L horn-cores with part of the frontal; KW 10173, KW 9611, KW 10704, KW 10183, R horn-cores; KW 9862, horn-core fragment; KW 10410, occipital bone. **NISP** = 7; **MNI** = 5.

Description – KW 10410 is an occipital bone preserving the occipital condyles, part of the left petrous bone with the temporal and about half of the basioccipital. The specimen is similar in size to the living springbok *A. marsupialis*. The external occipital crest is strong and projected backwards. The occipital surface faces posteriorly and is large, creating an elongated rectangular plateau in the posterior view. The temporal ridges approach moderately toward the superior occipital crest and are not so closely together as in Peleini or Aepycerotini. In lateral view, the cranial roof is slightly inclined. KW 10410 is almost indistinguishable from the living *A. marsupialis*, but because we do not have access to comparable fossils of the extinct springbok species, as well as the lack of other evidence for the presence of the modern species at Kromdraai, it is, therefore, more parsimonious to keep a generic identification for this specimen.

Genus *Raphicerus* Smith, 1827.

Raphicerus campestris (Thunberg, 1811)

Material examined – KW 6746, LP^3; KW 7993, $LP^{2\text{ and }3}$. **NISP** = 3; **MNI** = 2.

Description – KW 6746 (**MD** = 6.65; **BL** = 6.62; **CH** = 7.1) and KW 7993 (P^2: **MD** = 7.91; **BL** = 5.1; **CH** = 6.45; P^3: **MD** = 8.12; **BL** = 6.44; **CH** = 7.08) both belong to old individuals. By direct comparison, the material from Kromdraai is indistinguishable from the modern steenbok *R. campestris*.

Raphicerus sp.

Material examined – KW 10968, R mandible (diastema). **NISP** = 1; **MNI** = 1.

Description – The right mandible KW 10968 is similar in size and general morphology to the modern steenbok *R. campestris*. However, because of the absence of dental material, it is impossible to be too confident about its specific identification.

Antilopini indet.

Material examined – KW 6711, KW 8870, KW 8443, KW 9265, KW 9326, KW 9369, KW 9580, KW 9963, KW 10207, KW 10399, KW 10670, KW 10982, KW 11040, horn-core fragment; KW 9757, maxillary with RP^4-RM^1; KW 11044, R mandible with P2-M1 and M3; KW 10882, mandible fragment with rdp4; KW 7652b, KW 8337, KW 8425, KW 8512, KW 10970, KW 11031, mandible fragment; KW 6327, left incisor; KW 9545, ldp3; KW 10234, rdp3; KW 9813, dp4; KW 10277, LP4; KW 6284, KW 7196, LM1; KW 9609, RM3; KW 8574, KW 8731, KW 9863, KW 10290, KW 10217, KW 10263, KW 10266, KW 10270, KW 10344, lower molar; KW 9136, RM^1; KW 9106, KW 10330, RM^2; KW 7257, LM^3; KW 6259, KW 6747, KW 7458, KW 8050, KW 9705a, upper molar; KW 8757, KW 9799, mandibular branch fragment. NISP = 50.

Description – All of this material is attributed to the tribe Antilopini (Size Class I/II). The KW 10882 mandibular specimen belongs to a neonate (dp_4 unworn). We observe very sharp lobes as well as a small basal pillar between the third and second lobes. This specimen probably belongs to *Gazella*, but it is too fragmentary to be identified beyond the tribe level.

Tribe Reduncini Knottnerus-Meyer, 1907.

Genus *Redunca* Smith, 1827.

Redunca sp.

Material examined – KW 6380, partial skull; KW 8419, L pedicel with part of the horn-core; KW 9013, R incomplete horn-core; KW 7208, R pedicel with part of the horn-core. **NISP** = 4; **MNI** = 3.

Description – KW 6380 is a partial skull preserving the occipital part of the left petrous bone and the auditory bulla, the temporal, parietal, and posterior part of the two frontals and about half of the basioccipital bones. The external occipital crest is strong, projected backward, and the occipital surfaces are oriented laterally more than posteriorly. The temporal ridges approach closely toward the occipital. In lateral view, the cranial roof is horizontal and from a sharp angle with the occipital bone. KW 6380 is similar to the living *Redunca fulvorufula* (Afzelius, 1815) and is about the same size. However, it slightly differs from the modern mountain reedbuck by the following characters: an inter-frontal suture that is much more raised between the horns; an external auditory meatus that is wider and oriented dorsally more than laterally; a larger auditory bulla; a stronger occipital crest.

KW 8419 is a left horn-core pedicel preserving approximately the first third of the horn (**APD** = 21.37; **TD** = 17). The vascular grooves are deep and well-defined, especially on the medial side. The lateral surface is flat. The horn is divergent, inserted slightly behind and above the orbit, going backwards and then slightly curved upward. There is no significant swelling, although the flat lateral surface accentuates the convex curvature of the medial part in the anterior view. The postcornual fossae is well-developed.

KW 9013 is a tip fragment of the right horn-core. It has the same anatomical features as KW 8419, and they could belong to the same individual.

KW 7208 is a right horn-core pedicel which is inclined in the lateral view and slightly divergent. The postcornual fossae are also well-defined, but we cannot observe the lateral flattened surface that is the characteristic of KW 8419 and 9013. The cross-section is rounded, and the pedicel is more developed. KW 7208 is about the same size as KW 8419 and 9013.

Discussion – The horn-cores KW 8419 and KW 9013 are broadly similar to the living mountain reedbuck *R. fulvorufula*. However, they differ in its relatively small size compared to modern specimens. KW 7208 has similarities with *Redunca*, but significantly differs from KW 8419 and 9013. The cross-section is much rounder, without the lateral flattened surface, and the pedicel is more developed. Because female reedbucks do not possess horn-cores, we postulate here that the divergence in anatomical characters between KW 8419–9013 and KW 7208 does not reflect sexual dimorphism, but they possibly belong to different species.

Genus *Kobus* Smith, 1840.

Kobus sp.

Material examined – KW 6623, upper decidual premolar; KW 7258, Ldp^3; KW 8982, $Rdp^{3\text{ or }4}$; KW 10708, incomplete horn-core; KW 10924, Rdp^4. **NISP** = 5; **MNI** = 1.

Description – The horn-core KW 10708 is badly preserved and represents approximately half of the original specimen. We can observe the presence of a well-defined swelling at the base of the horn-core. It curves gently backwards and then upward, providing a concave profile in the lateral view. There is also the presence of remnant transverse

ridges.

The dental material (NISP = 4) has styles (parastyle, mesostyle and metastyle) and ribs that are well-developed. The lobes are generally squared rather than pointed and the occlusal outline is moderately complex.

Discussion – In its general morphology (e.g., swelling, remnant ridges), KW 10708 is attributable to the *Kobus* genus. Its size falls in between the lechwe *Kobus leche* Gray, 1850, and the waterbuck *Kobus ellipsiprymnus* (Ogilby, 1933). The dental specimens all belong to the same juvenile individual and are about the size of the modern *K. leche*. The porous surface aspect of the horn-core KW 10708 also indicates that it could belong to a juvenile individual. Therefore, we decided to associate this material and consider that they all correspond to a juvenile *Kobus*.

Tribe Peleini Gray, 1872.

Genus *Pelea* Gray, 1850.

Pelea sp.

Material examined –KW 7806, KW 9690, incomplete horn-cores; KW 6518, $RM_{1\text{-}2}$; KW 8783a R maxillary with P^3-M^1; KW 8783 b L maxillary with P^4-M^1; KW 10291, RM^1. **NISP** = 6; **MNI** = 2.

Description – KW 7806 (**APD** = 14.9; **TD** = 14.76) and KW 9690 (**APD** = 14.31; **TD** = 14.5) are both incomplete horn-cores displaying a small pedicel and a slightly inclined insertion. The cross-section is mostly rounded, but the posterior surface is flat, which creates an asymmetric ovoid shape. The vascular grooves are visible but not very deep. On the KW 7806 specimen, we can observe a slight compression on the anterior part of the horn, but not pronounced enough to form a proper keel. In anterior view, they are moderately divergent, and they somewhat curved backwardly in lateral view.

KW 8783a and 8783b belong to the same individual. The teeth are brachyodont, and the styles remain well-defined despite the advanced wear stage. The ribs between the styles are discrete. The lobes are pointed, and the occlusal enamel pattern is simple.

KW 10291 (RM^1) is brachyodont, in medium wear, with the styles well developed. The ribs between the styles are shallow and almost absent. The anterior lobe is squared and the posterior one is more rounded.

KW 6518 is at an advanced stage of wear and belongs to an old individual. It is similar in morphology to the extant *Pelea capreolus* (Förster, 1790).

Discussion – KW 8783a and KW 8783b belong to the same elderly adult specimen. They are similar in morphology to the extant *P. capreolus* but the P^3 is more developed than the living grey rhebok. Moreover, these specimens are more robust (shorter length with greater width) than the modern species (Fig. 7). KW 10291 is similar to the extant *P. capreolus* but with a simpler enamel outline in the occlusal view. It is more like *Antidorcas*, with a more squared shape and less pointed anterior lobe. Based on the morphology, we decided to attribute this specimen to *Pelea* instead of *Antidorcas* because of the general brachyodont conformity, which contrasts with the well-developed hypsodonty observed in the Antilopini tribe.

All these specimens could be conspecific and probably represent an early form of *P. capreolus*. However, there is still a need for more specimens in a better preservation state in order to be certain about their taxonomic statue.

Tribe Hippotragini Sundevaal, 1845.

Genus *Hippotragus* Sundevaal, 1845.

Hippotragus sp.

Material examined – KW 7058a, $RM^{1\text{-}2}$; KW 9293, LM_2. **NISP** = 2; **MNI** = 2.

Description – KW 7058 is an unworn upper molar. The tooth is relatively hypsodont, with well-developed ribs and styles on the labial wall. The basal pillar is well defined. There is an additional ridge in the internal part of the posterior infundibulum. The lobes are rounded, and the tooth is generally squared. The specimen is relatively small (**MD** = 20.4 mm; **BL** = 12.7 mm), smaller than a juvenile *Hippotragus equinus* (Geoffroy Saint-Hilaire, 1803). Therefore, we decided to keep the identification to the genus level only.

KW 9293 is a lower left well-worn second molar. The lobes are round, the posterior one being slightly constricted. There is a basal pillar and a goat-fold. The ridges are well-developed as well. The lobes have a rugose enamel on the labial side. The tooth looks similar to the extant *H. equinus* but is much less hypsodont – even after considering the degree of wear – and has a smaller basal pillar.

Tribe Alcelaphini (de Rochebrune, 1883)

Genus *Parmularius* Hopwood, 1934.

Parmularius sp.

(Fig. 8b)

Referred material – KW 6296, L horn-core. **NISP** = 1; **MNI** = 1.

Description – KW 6296 is an almost complete left horn-core lacking the end of the tip. It is about 17 cm long and shows a slight medio-lateral compression (**APD** = 43 mm; **TD** = 41 mm) with an oval cross-section at the base. The horn-core is hollowed at the base. It is inserted upright, slightly divergent at the base and converges toward the end. The horn curves backwards in lateral view with an anticlockwise torsion from the base to the tip. The bone surface is badly preserved because of cave corrosion, but we can observe what could be the remains of transverse ridges along the horn. A swelling is present on the anteromedial part of the base. Moreover, there is a keeled tendency, although slightly, along the postero-lateral side, which gently follows the torsion.

Discussion – The KW 6296 specimen belongs to a medium-sized alcelaphine (Fig. 8b). The presence of the swelling, slight torsion and the lack of significant compression are not consistent with *Damaliscus* Sclater and Thomas, 1894. The swelling at the base, the lack of pronounced compression, the slight divergence at the base and the moderate ridges on the anterior part of the horn fit pretty well with *Parmularius*. However, the position of the swelling (in the antero-medial part) and the shallow anticlockwise torsion of the horn challenge this



Fig. 8. *Numidocapra* cf. *porrocornutus* and *Parmularius* sp. from Kromdraai Unit P. *N.* cf. *porrocornutus*: (a) R horn-core from lateral and anterior view (KW 9421); (c) horn-core in anterior view (KW 7672); (d) horn-core in posterior and lateral view (KW 8122), black lines indicate the remnant transverse ridges. *Parmularius* sp.: (b) L horn-core (KW 6296). Scales = 5 cm.

identification. Vrba (1978) discussed the presence of problematical small alcelaphine dentitions from Kromdraai and described a new species, *Parmularius parvus* Vrba (1978) based on a skull lacking horn-cores. KW 6296 is obviously larger, slightly bigger than the modern *Damaliscus dorcas* (Pallas, 1766), and could not belong to this species. KW 6296 shares similar morphological features with *Parmularius braini* from Makapangast Member 2 and 3 (Vrba, 1977), notably the transverse ridges. However, direct comparison with the holotype M8326 shows that KW 6296 is significantly smaller, lacking the posteromedial swelling and the abrupt bent back curvature in lateral view. Finally, *Parmularius vrbae* Reed (1996) is a cryptic species that could benefit from a revision and proper description. For these reasons, we kept the generic identification for the Kromdraai Unit P specimen.

cf. *Parmularius* sp.

Referred specimens – KW 6511, R mandible with dp_4-m_1; KW 7195, R mandible with $dp_{3\text{-}4}$; KW 9624, L mandible fragment; KW 9965c, Rdp_4; KW 9965d, RM_1; KW 7000, LM_1; KW 6512, KW 6754, KW 10176, RM_3; KW 9715, LM_3; KW 10830, $RM^{1\text{-}2}$; KW 6375, LM^2; KW 6435, LM^3; KW 6514, KW 10832, KW 10896, L lower molar; KW 6609, R lower molar; KW 6379b, lower molar. **NISP** = 18; **MNI** = 5.

Description – This small-sized alcelaphini dental material is characterized by an extreme hypsodonty. Specimens fall in between the size of *Damaliscus lunatus* (Burchell, 1824) and *Alcelaphus buselaphus* (Pallas, 1766) but with an enamel occlusal outline that is less complicated. The molars are more compressed buccolingually, and the labial lobes of the lower molars are much more open and divergent. The metastylid and the third lobe of the lower third molar are more developed. The lobes have little to no constriction. KW 9965d and KW 7000 are both similar to the fragmentary left mandible M6279 *P. braini* from Makapansgat, except that KW 9965d is much smaller.

Discussion – Three species of *Parmularius* have been recognized in the Plio-Pleistocene of South Africa: *P. braini*, *P. parvus* and *P. vrbae*. *Parmularius braini* has been described from Makapansgat Members 2 and 3 (Vrba, 1977) and *P. parvus* from Kromdraai (Vrba, 1978). Subsequently, Reed (1996) assigned some dental and horn-core material to a new species, *Parmularius vrbae* from Makapansgat Member 3. These descriptions rely mainly on horn-core material associated – or assumed association – with dental specimens. *Parmularius vrbae* has been characterized by "its extremely small size, relatively shallow mandible, horn cores shorter with more mediolateral compression than the most compressed species (*P. braini*)" (Reed, 1996: 183). However, as both male and female alcelaphines bear horns, this gracile morphology could reflect sexual dimorphism more than specific differences. Moreover, *P. parvus* holotype is a mandible (KA 646A) with a juvenile fragmentary cranium (KA 731) and face (KA 1601A) as paratypes, while the holotype of *P. braini* is an almost complete pair of horn-cores (M8244). It is, therefore speculative to separate both species as the original material is difficult to compare. It is plausible that all this material is conspecific, with *P. vrbae* and *P. parvus* being the females of *P. braini*.

Although we observe morphological similarities with the Makapansgat material, the identification of the new dental specimens from Kromdraai Unit P is currently uncertain. Material attributed to *Parmularius* from South African deposits should first be re-examined.

Genus *Damaliscus* Sclater and Thomas, 1894.

Damaliscus cf. *lunatus* (Burchell, 1824)

Material examined – KW 7349, KW, 7399, R horn-cores. **NISP** = 2; **MNI** = 2.

Description – Two fragmentary horn-cores have been recovered from Kromdraai Unit P. They both have vascular grooves, important medio-lateral compression, and are slightly curved backwards. They do not belong to the same individual as they both correspond to right horn-core, and as KW 7399, they most likely belong to a young individual. They are both morphologically close to the living *D. lunatus*.

Genus *Connochaetes* Lichtenstein, 1812.

Connochaetes sp.

Material examined – KW 7662, basioccipital bone; KW 9721, P^4-M^2; KW 10532, R mandible with dp_4-M_1; KW 6379a, L mandible preserving M_2 and M_3; KW 10204, M_2 and M_3; KW 10114, LM_2; KW 6114, incisor; KW 6625, dp^4; KW 7987, $LP^{3\text{-}4}$; KW 6323, RM^1; KW 9969c, RM^2; KW 7652a, $RM^{1\text{-}3}$; KW 8219, LM^1; KW 9711, $LM^{1\text{-}3}$; KW 9679, upper premolar; KW 6513, KW 7593, KW 10826, KW 10828, upper molar. **NISP** = 20; **MNI** = 6.

Description – KW 7662 is a fragmentary basioccipital bone. It lays among the size variation of the modern *Connochaetes gnou* and has an undistinguishable morphology. The black wildebeest is generally smaller than the blue one, *Connochaetes taurinus* (Burchell, 1824). The occipital condyles are more gracile and less developed than in *C. taurinus*, also, the basioccipital is less wide and more elongated in *C. gnou*.

All these dental specimens are indistinguishable from the modern *Connochaetes* forms. They are not preserved well enough to be identified at the species level. Moreover, most of these specimens are isolated teeth, and it is, therefore impossible to be distinguished between *C. taurinus* and *C. gnou*.

Genus *Megalotragus* van Hoepen, 1932.

Megalotragus sp.

Material examined – KW 10727j, RP_4; KW 10727i, LP_4; KW 10727a, RM_3; KW 8201, LM_3; KW 10629, LP^4; KW 10727d, RM^1; KW 10727c, RM^2; KW 10710, RM^3; KW 10727b, KW 9725, LM^3; KW 8762, $RM^{2\text{-}3}$; KW 10059, $RM^{1\text{-}3}$; KW 10727f, lower premolar; KW 6388, KW 10727e, lower molar. **NISP** = 15; **MNI** = 5.

Description – Several dental specimens exhibit typical alcelaphine characters and are morphologically similar to *Connochaetes*. However, this material is much larger than the modern alcelaphine forms (Fig. 9). The specimens KW 10727a-j are about the size of the dental material from Swartkrans and attributed to cf. *Connochaetes* sp. aff. *africanus* Hopwood, 1934. However, KW 10727 is a young juvenile individual and would be expected to be much larger at its adult age. According to Vrba (1974) and Gentry and Gentry (1978), all the large alcelaphines of the South African Pleistocene could be attributed to the species *Megalotragus priscus* (Broom, 1909).

Genus *Numidocapra* Arambourg, 1949.

Numidocapra cf. *porrocornutus* (Vrba, 1971)

(Fig. 8)

Material examined – KW 9421, R horn-core; KW 7449, KW 7645, KW 7672, KW 8122, KW 9086, KW 10161, horn-core. **NISP** = 6; **MNI** = 3.

Description – Incomplete horn-cores have been recovered from Kromdraai Unit P that are all characterised by medio-lateral compression (KW 9421: **APD** = 40.8 mm; **TD** = 33.2 mm; **CI** = 1.2; KW 7645: **APD** = 40.9 mm; **TD** = 39.4 mm; **CI** = 1.04) – unlike *Alcelaphus* – a clockwise torsion on the right horn-core and very weak to strong transverse ridges on the medial side of the horn – unlike *Damaliscus*. From the lateral view, the horn curved forward with well-defined vascular grooves. This character association corresponds to the specific diagnosis of the extinct species *Numidocapra porrocornutus*, described by Vrba (1971) on a fragmentary skull from Swartkrans Member 1 (Brain, 1981). Some anatomical features (i.e. transverse thickness in anterior position, sharp posterolateral edge, little compression, flattened posterolateral surface, slight transverse ridge) of KW 7449 (**APD** = 28.7; **TD** = 20.9 mm; **CI** = 1.37) and KW 9086 (**APD** = 34.6; **TD** = 27.8; **CI** = 1.24) permit to rise the hypothesis of an affinity with the Aepycerotini tribe. The compression index (CI) of the Kromdraai specimens is similar to the SHK II Olduvai specimen BM(NH) M 26826 (CI = 1.22) attributed to *Aepyceros* sp. indet. (Gentry and Gentry, 1978). Unfortunately, there are no definitive *Aepyceros* horn-core specimens from the Late Pliocene – Early Pleistocene in South Africa.

Alcelaphini indet.

Material examined – KW 8872, KW 10184, frontal bone; KW 10825, L parietal and temporal bones with part of the horn base; KW 6390, KW 6930c, KW 7626, KW 7644, KW 7671, KW 8056, KW 8250, KW 8918, KW 9497, KW 9548, KW 9587, KW 9626, KW 9847, KW 9955, KW

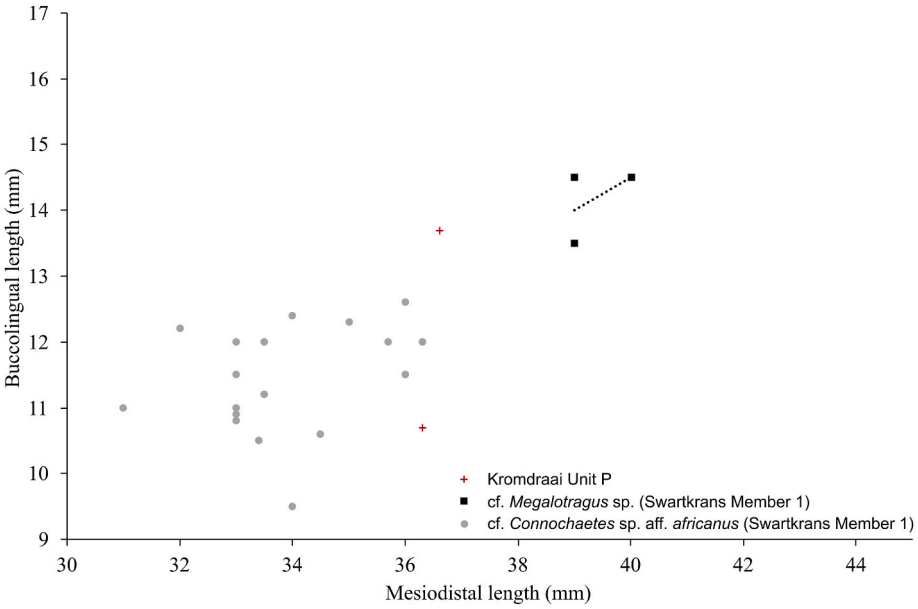


Fig. 9. Comparison of the M_3 dimensions between Kromdraai Unit P and large alcelaphines from Swartkrans. Both the specimens are close to the upper limit size of cf. *Connochaetes* sp. aff *africanus*. However, it is important to note that KW 10727a belongs to a young juvenile individual. Comparative data was obtained from Vrba (1974).

10060, KW 10228, KW 10441, KW 10711b, KW 10815, KW 11069, horn-cores; KW 6415, premaxillary fragment; KW 10449, maxillary; KW 8572, R mandible fragment; KW 9030, L mandible with P4 and M3; KW 9695, KW 10556, KW 10591, L mandible fragment; KW 9765, mandible fragment; KW 6418, incisor; KW 9678, RP^{2-3}; KW 6625, KW 6983, Ldp4; KW 10216, Ldp^4; KW 6605, KW 10727k, LP4; KW 8199, LM^1-M^3; KW 8239, RP^3; KW 6984, LP^3; KW 7684, RP^4; KW 7318, KW 1029, LP^4; KW 9019, P^4; KW 7841, lower premolar; KW 9691, RM^3; KW 8424, LM^{1-2}; KW 9601, KW 10342, LM^1; KW 7218, LM^3; KW 9702, KW 10133, M3; KW 6379c, KW 6517, KW 7234, KW 8361, KW 8966, KW 9122, KW 9456, KW 9573, KW 9699, KW 10084, KW 10348, KW 10503, KW 10515, KW 10521, KW 10571, KW 10582, KW 10690, KW 10727h, KW 10809, lower molar; KW 6793, KW 7265, KW 7763, KW 7863, KW 8125, KW 8478, KW 8507, KW 8632, KW 8636, KW 8657, KW 8776, KW 8938, KW 9035a, KW 9604, KW 9621, KW 9636, KW 9652, KW 9681a, KW 9687, KW 9738, KW 9828, KW 10229, KW 10233, KW 10237, KW 10645, KW 10869, KW 10905, upper molar; KW 7474, KW 8186, KW 8703, KW 10066, KW 10716, molar. NISP = 102.

Description – This material is attributed to Alcelaphini based on their hypsodonty, distinct rounded lobes, no basal pillar and the simple enamel occlusal outline for the dental material, and on the presence of extensive internal sinuses and transverse ridges sometimes associated with torsion and curvature for the horn-cores. However, these specimens are too fragmentary to be identified beyond the tribe level.

Tribe Caprini Gray, 1872.

Genus *Makapania* Wells and Cooke, 1956.

Makapania cf. *broomi* Wells and Cooke (1956).

Referred specimens – KW 10816 LP_3; KW 6591 L mandible preserving dp_4 – m_1; KW 10139, L and R dp_4. **NISP** = 3; **MNI** = 2.

Description – Three teeth and a partial mandible display an unusual morphology among the Kromdraai bovid specimens. They are characterized by an mesiodistal elongated shape and a narrow buccolingual width, associated with pointed lobes, simple occlusal outline, moderately hypsodont and a projected parastylid on the lingual side.

Discussion – This material mimics Antilopini morphology, but the teeth are extremely large and too buccolingually compressed, with the mandibular body narrower to belong to this tribe. After a direct comparison, the specimens from Kromdraai seem indistinguishable from two juvenile mandible specimens (M6315 and M6264) from Makapansgat Member 3 attributed to the extinct Caprini species *Makapania broomi* which is housed at the ESI. They all exhibit the same specific set of characters and are all of the same size range.

Bovidae gen. and sp. indet.

Bovidae Size Class I.

Material examined – KW 6716, KW 7037, KW 7401, KW 7527, KW 8441, KW 8484, KW 8528, KW 8644, KW 10324, KW 10783, horn-core fragments; KW 7543, petrous; KW 10189a, maxilla; KW 6945, KW, 7170, KW 7504, KW 7594, KW 7685, KW 8543, KW 9448, KW 10351, KW 10536, mandible fragments; KW 7362, KW 7716, KW 8759, incisors; KW 9238, upper molar; KW 6620, lower premolar; KW 7032, KW 8654, KW 9268, P_2; KW 7669, rdp_4; KW 7247, lower molar. **NISP** = 31.

Bovidae Size Class II.

Material examined – KW 6947, KW 7061, KW 7620, KW 8181, KW 8976, KW 9412, KW 9848, KW 9873, KW 9966b, KW 10286, KW 10448, KW 10469, KW 10491, KW 10580, KW 10664, KW 10755, KW 10855, KW 10927b, KW 11032, skull fragments; KW 6677, KW 6783, KW 6928, KW 7224, KW 7465, KW 7503, KW 7510, KW 8010, KW 8029, KW 8049, KW 8059, KW 8062, KW 8166, KW 8164, KW 8354, KW 8621, KW 9766, KW 10071, KW 10131, KW 10631, KW 10651, KW 10652b, KW 10711a, KW 10957, KW 11061, horn-core fragments; KW 6341, KW 7187, KW 7279, KW 7949, KW 8452, KW 8601, KW 10461, KW 10618, KW 10792, petrous; KW 10665a, premaxilla; KW 7791, KW 8326, KW 8957, maxilla; KW 6899, KW 7038, KW 7392, KW 7395, KW 8037, KW 8511, KW 8815, KW 9140, KW 9667, KW 9915, KW 10554, mandible fragments; KW 6362, KW 6633, KW 6635, KW 6689, KW 6937, KW 7188, KW 7193, KW 7293, KW 7457, KW 7696, KW 7711, KW 7717, KW 7859, KW 8460, KW 8643, KW 8744, KW 9109, KW 9310, KW 9728, KW 9794, KW 10110, KW 10260, KW 10300, KW 10329, KW 10405, KW 10514, KW 10613, KW 10617, incisors; KW 6198, KW 8480, KW 9541, KW 11010, upper molars; KW 7538, lower molar; KW 6573, KW 7106, KW 8216, KW 8515, KW 8610, KW 9437, KW 9485, KW 10024, KW 10687, KW 10727L, premolars; KW 7547, KW 7984, KW 8456, KW 8960, KW 9479, KW 9982, KW 10683, molars; KW 8220, P^3; KW 10261, P^4; KW 8382, dp4; KW 6613, KW 8929, P2; KW 10727, enamel fragments. NISP = 122.

Bovidae Size Class III.

Material examined – KW 6715, KW 6729, KW 8140, KW 9682, KW 9729, KW 9732, KW 9750, KW 10206, KW 10722, KW 10747, KW

10842, KW 10868, skull fragment; KW 6381, KW 6749, KW 7210, KW 7296, KW 8587, KW 8603, KW 10006, KW 10662, KW 10685, petrous; KW 6930, KW 6990, KW 7071, KW 7412, KW 7422, KW 8099, KW 8420, KW 8880, KW 10070b, KW 10403, KW 10579a, horn-core fragments; KW 10096, premaxilla; KW 7621, KW 8128, KW 9470, KW 10734, mandible fragments; KW 6650, KW 6757, KW 7773, upper molars; KW 7319, KW 7898, premolars; KW 6795, KW 8186, KW 8415, molars; KW 10944, I2; KW 6400, KW 6541, KW 7325, KW 8096, KW 9442, KW 9455, KW 9467, KW 9511, KW 9576, KW 9693, KW 10697, incisors; KW 9477, LP4; KW 6526, KW 6598, KW 7525, KW 7590, KW 7757, KW 8667, KW 8975, KW 9705b, enamel fragments. NISP = 65.

Bovidae Size Class IV.

Material examined – KW 9826, horn-core; KW 9016, mandible fragment; KW 7216, incisor. **NISP** = 3.

Bovidae Size Class indet.

Material examined – KW 7407, skull fragment; KW 6683, KW 8027, petrous; KW 9551, horn-core; KW 8071, mandible fragment; KW 10637, incisor; KW 1211, KW 6191, KW 6379, KW 6540, KW 6596, KW 6621, KW 6622, KW 7103, KW 7236, KW 7323, KW 7348, KW 7376, KW 7423, KW 7440, KW 7516, KW 7540, KW 7584, KW 7587, KW 7589, KW 7652c, KW 7659, KW 7678, KW 7682, KW 7779, KW 8004, KW 8176, KW 8309, KW 8462, KW 8470, KW 8675, KW 8718, KW 8886, KW 8952, KW 8962, KW 9029, KW 9239, KW 9346, KW 9348, KW 9353, KW 9560, KW 9575, KW 9593, KW 9602, KW 9708, KW 9739, KW 9795, KW 9803, KW 9963, KW 10063, KW 10113, KW 10122, KW 10257, KW 10264, KW 10274, KW 10393, KW 10451, KW 10535, KW 10558, KW 10805, KW 10969, enamel fragment. NISP = 66.

4. Palaeoecology

4.1. Bovid assemblage composition

The bovid fossil assemblage from Kromdraai Unit P is largely dominated by the Alcelaphini (NISP = 57%; MNI = 41%) and Antilopini tribes (NISP = 30%; MNI = 30%; Fig. 10 and Table 6). By putting all the other tribes together, they account for only 14% of the NISP and 30% of the MNI. The Reduncini is the third most common tribe, with only six individuals. The Tragelaphini tribe is represented by three individuals, and Caprini and Hippotragini by only two individuals. Bovini, Oreotragini and Cephalophini yielded only one individual. Therefore, the bovid assemblage from Kromdraai Unit P has an Alcelaphini + Antilopini ratio of 70% (AA = 38/54; Table 6).

Our bovid list of the Kromdraai Unit P slightly differs from the previous and preliminary accounts of the bovid composition in this deposit (Table 6; Braga and Thackeray, 2016; Fourvel et al., 2018). For example, four taxa identified by Fourvel et al. (2018) are absent from the material examined in this study: *Taurotragus oryx* (Pallas, 1766), *C. taurinus*, cf. *Numidocapra crassicornis* Arambourg, 1949 and *Ourebia ourebi* (Zimmermann, 1783). It is highly probable that the eland (*T. oryx*) corresponds to some of the *Tragelaphus* sp. material similar to the *T.* cf. *strepsiceros* from Swartkrans (Vrba, 1974) and the cf. *N. crassicornis* to *N.* cf. *porrocornutus*. All these taxa were identified by few specimens and do not represent the majority of the total assemblage (Fourvel et al., 2018: 84, Table 2).

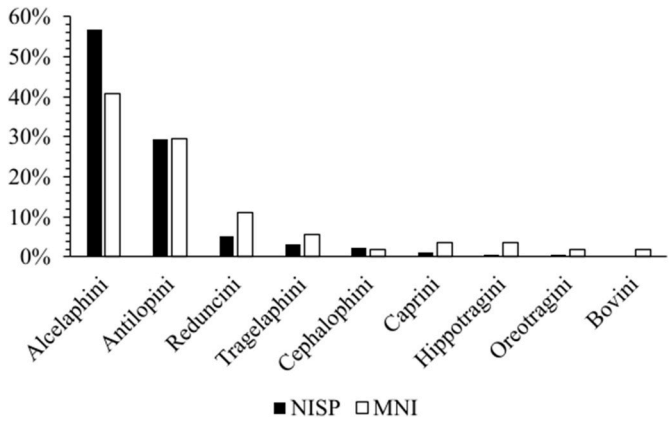


Fig. 10. Distribution of bovids according to their tribe at Kromdraai Unit P.

4.2. Bovid palaeocommunity and ecology

The multiple correspondence analyses performed on the bovid tribe abundance of 16 Plio-Pleistocene deposits from South Africa show a distribution around two main clusters (Fig. 12a). Correspondence analysis is a data visualization technique that reveals clusters of points representing similar, closely related variables, while dissimilar variables appear farther apart from each other. The first cluster is composed of deposits characterised by the overrepresentation of Alcelaphini and Antilopini (DMQ, CD, SHKR, SKLB, SKM2, SKM3, ST5AL, ST5OL and Kromdraai Unit P). In contrast, the second cluster (MKM3, MKM4, MKM5, MAL) is characterised by the presence of more Reduncini, Tragelaphini, Cephalophini and Boselaphini taxa, which indicates a better representation of closed and wet environments. It is worth noting that the clusters reflect neither chronology nor geography of the deposits but rather ecology. The first cluster is composed of deposits including only *Paranthropus* and/or *Homo* specimens, while the second cluster is composed only of deposits yielding *Australopithecus* remains. Interestingly, Sterkfontein Members 2 and 4 are distant from the two clusters. The Sterkfontein Member 4 is the only deposit to have two distinct species of *Hippotragus* (*H. equinus* and *Hippotragus cookei* Vrba, 1987), while Sterkfontein Member 2 has only yielded remains attributed to *Makapania broomi*. Motsetse falls in between the two clusters. Motsetse still needs deeper taxonomic investigation as its published faunal list is still preliminary (Berger and Lacruz, 2003).

This distribution of the deposits between open-dry and closed-wet clusters is consistent with the results on the bovid habitat preferences (Fig. 11b). Although the distinction is less clear, we can see that Malapa and Makapansgat deposits are closer to woodland and closed-wet adapted taxa, even though Malapa has a much smaller sample size compared with Makapansgat. The other deposits lay along the grassland-adapted taxa.

As far as the bovid diet is concerned (Fig. 11c), browsers and fresh-grass eaters are more common at Malapa and Makapansgat than in other deposits. Kromdraai Unit P is marked by a strong mixed-feeders component with an equal presence of both grazing and browsing species.

When we look at the distribution of bovids according to their water requirements (Fig. 11d), Kromdraai Unit P falls somewhat closer to the taxa that are independent of the presence of a nearby permanent water source.

The cluster analysis performed on the presence and absence of bovid taxa at each site (Fig. 12) shows the same result, with a clear distinction between the two main clusters. The first cluster consists of deposits with most grassland-adapted taxa (DMQ, CD, STM4, ST5AL, ST5OL, SKHR, SKLB, SKM2, SKM3, MOT, MAL and Kromdraai Unit P). The second cluster corresponds to the deposits that have a stronger closed-wet environmental signal (MKM3, MKM4, MKM5, STM2). Interestingly, except for the Sterkfontein Member 4, all the *Australopithecus* deposits are grouped together as well as all the *Paranthropus* and *Homo* deposits (see discussion).

5. Discussion

5.1. Biochronology

The taxonomic analysis provided in this paper permits us to discuss the temporal resolution of the Kromdraai Unit P (Fig. 13). This is particularly important as the chronology of the Kromdraai stratigraphy

Table 6
Bovid list and detailed demography from Kromdraai Unit P.

Subfamily	Tribe	Taxon	NISP	MNI	Juvenile	Adult	Old	Male	Female
Bovinae	Bovini	*Syncerus* sp.[a]	1	1	–	1	–	–	–
	Tragelaphini	*Tragelaphus strepsiceros*[a]	2	2	2	–	–	–	–
		Tragelaphus sp.	3	1	–	1	–	–	–
		Tragelaphini indet.	4	–	–	–	–	–	–
Antilopinae	Oreotragini	*Oreotragus oreotragus*[a]	2	1	–	1	–	–	–
	Cephalophini	*Sylvicapra* sp.[a]	2	1	–	–	1	–	–
		Cephalophini indet.[a]	5	–	–	–	–	–	–
	Antilopini	*Gazella gracilior*[a]	9	3	2	1	–	2	1
		Antidorcas recki[a]	15	5	1	4	–	5	–
		Antidorcas sp.[a]	7	5	–	5	–	–	–
		Raphicerus campestris[a]	3	2	–	2	–	–	–
		Raphicerus sp.[a]	1	1	1	–	–	–	–
		Antilopini indet.	50	–	–	–	–	–	–
	Reduncini	*Redunca* sp.[a]	4	3	–	3	–	–	–
		Kobus sp.[a]	5	1	1	–	–	–	–
		Pelea sp.[a]	6	2	–	1	1	–	–
	Hippotragini	*Hippotragus* sp.[a]	2	2	1	1	–	–	–
	Alcelaphini	*Parmularius* sp.	1	1	–	1	–	–	–
		cf. *Parmularius* sp.	18	5	2	3	–	–	–
		Damaliscus cf. *lunatus*	2	2	–	2	–	–	–
		Connochaetes sp.	18	6	2	4	–	–	–
		Megalotragus sp.	15	5	2	3	–	–	–
		Numidocapra cf. *porrocornutus*[a]	6	3	–	3	–	–	–
		Alcelaphini indet.	98	–	–	–	–	–	–
	Caprini	*Makapania* cf. *broomi*[a]	3	2	2	–	–	–	–
Indeterminate	Indeterminate	Size Class I	31	–	–	–	–	–	–
		Size Class II	121	–	–	–	–	–	–
		Size Class III	64	–	–	–	–	–	–
		Size Class IV	3	–	–	–	–	–	–
		Size Class indet.	64	–	–	–	–	–	–
		TOTAL	567	54	16	36	2	7	6

[a] Previously unidentified taxa.

has long been debated (Vrba, 1975; Thackeray et al., 2002; Braga et al., 2013, 2017, 2022b).

In general, the bovid faunal assemblage from Kromdraai Unit P is characterized by the presence of extinct and extant taxa. Among the oldest extinct taxa, we found *M. broomi*, *Megalotragus* sp., *G. gracilior* and *A. recki* from Sterkfontein Member 2 (3.9–3.5 Ma; Granger et al., 2015), Member 4 (3.7–3.3 Ma; Kibii, 2007; Granger et al., 2022), the Stw 53 Infill (1.8–1.5 Ma; Pickering, 1999; Herries and Shaw, 2011), Makapansgat Member 3–5 (3.0–0.8 Ma; Reed, 1996; Herries et al., 2009) and Malapa (1.95 Ma; Dirks et al., 2010; Brophy et al., 2016). The first appearance of *Megalotragus* in South Africa is at Matjhabeng around 4.0–3.5 Ma (de Ruiter et al., 2010), and the genus survived until the end of the Pleistocene (Faith, 2014). *Gazella gracilior* is only known at Makapansgat Member 3 (Reed, 1996) and possibly Sterkfontein StW 53 Infill (Pickering, 1999). *Antidorcas recki* probably first appeared at Sterkfontein Member 4 (Kibii, 2007) or at Hoogland (2.6 Ma; Adams et al., 2010). Based on the presence of *G. gracilior*, we can propose a *terminus post quem* date of 2.9 Ma for the deposition of Kromdraai Unit P.

The identification of *N. porrocornutus* is especially interesting in terms of biochronology. The presence of *Numidocapra* at Kromdraai Unit P has already been proposed (Fourvel et al., 2016, 2018) but under another form (*N. crassicornis*). However, this previous identification was based on postcranial remains (Fourvel et al., 2016) and can therefore be questioned. Our results provided anatomical evidence for the presence of *N. porrocornutus* based on cranio-dental specimens. This species is known only from Swartkrans Member 1 Hanging Remnant (2.3–1.8 Ma; Vrba, 1971; Pickering et al., 2019). This species can be used as a marker for a *terminus ante quem* at 1.8 Ma.

An interesting fact about the Kromdraai Unit P bovid assemblage is the simultaneous presence of both *Gazella* and *Antidorcas*. By dismissing *G. gracilior* from Sterkfontein StW53 Infill and *A. recki* from Bolt's Farm Aves Cave I (Gommery et al., 2016) because of their questionable geochronological context, we observe that *Antidorcas* replaced *Gazella* in South Africa around 2.6 Ma, *Gazella* disappeared at Makapansgat Member 3 and *Antidorcas* appeared at Hoogland (Adams et al., 2010) and Swartkrans Member 1 Hanging Remnant (Vrba, 1974; de Ruiter, 2003). Moreover, the only *Antidorcas* species identified yet at Kromdraai Unit P is the extinct *A. recki*. The absence of the extant springbok *A. marsupialis* could indicate an age older than 2.3 Ma for Kromdraai Unit P, as the species is represented at Haasgat Cave (2.3–2.0 Ma; Adams, 2012) and Swartkrans Member 1 Lower Bank (2.2 ± 0.1 Ma; Vrba, 1974; de Ruiter, 2003; Kuman et al., 2021).

Therefore, based on the bovid faunal evidence, we can conclude that Kromdraai Unit P most likely accumulated during the first half of the Makapanian age, between 2.9 and 1.8 Ma. This would also imply that Kromdraai Unit P holds ancient specimens of *Numidocapra* and *Damaliscus lunatus*. A Plio-Pleistocene transition age for Kromdraai Unit P was already proposed on the basis of a preliminary study of the faunal assemblage comprising Aves, Bovidae and Carnivore evidence (Fourvel et al., 2016). For instance, the carnivore assemblage and the unique association of *Dinofelis barlowi*, *Chasmaporthetes silberbergi*, *Protocyon recki*, *Canis hewitti* and *Prepoecilogale bolti* suggested an age older than 2.0 Ma (Fourvel, 2018; Fourvel and Thackeray, 2022).

5.2. Implication for hominin evolution

If confirmed, our biochronological interpretation would be in line with the hypothesis that the accumulation of Unit P and the geologically younger Units Q-R (previously 'Member 3'), recorded the evolutionary history of ancient representatives of the *P. robustus* lineage in South Africa (Braga et al., 2013, 2022a). Likewise, the analysis of one cranium from the site of Drimolen led to the proposition that it documented an earlier evolutionary stage in the *P. robustus* lineage (Martin et al., 2020). When compared to the geologically younger subadult holotype of *P. robustus* from Kromdraai and other specimens of this species from Swartkrans, *P. robustus* from Unit P is notably smaller (as indicated by the overall size of the mandible, maxilla and temporal bone) (Braga and Grine, 2024), and evinces more plesiomorphic features (Braga et al.,

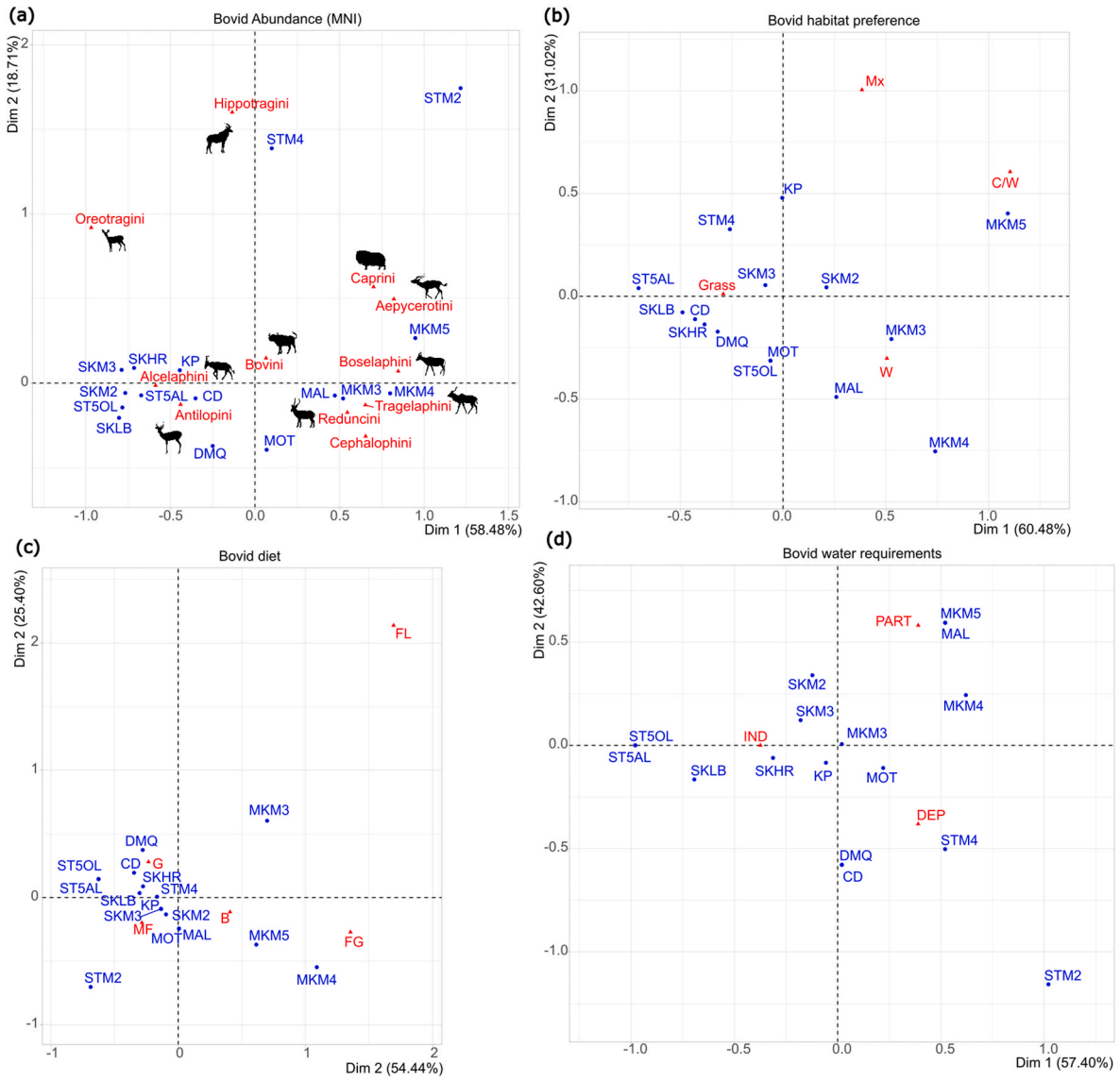


Fig. 11. Multiple correspondence analyses on (a) bovid abundance (in MNI) per tribe and on the distribution of bovids according to their (b) habitat, (c) diet and (d) water requirements. Data from Supplementary Material S2 and the contribution of each variable in Supplementary Material S3. Details on the comparative assemblages are provided in Table 3.

2022a). Alternatively, morphological distinctions between site-specific *P. robustus* sample may illustrate differences in body size (Braga et al., 2022a). Indeed, the analysis of new *P. robustus* craniodental remains from Kromdraai Unit P also reinforce the presence of a significant degree of sexual dimorphism in this species (Braga and Grine, 2024). Unfortunately, the dearth of biochronologically informative faunas from Drimolen prevents detailed comparisons with the bovid evolutionary pattern observed within Kromdraai Unit P. It, therefore, remains an open question whether other vertebrate species from Kromdraai Unit P showed trait distributions with microevolutionary shifts.

The bovid faunal evidence provided in this paper provides insights into hominin palaeoecology. The most relevant piece of evidence is the cluster analysis (Fig. 12). Our analysis combining both *Australopithecus* and *Paranthropus*-bearing sites, showed a distinction between two well-defined clusters composed of either open-dry or closed-wet adapted taxa. Interestingly, all the deposits in the open-dry cluster have yielded *Paranthropus* and/or *Homo* sp. specimens, except for STM 4, which had yielded only *Australopithecus* and Motsetse, from which no hominins have been discovered so far. In contrast, the closed-wet cluster is composed of *Australopithecus* assemblages only.

Previous research has already pointed out the distinction between the *Australopithecus* deposits from Makapansgat and the *Paranthropus/Homo* deposits from Gauteng in terms of palaeoenvironments (Reed, 1996, 1997). *Paranthropus* and *Homo* deposits are all in the same open-dry cluster, but they also show ecological variation within bovid taxa, like the presence of the two reduncines, *Kobus* sp. and *Redunca* sp. at Kromdraai, which are both dependent on the presence of a water source and close/wet environments. A distinction between habitat preferences and habitat association for *P. robustus* has been made previously (de Ruiter et al., 2008), stating that the association of *P. robustus* remains with open grassland habitats does not necessarily reflect its habitat preferences. This result supports the hypothesis of *P. robustus* as a eurytopic species (generalist) more than stenotopic (specialist), which is consistent with previous research (Wood and Strait, 2004; de Ruiter et al., 2008, 2012; Steininger, 2011; Lüdecke et al., 2018; Wynn et al., 2020; Hanon et al., 2022; Sponheimer et al., 2022).

6. Conclusion

In this paper, we provided the first taxonomic analysis of the bovid

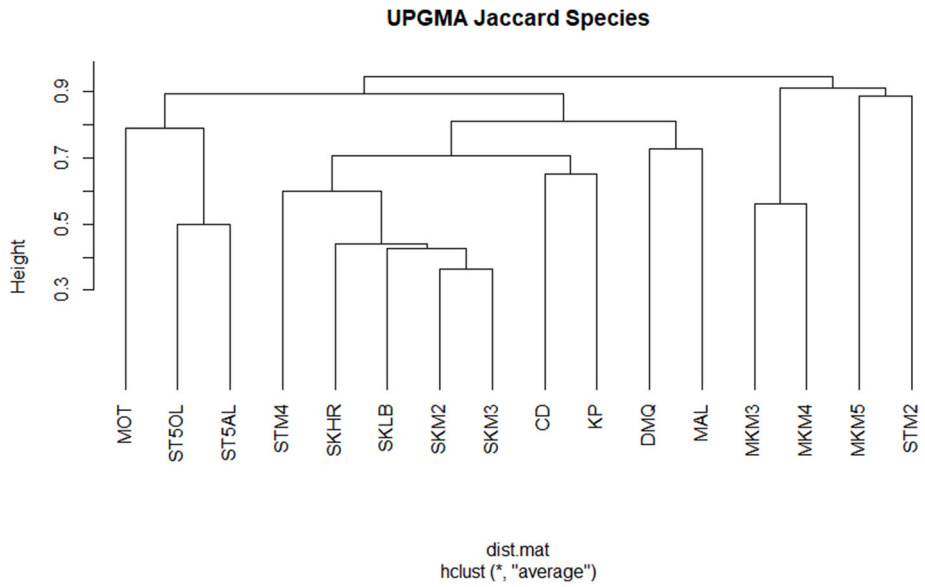


Fig. 12. Cluster analysis was performed on the presence and absence of bovid taxa. Data from Supplementary Material S4.

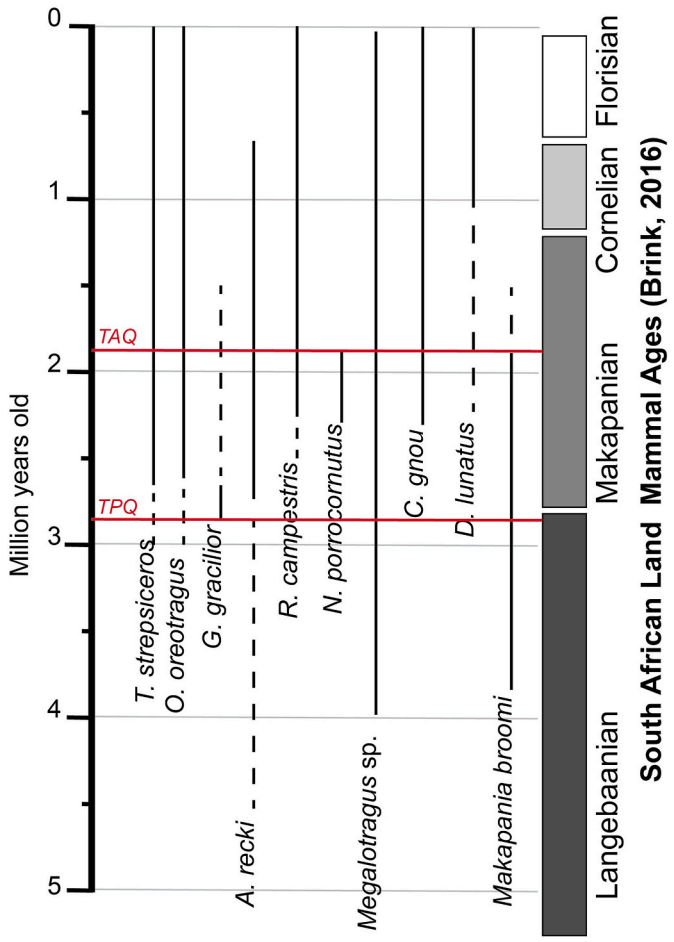


Fig. 13. Temporal distribution of key bovid species from Kromdraai Unit P. Thick black lines represent the confident temporal distribution of a taxon. Dashed black lines represent the uncertain temporal distribution of a taxon because of its doubtful identification (cf.) or of its unclear context of discovery (non-radiometrically dated sites). TPQ = *Terminus post quem*; TAQ = *terminus ante quem*.

assemblage from Kromdraai Unit P. Bovid species adapted to open and dry grassland environments dominate the assemblage, notably by the overrepresentation of Alcelaphini-Antilopini species. By comparing the distribution of bovids among the three ecovariables (habitat preference, diet and water requirement) of hominin-bearing sites in South Africa, we showed that *Australopithecus* is associated with bovids adapted to closed and wet environments. In contrast, bovid assemblages associated with *Homo* are characterized by an important open and dry adaptation component. Interestingly, *Paranthropus* is associated with bovid fauna, showing an important variety of adaptations. Therefore, this result is consistent with the hypothesis of a eurytopic behaviour for *P. robustus*.

Moreover, the bovid assemblage from Kromdraai Unit P is characterized by the presence of both extinct Pliocene species (*G. gracilior, M. broomi, Numidocapra*) and younger Quaternary taxa (*T. strepsiceros, R. campestris, O. oreotragus, D. lunatus*). We therefore argue that Unit P accumulated between 2.9 and 1.8 Ma, as already suggested by the carnivore association which indicate an age older than 2.0 Ma (Fourvel et al., 2016; Fourvel and Thackeray, 2022). If this hypothesis is confirmed in the future, Kromdraai Unit P could, therefore, potentially provide the oldest appearance of *Paranthropus robustus*, *Numidocapra* and *Damaliscus* in southern Africa.

CRediT authorship contribution statement

Raphaël Hanon: Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing. **Jean-Baptiste Fourvel:** Investigation, Writing – review & editing. **Recognise Sambo:** Investigation, Writing – review & editing. **Nompumelelo Maringa:** Investigation, Writing – review & editing. **Christine Steininger:** Supervision, Writing – review & editing. **Bernhard Zipfel:** Data curation, Writing – review & editing. **José Braga:** Supervision, Project administration, Funding acquisition, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The date is available in the Supplementary Material

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2024.108621.

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