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Stretching the time span of hominin evolution at Kromdraai (Gauteng, South Africa): Recent discoveries

Extension de la durée de l'évolution humaine à Kromdraai (Gauteng, Afrique du Sud) : découvertes récentes

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ABSTRACT

The Plio-Pleistocene locality of Kromdraai B has yielded the type specimen of *Paranthropus robustus*, as well as 27 additional fossil hominin specimens. In a number of both cranial and dental features, the states shown by the Kromdraai *Paranthropus* are more conservative when compared to the more derived conditions displayed by both South African conspecifics and the post-2.3 Ma eastern African *Paranthropus boisei*. Since 2014, we excavated the earliest known infilling of the Kromdraai cave system in a previously unexplored area. This new locality provided as yet 2200 identifiable macrovertebrate fossils, including 22 hominins, all tied in the earliest part of the stratigraphic sequence, representing three distinct depositional periods. Since we report here, for the first time, the occurrence of fossil hominins in Members 1 and 2, our discoveries stretch the time span of hominin evolution at Kromdraai and contribute to a better understanding of the origin of *Paranthropus* in southern Africa.

RÉSUMÉ

La localité Plio-Pléistocène de Kromdraai B a livré l'holotype de *Paranthropus robustus* ainsi que 27 autres spécimens d'homininés fossiles. Pour un certain nombre de traits dentaires et crâniens, les états présentés par les *Paranthropus* de Kromdraai sont davantage conservés par comparaison aux conditions plus dérivées observées à la fois sur les individus du même genre en Afrique australe et les *Paranthropus boisei* postérieurs à 2,3 Ma. Depuis 2014, nous avons fouillé les dépôts les plus anciens de la grotte de Kromdraai, dans une zone jusqu'ici inexplorée. Cette nouvelle localité a livré 2200 vestiges identifiables de macrovertébrés, dont 22 homininés fossiles, tous précisément

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localisés dans la première partie de la séquence stratigraphique, représentant trois périodes de dépôt distinctes. Parce que nous communiquons ici, pour la première fois, sur la présence d'homininés dans les Membres 1 et 2, nos découvertes étendent la durée de l'évolution humaine à Kromdraai et contribuent à une meilleure compréhension de l'origine de *Paranthropus* en Afrique australe.

1. Introduction

1.1. The Kromdraai A and Kromdraai B localities

The Plio-Pleistocene site of Kromdraai, Gauteng province, South Africa (26°00′41″S, 27°44′60″E), is an unroofed dolomite cave partially shaped by the erosional surface and filled with fossil-bearing deposits, situated approximately 2 km east of Sterkfontein Caves, on the southern side of the Blaauwbank stream (Fig. 1). It has long been considered as two distinct localities of relatively limited extent: Kromdraai A (KA) and Kromdraai B (KB) (Fig. 2).

The younger KA locality is situated about 30 m to the west of KB (Fig. 2) and has not yielded fossil hominins yet. The KB locality yielded the type specimen of *Paranthropus robustus*, TM 1517, the only partial skeleton of this species known thus far (Broom, 1938a, b, 1942, 1943), as well as 27 other fossil hominin individuals discovered from 1938 to 2009 (Braga and Thackeray, 2003; Braga et al., 2013; Thackeray et al., 2001). Until 2014, the KB sedimentary deposits occuring on either side of a rib of 'dolomitic bridge' located near the western end of the locality (named 'KB East' and 'KB West' Formations) were considered to fill a deep fissure of about 46 m from east to west, but only 1 to 3 m from south to north (Fig. 2). The southern dolomitic wall of this paleo-cavity is still visible. However, until 2014, the northern wall of KB was only identifiable in the western part of the site. New excavations initiated in 2014 indicate that KB extends more than 30 m towards the north.

1.2. Why Kromdraai hominins are important?

The KB *P. robustus* hominins have long been considered as distinct from their congenerics from the nearby site of Swartkrans. The Swartkrans *Paranthropus* sample was first suggested to represent a distinct species – *Paranthropus crassidens* – with much larger teeth (Broom, 1949, 1950; Howell, 1978). This specific distinction between *P. robustus* from Kromdraai and *P. crassidens* from Swartkrans was changed into a subspecific one by Robinson (1954) on the basis of differences in the deciduous first molar and canine. However, the initial specific distinction was subsequently supported on the basis of features mainly related to wear, morphology and size observed on the mandibular deciduous first molar, the canine and the first permanent mandibular molar (Grine, 1982, 1985, 1988). Subsequent studies of dental remains from Drimolen, the second largest sample of *Paranthropus* in South Africa (after Swartkrans) favoured the hypothesis of a single and variable *P. robustus* species (Keyser et al., 2000; Moggi-Cecchi et al., 2010). However, in the absence of a larger hominin sample from Kromdraai, it is still uncertain as to whether the size and shape pattern of the KB cranial, dental and postcranial hominin specimens represent distinctions as expected as normal variation within a single *P. robustus* species with a relatively limited time span.

While the dating of the KB hominins remains problematic, it has been suggested that at least some specimens lie close to the origin of a putative *Paranthropus* monophyletic clade (Kaszycka, 2002; Tobias, 1988). In a number of cranial and dental morphological features, the states shown by at least some KB hominins may represent the primitive condition for *Paranthropus* and were interpreted intermediate between the more plesiomorphic hominins from Makapansgat Members 3/4 and Sterkfontein Member 4, on the one hand, and the more derived conditions displayed by South African hominins from the nearby site of Swartkrans, on the other hand. Several dental and cranial features observed on the more generalized *Paranthropus* at KB contrast to the more derived conditions displayed not only by other southern African congenerics sampled thus far (Braga et al., 2013; Grine, 1988; Kaszycka, 2002), but also by the post-2.3 millions of years ago (Ma) eastern African *P. boisei* (Suwa, 1988). As stated by Tobias (1988: 305), "the population represented by the Kromdraai hominid may throw light on the nature of the cladogenetic trans-specific change from the postulated 'derived *A. africanus*' [. . .] to the earliest 'robust' australopithecine sensu stricto." However, most scenarios consider that *Paranthropus* did not occur in southern Africa prior to 2.0 Ma (e.g., Kimbel, 2007; Wood and Boyle, 2016).

The chronological gap between the purported origin of the *Paranthropus* clade and its diversification into eastern and southern African forms (hereinafter called *P. boisei* and *P. robustus*, respectively) is often set during the 2.7–2.3 Ma period. The fossil hominin assemblage documenting this period is dominated mainly by: (i) the eastern African and geographically widely distributed *P. aethiopicus* (from Laetoli, in Tanzania, to the Omo-Turkana basin, in Kenya and Ethiopia), with its highly mosaic and plesiomorphic face at ca 2.7–2.3 Ma; (ii) the conventionally defined *Au. africanus* species with its extensive range of variation sampled at Sterkfontein, Makapansgat and Taung, South Africa (but see below), here set between ca. 3.7 and 3.0–2.6 Ma, based on the combination of faunal evidence (McKee et al., 1995) and absolute dates (Granger et al., 2015). The hypothesis of the *aethiopicus* species as a potential ancestor of *Paranthropus* is most commonly accepted. An alternative phylogenetic model rests on the discovery of non-*aethiopicus*-like but more *P. robustus*/*P. boisei*-like hominins securely dated from between 3.0 and 2.3 Ma. In the event of the occurrence of a pre-2.3 Ma *P. robustus* southern African form, this alternative hypothesis would entail the parallel evolution of certain ‘robust’ craniodental traits in the *aethiopicus* species. It would also posit that some populations of *P. robustus* predated the first appearance of *P. boisei* at 2.3 Ma in East Africa, gave rise to this latter species and survived the split to persist in South Africa. If at least some KB hominins were older than the first appearance of *P. boisei* in East Africa at ca 2.3 Ma, their chronology would be in line with their morphology to represent an ancestral population of *Paranthropus* sensu stricto before 2.3 Ma in the southern African record. Further discoveries and analyses of fossil hominins at Kromdraai, as well as closer comparisons with *Au. africanus*, may affect our current interpretation of the source populations for *Paranthropus*.

1.3. Aims of this paper

This paper mainly aims to provide a brief historiographic framework of previous work at Kromdraai and, for a better evaluation of the potential of this site, to present preliminary results obtained during recent fieldwork. It is important to note that the current lack of consideration of previous publications has led to unsubstantiated statements, misinterpretations or errors. For example, until recent excavations started in 2014, the large majority of the KB fossils have been found from *ex situ* breccia blocks (Broom, 1938a, b, 1942, 1943), or from decalcified breccias with no ascertained stratigraphic context (Brain, 1981). Despite several previous published reports (e.g., Vrba, 1981: 19; Vrba and Panagos, 1982: 21), it is disappointing to read that most studies treat the Kromdraai fossils (including its hominin sample) as a temporally homogeneous sample (e.g., Herriès et al., 2009; Kaszycka, 2002; Skinner et al., 2013).

Here we explain why the current KB faunal and archaeological samples are primarily derived from at least three distinct depositional phases securely tied in a stratigraphic context (Braga et al., 2013) and we present recent data gathered at Kromdraai in order to discuss how the variation seen among the fossil-bearing deposits, faunal and hominin samples at this site stretch a longer timeline of human evolution than previously thought.

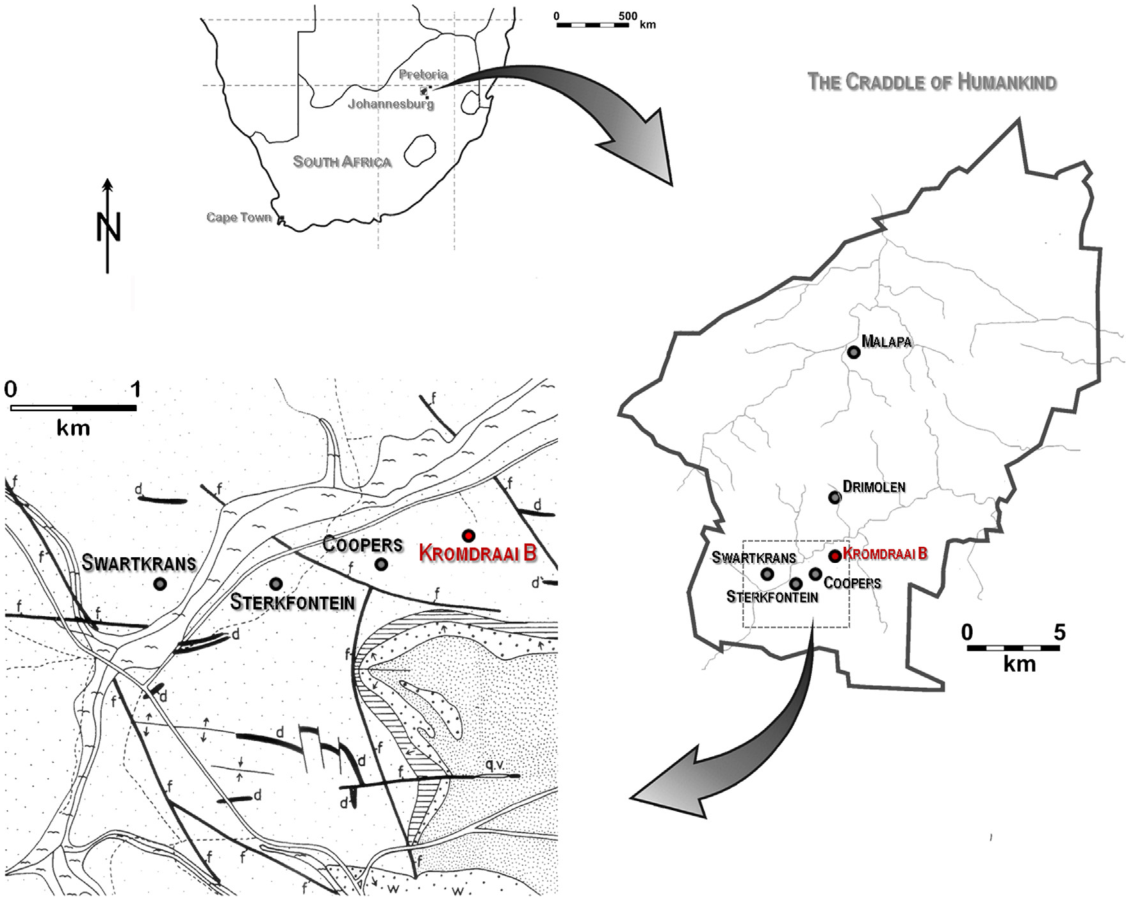

Fig. 1. Map showing the location of the site of Kromdraai (Gauteng, South Africa).

Fig. 1. Carte de localisation du site de Kromdraai (Gauteng, Afrique du Sud).

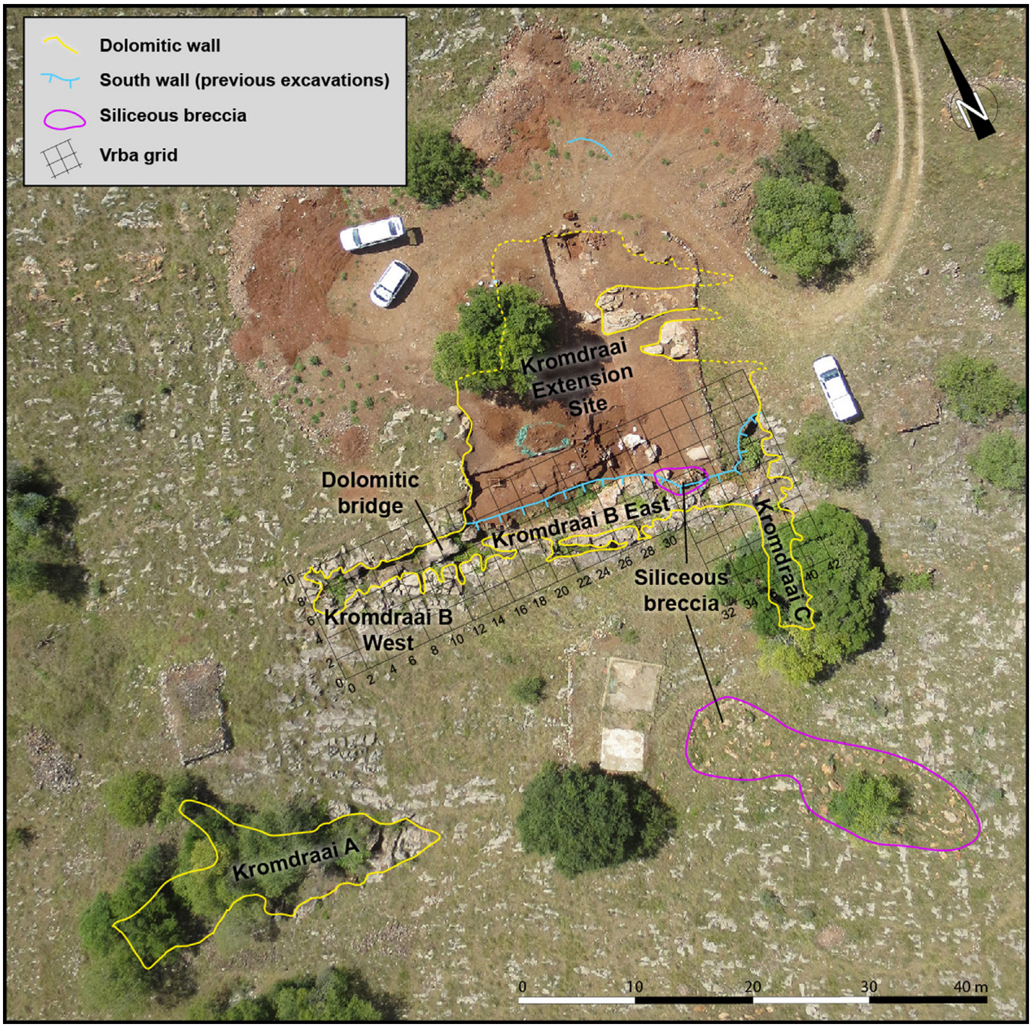

Fig. 2. Aerial view of the Kromdraai site with locations of its main features.

Fig. 2. Vue aérienne du site de Kromdraai et localisation de ses principaux éléments.

2. The construction of the Kromdraai B fossil and archaeological assemblages

The KB fossil assemblage discovered before 2014 (see below) comprises 6067 specimens in total, all stored at the Ditsong National Museum of Natural History in Pretoria and accessioned into the catalogue system with the KB prefix (the last published KB fossil, KB 6067, is a partial temporal bone of a juvenile hominin; Braga et al., 2013). The KB fossils and cultural artefacts were recovered during five distinct periods, as reported below.

2.1. Broom's excavations (1938–1944)

The exact circumstances of the discovery of the holotype of *P. robustus* (TM 1517) at KB are not clear. The fossil bones, regarded as belonging to this single individual, have been published in a series of four papers (Broom, 1938a, b, 1942, 1943). In his first report of the discovery of the left half of a subadult calvarium (TM 1517a), an associated right mandibular corpus (TM 1517b) and several isolated teeth (TM 1517c), no mention was made as to whether these specimens have been found *in situ* or in a loose block (Broom, 1938a). Broom (1938b) subsequently reported the discovery of the distal end of a humerus (TM 1517g), part of the proximal end of a ulna (TM 1517e), and a manual distal phalanx from rays II to V (TM 1517o, possibly of a baboon; Day, 1978; see Skinner et al., 2013) which he assigned to the same individual as TM 1517a, b and c and all reported to come from the same area (Broom, 1938b: 897). After more preparation of "the matrix on which the maxilla rested", Broom (1942: 513) reported the discovery of several isolated hand and foot bones that he also assigned to TM 1517, but most of them (except TM 1517k) are now identified as cercopithecoid specimens (TM 1517 h, i, j, l, m, n, o; for more details, see Broom and Schepers, 1946; Day, 1978; Day and Thornton, 1986; Skinner et al., 2013). A year later, Broom (1943: 689) reported the discovery of a right talus (TM 1517d) from the same "block of matrix" in which other TM 1517 fossils came from. Further work at KB produced more remains attributed to *P. robustus*: (i) a mandible of a child (TM 1536, in 1941) found "within four feet of the place where the type skull lay" (Broom and Schepers, 1946: 109–110); (ii) the crown (with no developed roots) of a upper left third molar assigned to the TM 1517 individual (TM 1603, in 1944), found on the "tailings from the Kromdraai skull site" (Broom and Schepers, 1946: 98–99).

2.2. Brain's excavations (1955–1956)

The large majority of the KB fossil sample known thus far has been found during the 1955–1956 fieldwork leaded by Brain (Brain, 1958, 1975, 1978, 1981; Freedman and Brain, 1972). Almost nothing about the geology of KB was available at this time. Brain's excavation concentrated on mainly decalcified breccia along what he believed to be "the northern wall" of the KB East Formation (between E-W coordinates 20 and 30 m, according to E. Vrba's grid system) (Fig. 2) to a maximum depth of about 5 m. Brain (1975: 226) considered that "the dolomite wall [was] preserved in its original form only along the southern side of the deposit. On the northern side it [had] largely disappeared through solution, and the breccia, which was in contact with it, has been severely decalcified".

The fossil finds were grouped into three layers according to their depth in the excavation and were regarded as representing a single depositional phase (Brain, 1958, 1975, 1981). As emphasized by Brain (1958), contrary to several subsequent and unsubstantiated statements (including in the recent literature), the horizontal delineation of decalcified deposits had "little meaning". As already emphasized by others (Vrba, 1981; Vrba and Panagos, 1982; see Brain, 1981), Brain's KB fossil sample (including five hominin specimens; see Table 1) could not be tied precisely to any of the five successive breccia members of KB, as defined by Partridge (1982) (see below). Brain's excavations led to the first discoveries of cultural material at KB. This material consisted of at least one unquestionable flake of chert interpreted as possibly "artificially introduced" (Brain, 1958).

2.3. Vrba's excavations (1977–1980)

During the 1977–1980 fieldwork leaded by Vrba (Grine, 1982; Vrba, 1981; Vrba and Panagos, 1982), a grid system was established for the first time at KB (Fig. 2). The KB East Formation was interpreted to represent a single debris cone whose initial geometry was assessed by extrapolating the inclinations of the interfaces [either observed on the surface or probed by drilling between five Members (Partridge, 1982)]. From the extrapolation of the slopes, the location of the original cave opening was assessed towards the eastern end of the site, between E-W coordinates 29 and 33 m, likely between 5 and 10 m above the present erosion level (Partridge, 1982; Vrba, 1981: 22).

The vast majority of the macrovertebrate sample recovered during Vrba's excavation was found in Member 3, on the central part of the KB East Formation, between E-W coordinates 22 and 30 m (Fig. 2), which failed to produce any further artefacts. Primates featured prominently in the faunal sample that contained almost no bovids. Carnivores represented the second most occurring group. Only a few remains were discovered from Member 1, with Member 2 considered as sterile (Vrba, 1981).

2.4. Thackeray's excavations (1993–2002)

In 1993, Thackeray started new excavations at KB with a 100 m^2 eastern extension of Vrba's grid system. This fieldwork focused on an area 30–40 m north and 0–10 m east of Vrba's datum point (see Fig. 2 in Kuman et al., 1997). Fossil bone discoveries (beginning with the number KB 5500) were reported, including one fossil hominin specimen (KB 5503). This excavation led to the discovery of the only provenanced Oldowan polyhedral core from KB (Kuman et al., 1997). A revised list of the KB hominins (Thackeray et al., 2001) and the only palaeomagnetic analyses yet conducted at this site (Thackeray et al., 2002) were also published.

2.5. The Kromdraai Research Project (since 2002)

After the discovery of additional fossil material at KB in 2002 (Thackeray et al., 2005), the Kromdraai Research Project (KRP) was established. We started to clean the KB solid breccias with acetic acid (10%) and a high pressure cleaner to be able to analyse their texture and geometry. We also cleaned the bottom and the sections of Brain's excavation conducted along the wall interpreted as the northern side of KB. From this first step, we reached the conclusion that the Kromdraai site had a larger extension toward the north than it was previously thought. We inferred that this extension (Fig. 2) represented mainly decalcified infillings of a single Kromdraai cave system (which has lost its roof through erosion) accessible from the surface, with a total area of exposed fossiliferous deposits of around 600 m^2 (Fig. 2). Test pits and sections in the purported extension of the Kromdraai site (KE; Fig. 2) revealed that approximately the first top meter of the deposits was affected by pedogenesis that lead to the formation of a ferruginous soil. It was associated with a severe decalcification in which only pieces of weathered cherts and gravels remained in place. Therefore, no fossils could be found in the first top meter from the natural surface. In order to reach potentially new fossiliferous deposits free of decalcification in KE, we started to remove the residualised and sterile first top meter of soil on a surface of approximately 300 m^2. Not even a single bone was found during this phase. When the sediments became darker, less than one unidentifiable bone fragments per m^2 was found between a depth of approximately 1 and 1.20 m. We reached the levels not affected by the pedogenetic process at a depth of 1.20 m. In April 2014, we started finding numerous macrovertebrate fossils (including two fossil hominin specimens, KW 6087 and KW 6167) (Braga, 2016) at a minimal depth of 1.2 m (below datum point) where both soft and solid breccias were preserved.

During seven field seasons from April 2014 to February 2016, we recovered more than 2200 identifiable fossils (including 22 hominin specimens) in the KE locality, all precisely tied in the stratigraphy. These fossil discoveries confirm that the Kromdraai site is at least six times larger than previously thought and particularly rich in

Table 1
List of the Kromdraai B fossil material found before 2014 and unambiguously attributed to hominins.
Tableau 1
Liste des vestiges fossiles de Kromdraai B découverts avant 2014 et attribués sans équivoque à des homininés.

Catalogue No.	Description	Provenance	References	Assoc., biol. age
TM 1517a	Left part of a calvarium with P3 to M2	Ex situ (possibly Mb.4), 1938	Broom (1938a) and Broom and Schepers (1946) (Pl. 8–9)	Ind. 1, late adolescent
TM 1517b	Right part of a mandibular corpus with C root, C crown (impression), P3 to M3	Ex situ (possibly Mb.4), 1938	Broom (1938a) and Broom and Schepers (1946) (Pl. 10)	Ind. 1, late adolescent
TM 1517c	LLP3-LLP4 and URP3 to M3	Ex situ (possibly Mb.4), 1938	Broom and Schepers (1946) (Pl. 9)	Ind. 1, late adolescent
TM 1517d	Right talus	Ex situ (possibly Mb.4), 1943	Broom (1943)	Ind. 1, late adolescent
TM 1517e	Right proximal ulna	Ex situ (possibly Mb.4), 1938	Broom (1938b) and Broom and Schepers (1946) (Pl. 12)	Ind. 1, late adolescent
TM 1517g	Right distal humerus	Ex situ (possibly Mb.4), 1938	Broom (1938b) and Broom and Schepers (1946) (Pl. 12)	Ind. 1, late adolescent
TM 1517k	Distal phalanx, possibly from hallux	Ex situ (possibly Mb.4), 1942	Day and Thornton (1986), Day (1978), Skinner et al. (2013)	Ind. 1, late adolescent
TM 1517n	Intermediate phalanx, possibly cercopithecine	Ex situ (possibly Mb.4), 1942	Broom (1942), Day and Thornton (1986), Day (1978)	
TM 1517o	Distal manual phalanx, ray II-V, possibly baboon	Ex situ (possibly Mb.4), 1938	Broom (1938b) and Broom and Schepers (1946) (Pl. 12), Day and Thornton (1986), Day (1978), Skinner et al. (2013)	
TM 1536	Left mandibular corpus (fragmentary) with I1, I2, di2, dm1-2, M1; L dC	Ex situ, 1941	Broom (1941) and Broom and Schepers (1946) (Pl. 11)	Ind. 2, juvenile
TM 1600	Left mandibular corpus fragments (2) with M2-M3 (fragmt.1) and P3 (fragmt.2)	Decalcified breccia, Unprov., 1955–1956	Brain (1981)	Ind. 3, adult
TM 1601a	Lower right dm1	Decalcified breccia, Unprov., 1955–1956	Brain (1981)	Ind. 4, juvenile
TM 1601b to d	Respectively, Lower right P3, C, P4 germs	Decalcified breccia, Unprov., 1955–1956	Brain (1981)	Ind. 4, juvenile
TM1601e	Upper left M1 germ	Decalcified breccia, Unprov., 1955–1956	Brain (1981)	Ind. 4, juvenile
TM1601f	Lower right dc	Decalcified breccia, Unprov., 1955–1956	Brain (1981)	Ind. 4, juvenile
TM 1602	Right maxillary fragment with root of P4 to M3	Decalcified breccia, Unprov., 1955–1956	Brain (1981)	Ind. 5, adult
TM 1603	Upper left M3	Dump, 1944	Broom and Schepers (1946) (pp. 98–99)	Ind. 6[a], adolescent
TM 1604	Lower left dm2 associated with breccia matrix	Decalcified breccia, Unprov., 1955–1956	Brain (1981)	Ind. 7, juvenile
TM 1605	Left innominate	Decalcified breccia, Unprov., 1955–1956	Brain (1981), Robinson (1972)	Ind. 8, adult
KB 5063	Upper right M1	Unprov., 1977–1980	Vrba (1981)	Ind. 9, adult
KB 5163	Lower right C	Ex situ (Ditsong Museum, Pretoria)	de Ruiter (2004)	Ind. 10, adult
KB 5222	Upper left M3	Unprov., 1977–1980	Vrba (1981)	Ind. 11[b], juvenile
KB 5223	LL dc, dm1-2; LR dm2; Lower permanent incisors; LR and LL M1s	MB.3, 1977–1980	Vrba (1981), Grine (1982), Braga and Thackeray (2003)	Ind. 12, juvenile[c]
KB 5226	Lower left M3	MB.3, 1977–1980	Vrba (1981)	Ind. 13, adult
KB 5383	Upper right M1	Unprov.[d], 1977–1980	Vrba (1981)	Ind. 14, adult
KB 5389	Upper left I1	Ex situ (Ditsong Museum, Pretoria)	de Ruiter (2004)	Ind. 15, adult
KB 5503	Lower right dm2	Unprov.	Thackeray et al. (2001)	Ind. 16, juvenile
KB 5522	Left humerus shaft fragment	Possibly MB 5 (KRP), 2002	Thackeray et al. (2005)	Possibly Ind. 1[d]
KB 5524	Lingual side of a worn molar crown, possibly M1 or M2	MB.5 (KRP), 2002	Braga et al. (2013)	Possibly Ind. 1[e]
KB 6067	Petrous part of a left temporal bone	MB.3 (Ditsong Museum, Pretoria)	Braga et al. (2013)	Ind. 17, juvenile

KRP: Kromdraai Research Project; MB: Member; Unprov.: Unprovenianced in stratigraphy; Ind. Individual; L: Left; R: Right; L: Lower; U: Upper.

[a] KB 542 (metacarpal), KB 3133 (left cuboid), and KB 3297 (right calcaneus) have been found ex situ and were unconvincingly considered as possible hominins.

[b] KB 5222 has been attributed to the same individual as TM 1600, even though these two specimens are likely from distinct stratigraphic units.

[c] We cannot determine whether the roots have been broken or were not formed as yet.

[d] For more details, see Thackeray et al. (2001) and Braga et al. (2013).

[e] Same provenience as KB 5063.

macrofauna (including fossil hominins). All these newly discovered specimens are curated at the Evolutionary Studies Institute of the University of the Witwatersrand in Johannesburg, and are accessioned into the catalogue system with the 'KW' prefix (numbered from KW 6068 to KW 8280, in the current stage of the excavation). The former distinction between KA and KB is not any more justified because the KA locality contains sediments also represented at KB. We therefore use the new prefix 'KW' that corresponds to a single stratigraphic succession, with no distinction between KA, KB and KE localities.

The main geological features and the fossil discoveries are recorded on a topographical database generated by a total station theodolite, instead of a grid system. We also use multi-image photogrammetry and close range laser scanning for capturing high-resolution 3D surfaces with complete texture at two different scales, from a few kilometres to a few metres, with respectively centimetre and sub-centimetre accuracies. Close range laser scanning is used for the detailed recording of objects (e.g., fossils) and some aspects of the ground surface (e.g., contacts between breccias, flowstones) at a sub-centimetre scale. Finally, we use micro-computed tomography to observe fossils that have been preserved inside plaster caps during the excavation for their safe removal from the site. Therefore, we record the successive excavations and assess the changes of the site with a precise location and visualisation of the better-preserved fossil specimens (particularly, the articulated bones) within their sedimentary units.

3. Kromdraai litho- and biostratigraphy

The Kromdraai lithostratigraphy corresponds to a single talus cone interbedded with flowstones and includes several successive cycles, each indicating depositions, mineralizations, demineralizations and erosions. It therefore subsumes a complex succession of more than a single time period. A detailed account of the new stratigraphic interpretation of Kromdraai is published elsewhere (Bruxelles et al., 2016). Here, we very briefly summarize the lithostratigraphic interpretation first proposed by Partridge (1982).

3.1. Partridge's (1982) stratigraphic interpretation of KB

First of all, it is interesting to note that throughout the following succession of the KB five Members reported by Partridge (1982), all the upper contacts were considered as eroded and disconformable, representing a depositional hiatus:

- member 1 was reported at the eastern end of KB (KB East Formation) (Fig. 2) to consist of breccias containing abundant chert pebbles, cobbles and boulders, but with rare bone fragments and scattered fine pyrolusite concretions;
- member 2 was divided into two facies occurring to the east and west of the apex of the debris cone constituting Member 1. The top surface of Member 2 bears a stalagmite currently under study for absolute datings;
- member 3 was localized to the west of Member 2, where it thickened in this direction. Its breccia was reported as very fossiliferous;
- members 4 and 5 were described to the west of Member 3 with only rare fossils.

Only a minority of the KB fossils (including the fossil hominin sample) can be unambiguously assigned to the Member 3 deposits (Brain, 1981; Thackeray et al., 2005; Vrba, 1981; Vrba and Panagos, 1982). The stratigraphic succession was considered as "generally less calcified than that at Sterkfontein [Partridge, 1978] due either to a lesser degree of initial cementation or, more probably, to "more extensive post-depositional decalcification" (Partridge, 1982: 11). The fine textured sediments (clays and silts) were reported to be "50% more abundant than in any of the members of the Sterkfontein Formation", indicating "a greater degree of weathering and pedogenesis outside the cave, both prior to and during the accumulation of the deposits" (Partridge, 1982: 11). A significantly more humid climate than the present climatic regime may be an explanation of this observation (Partridge, 1982).

3.2. Further stratigraphic interpretations at Kromdraai

Even though the accumulation of some Members may have been rapid, the different breccias record distinct periods of time separated by lengthy time-lapse unconformities corresponding to erosive phases after deposition, cementation and alteration. At this stage, we cannot determine whether the unformities correspond to longer time periods than those covered by the different sedimentary records. Bruxelles et al. (2016) distinguish two groups of breccias suggesting a radical change in the morphological evolution of the cavity. During the earliest phase of the deposition observed from Members 1 to 3, the breccias have accumulated in a relatively deep gallery where flowstones could form and where the walls and vault contributed to the sedimentation. However, during this first phase, hyenas were active inside the Kromdraai cave used as a shelter, as indicated by several coprolithes recently found in the base of Member 2 (Fourvel, 2016). During the second phase, the cavity was largely dismantled, as shown by the formation of Members 4 and 5 consisting mainly of colluvium inputs into an already largely filled cavity.

3.3. The Kromdraai biostratigraphy

Previous biochronological assessments of the KB faunal assemblage (e.g., Heaton, 2006; McKee et al., 1995) did not distinguish between the sample from the calcified Member 3 breccia (from Vrba's excavation) and Brain's sample from decalcified deposits with probable mixing of specimens from Members 1–4. These biostratigraphic interpretations of the total KB sample should be considered with caution. We urge the readers to consider the KB fossil samples (recovered from distinct excavation periods) separately because they were gathered from distinct geological contexts (solid versus decalcified breccias), from different lithostratigraphic provenience (i.e. Member 1 versus Member 3), or from various circumstances of discovery (i.e., *ex* *situ* versus *in situ*, or unknown). An example of the variety of these distinct samples is given for the fossil hominins (Table 1).

The KB fossils collected from *in situ* Member 3 predominantly consist of cercopithecoid monkeys (approximately 75% of the faunal sample), including leaf-eating forms (colobinae). The KB cercopithecinae sample is taxonomically diverse and includes three papionin species: (i) an extinct and large-bodied subspecies of the contemporaneous *Papio hamadryas*; (ii) the large *Gorgopithecus major*; (iii) the smaller *Papio angusticeps*. Heaton (2006) concluded that these three KB papionins represent the oldest and synchronous occurrence of these species (alongside *P. robustus*) in South Africa. On the basis of the first occurrence of the eastern African and large-bodied *Theropithecus oswaldi* at Sterkfontein Member 5 and Swartkrans Member 1, Heaton (2006) also considered these later deposits as younger than those of KB. Heaton (2006) suggests that the absence of *D. ingens* at Kromdraai Member 3 (instead found at Swartkrans Member 1) may represent an additional indice of its older age as compared to Sterkfontein Member 5, Drimolen, Swartkrans Member 1 and KA.

Faunal seriation using other macromammal groups than non-human primates support this conclusion (McKee et al., 1995). For example, Pickford (2013) inferred the presence of deposits at KB that might be contemporaneous with the oldest hominin-bearing southern African Pliocene faunal assemblages (as represented at Makapansgat Member 3 and by the low-lying fossiliferous breccias at Sterkfontein represented by Member 2 and Jacovec Cavern). Indeed, Pickford (2013: 30) assigned a single tooth recovered from the lowermost decalcified breccia layer during Brain's KB excavation (1958) to *Potamochoeroides hypsodont*, suggesting "the presence of an earlier [than 2.5 Ma] deposit at the site [KB], equivalent in age to part of the Makapansgat sequence (perhaps about 3.5–3 Ma)".

Previous studies highlighted the low diversity of the KB carnivore species, when compared to those of KA (respectively 8 and 14 taxa) (e.g., Hendey, 1973). Since 2014, we significantly increased the carnivore spectrum from KB. From 89 newly discovered specimens recovered from Member 1 to 3, we identified 12 KB carnivore genera referred to six families (Canidae, Felidae, Hyaenidae, Mustelidae, Herpestidae, Viverridae). Our future identification of the KB *Dinofelis* at the species level will be indicative in terms of biochronology. At this stage, the occurrence of the small mustelid *Prepoecilogale bolti* is also particularly interesting. This species likely evolved in Africa between 3.7 and 2.6 My (Werdelin and Peigné, 2010). Recents finds at Cooper's may extend its time span or instead, may illustrate a younger step of evolution of this species (O'Regan et al., 2013). *P. bolti* from KB appears much more similar to a specimen from Laetoli Upper Unit (Werdelin and Dehghani, 2011) and may thus indicate an older age than Cooper's.

In contrast to KB, the abundance of ungulates in the KA faunal assemblage considered as homogeneous and the absence of colobinae (leaf-eating monkeys) suggested a more open landscape. KA shows a large number of extant time-sensitive bovid species, as well as those species characteristic of the 'Cornelia Faunal Span'. However, KA has not yielded as many extant species as the possibly younger Swartkrans Members 2 and 3.

3.4. Uranium-lead dating and magnetostratigraphy of the Kromdraai deposits

No U-Pb dates are available for KB at the moment, because diagenetic recrystallisation of neocalcite, observed on two speleothems from 'KB East', may have led to the opening of the geochemical system, marked by the deplacement, the incorporation or the loss of uranium. This may have an as yet unknown impact on the absolute dates. Taking this into account, we will obtain in the future U-Pb dates for the top Member 2′ stalagmite, as well as for a recently discovered large stalagmite from the top of Member 1. U-Pb direct measures of enamel (Balter et al., 2008) may also provide radiometric dates of the Kromdraai fossils in the future. U-Pb dates are available for the nearby site of Swartkrans. The oldest *P. robustus* specimens from Swartkrans Member 1 may represent either a relatively short period averaging 1.99 or 1.8 Ma, or rather a duration of deposition from 2.19 to 1.80 Ma (Gibbon et al., 2014; Pickering et al., 2011). When considering previous faunal seriations of South African Plio-Pleistocene sites (McKee et al., 1995), these results are well in line with the cosmogenic maximal dates obtained for Sterkfontein Member 5 at 2.18 Ma (Granger et al., 2015), regarded as younger than KB Member 3.

To our surprise, it is often and incorrectly stated that "the Kromdraai material" yielded an age range of c. 1.8–1.6 Ma from paleomagnetic data (e.g., Wood and Boyle, 2016). To support this view, Herries et al. (2009) are wrongly cited since they never conducted paleomagnetic or stratigraphic analyses at Kromdraai, but instead re-interpreted the only measurements yet obtained at this site by Thackeray et al. (2002). Thackeray et al. (2002) analysed a capping flowstone stratigraphically younger than Member 3 and obtained an interval of reversed polarity that they interpreted as older than the normal Olduvai Event (between 1.95 and 1.78 Ma). This interpretation was well in line with the biostratigraphic data. Therefore, Herriès et al. (2009) miscorrelated Thackeray et al.'s (2002) paleomagnetic data and ignored the KB stratigraphy.

4. The taphonomy, archaeology and paleoenvironments at Kromdraai B

4.1. Accumulative agents and archaeology at KB

Brain (1975) noticed an extreme fragmentation of the KB bone found mainly in decalcified breccias. He interpreted this pattern as an indication of the hominin food remains. Vrba (1981) considered the fragmentation of the KB bones as a result of the decalcification process. In addition to the absence of stone artifacts in Member 3, Vrba (1981: 21) noticed "the anatomical association of fragments, the virtual absence of bovids, the good representation of cercopithecoids and large carnivores". She concluded that this assemblage likely accumulated not only as a result of carnivore feeding behaviors, but also as a deathtrap (Vrba, 1981). Even though our study of the newly discovered fossil assemblages from Kromdraai Members 1, 2 and 3 is only preliminary, we report here that carnivores clearly had some involvement in the accumulation of the last two deposits (Fourvel, 2016).

The presence of circa 100 artefacts associated with the Early Acheulean or developed Oldowan at KA (Kuman et al., 1997) indicates a hominin presence but, as suggested by faunal seriations, during a period likely younger than the one represented at KB (McKee et al., 1995). Only the easternmost part of KB yielded a single Oldowan stone tool (a polyhedral core) that, according to the new stratigraphic interpretation (Bruxelles et al., 2016), was deposited during the second phase of the cavity infill (Members 4 or 5). Interestingly, KB as a whole, has been considered as "nearly contemporaneous" with the Member 5 deposits at Sterkfontein (McKee et al., 1995: 244), which mark the appearance of the earliest lower Oldowan tools in South Africa, currently dated at 2.18 ± 0.21 Ma (Granger et al., 2015). Moreover, no stone tools were found in the earliest part of the Kromdraai deposits (Members 1 to 3). Even though some taphonomic processes may explain this absence of stone tools, we consider that Members 1 to 3 accumulated before the first appearance of the Oldowan in South Africa.

4.2. *Paleoenvironments*

Vrba (1975) defined an "alcelaphini + antilopini criterion" (AAC) to compare the bovid assemblages in the African Plio-Pleistocene. She considered that the percentage of AAC was never > 30% of the total bovid population in areas with considerable tree and bush cover, but always > 60% in areas with high grass cover but few trees and bushes. Based on this evidence, she argued for a major African faunal turnover at about 2.4–2.6 Ma in both East and South Africa (Vrba, 1975). This faunal change was considered to correlate directly with hominin evolution and global climate changes. Vrba and Panagos (1982:13) suggested that KB sediments lower than Member 3 might have registered "a continuation from Sterkfontein Member 4 of an early period of higher rainfall and less dominant grassland prevalence than succeeding phases represented by Swartkrans Member 1 and Sterkfontein Member 5". However, due to the unknown provenience of most of the KB faunal assemblage, the AAC criterion must be interpreted with caution. We hope that the newly discovered bovids and other fossils from Member 2 will lead to a better understanding of the paleoecological conditions that prevailed at this time, well before the deposition of KB Member 3.

4.3. *Isotopic evidence*

Even if faunal assemblage likely represents relatively crude snapshots of the past with an unknown length of time, hypotheses about palaeoenvironmental changes have also been tested with measurements of stable carbon isotope ratios (Kohn and Cerling, 2002). The comparisons between karstic hominin site paleoenvironmental contexts based on δ^{13}C values have been used to decide whether the observed differences were due to long- or short-term shifts in habitats, or instead were caused by adaptations and versatility of dietary behaviors.

Only a very limited isotopic dataset is currently available for KB fossils that mainly served for diagenetic tests in order to identify potentially altered material and to recover reliable biogenic signals, not influenced by the isotopic values of the depositional context (Kirsanow, 2009). A single *P. robustus* tooth δ^{13}C measurement made on TM 1600 (not precisely tied in the lithostratigraphy) revealed no significant difference with those obtained on *P. robustus* specimens from the nearby site of Swartkrans (Sponheimer et al., 2005).

5. A preliminary sketch of the KB fossil hominins

The KB hominin sample published as yet (from 1938 to 2013) comprises 28 craniodental and postcranial specimens, with a minimum number of 17 individuals (Braga et al., 2013; Thackeray et al., 2001) (Table 1) attributed to *P. robustus* (Broom, 1938a, b; Thackeray et al., 2001; Vrba, 1981) and early *Homo* (Braga and Thackeray, 2003; but see Grine et al., 2009). This KB hominin sample contains only three non-dental diagnostic cranial remains: (i) the geologically younger type specimen of *P. robustus* (TM 1517; Broom, 1938a, b, 1942, 1943), possibly from Member 4; (ii) a significantly older isolated temporal bone (KB 6067) from Member 3 (Braga et al., 2013); (iii) the unprovenanced TM 1602 adult palate (Brain, 1981). Only a few hominin postcranial specimens from Kromdraai have been thus far published.

Our view of the phylogenetic status of the KB hominins has been greatly influenced by the difficulties to obtain appropriate radiometric dates from the fossiliferous sedimentary formations of this locality and other South African hominin-bearing sedimentary formations, as well as the interpretation of the morphological variability within the conventionally defined *Au. africanus* hypodigm. Moreover, the taxonomic interpretations of the KB hominins have been obscured by the lack of studies on the morphological variability within and between *Au. africanus* and *P. robustus*. Even though it has already been demonstrated that the Kromdraai fossil hominins display a unique morphological pattern (Braga et al., 2013; Broom, 1949, 1950; Grine, 1982, 1985, 1988; Howell, 1978; Kaszycka, 2002; Robinson, 1954; Tobias, 1988), a larger sample from this site is needed to obtain a better evolutionary scenario and paleobiological portray of the southern African *Paranthropus*.

5.1. *The distinct KB hominin samples*

The KB hominin sample published before 2014 falls into four groups (Table 1): (i) two specimens found during Vrba's excavation (KB 5223 and KB 5226; Vrba, 1981) or in the KB faunal collection (KB 6067; Braga et al., 2013) are securely provenienced from Member 3; (ii) two additional and potentially geologically younger specimens (KB 5522, reported by Thackeray et al., 2005, and KB 5524, reported by Braga et al., 2013) found *in situ* during excavations undertaken by FT and JB (since 2002) on the easternmost part of 'KB East' (circa 36 m east of datum point) and likely corresponding to Member 4; (iii) four specimens from Brain's excavation that cannot be securely tied in the stratigraphy; (iv) all the other unprovenienced KB hominins (including TM 1517), recovered either by Broom between 1938 and 1944 (Broom, 1938a, b, 1942, 1943), by one of us (FT) in a loose block of breccia (KB 5503; Thackeray et al., 2001), in the KB faunal collection (KB 5163, KB 5389; de Ruiter, 2004), or during Vrba's excavations.

In addition to the yet published KB hominin sample, 22 hominin specimens newly announced here are currently under study. They were discovered across the three distinct Members 1, 2 and 3. The calcified and soft breccia deposits of Members 1 and 2 excavated so far at Kromdraai represent the oldest of these time periods and had not yet provided fossil hominins. The newly discovered Kromdraai hominin cranial, dental and postcranial material will be reported in detail when more comparisons will be made. With this respect, it will be especially important to determine whether the stratigraphically older hominins from Members 1 and 2 appear distinct from those securely derived from Member 3.

5.2. *Size: a hallmark of the KB hominin sample?*

From the currently published maxillo-facial, basicranial and postcranial evidence, small size represents an important hallmark of the KB hominins. A first example is given by the size of several craniodental features and, in particular, the mandibular corpus. When measured at the level of the first permanent molar (M_1), its area (calculated using the formula for an ellipse; see Wood, 1991) in the adult TM 1517b specimen (660 mm^2) falls below the range that we obtained from published measurements of corpus height and width in other *P. robustus* adult specimens from Swartkrans (668–750 mm^2) (Grine and Daegling, 1993; Wood, 1991). Another and more complete adult mandible from Kromdraai Member 3 newly reported here (KW 6220, a specimen to be described in detail elsewhere) shows the same trend (667 mm^2) as the small-sized TM 1517 specimen. Unfortunately, the corpus height dimensions at M_1 were not reported for the two DNH 7 and DNH 8 adult mandibles from Drimolen (Keyser et al., 2000), even though the former specimen appears smaller in its corpus breadth at M_1 (20.9 mm) than both TM 1517 and KW 6220 (respectively, 24.1 and 24.2 mm). Differences in mandibular corpus dimensions within *Paranthropus* species may reflect patterns of sexual dimophism rather than dietary adaptations (Chamberlain and Wood, 1985). However, detailed comparative studies of mandibular inner structures (e.g., cortical thickness distribution across the corpus) in fossil hominins are needed to investigate this aspect further. Simple mesiodistal and buccolingual diameters of deciduous and permanent teeth of other KB hominins (e.g., TM 1536) also indicate relatively small size. When we focus on the M_1 and compare the *P. robustus* samples in a sequence from the smaller to the larger, we obtain the Kromdraai-Drimolen-Swartkrans succession (Moggi-Cecchi et al., 2010).

Basicranial features also reveal the small size of KB hominins. For instance, in cochlea and oval window size, two cranial proxies of body size (Braga et al., 2015) not associated with the masticatory apparatus, the only KB specimen on which these two features could be measured (KB 6067) is 50% smaller (for oval window size) than the mean value ontained for *P. robustus* adults specimens from Swartkrans, or falls well below them (for cochlear length), and is more similar to some specimens from Sterkfontein Member 4, such as StW 329 and StW 255 (Braga et al., 2013). Interestingly, the later specimen may be associated with the partial cranium StW 252 (both specimens were found in June 1984 and in the same area of decalcified breccia), placed “morphologically and temporally to be a member of a species [*Au. Prometheus*; see Clarke, 2008] that was ancestral to and directly on the lineage of *Paranthropus*” (Clarke, 1988: 291). The small size of KB 6067 can therefore be interpreted as indicative of a small body size for an adult *P. robustus*, possibly showing closer affinities with some Sterkfontein Member 4 specimens.

Small size in the KB hominins is also represented by postcranial remains presumably associated with the partial cranium of TM 1517, the ‘type specimen’ of *P. robustus* (Table 1). Among the handful of limb fragments published yet to estimate body weight in *P. robustus*, the TM 1517b talus represents one of the smallest specimens used to predict the low 32–40 kg female range for this species (Susman et al., 2001). Moreover, as already noted by McHenry (1974: 335–336), if the three postcranial bone remains attributed to TM 1517 belong to a single individual, then the humerus appears to be much larger in relation to the talus than is the usual case in modern man, but not when compared to great ape data.

5.3. *A preliminary hypothetical scenario*

Given the close geographical proximity (less than 5 km) of the six known *Paranthropus*-bearing deposits in South Africa (Kromdraai, Sterkfontein Member 5, Swartkrans, Drimolen, Coopers and Gondolin) and the noticeable small dental, cranial and postcranial size of several hominin specimens from Kromdraai, how can we interpret the fossil assemblage from this site despite the limitations due to its paucity? The small size of several *Paranthropus* dental, cranial and postcranial specimens, including those from Kromdraai, has usually been considered as a good proxy for sex assessment. The predominance of small-sized specimens in most assemblages has even been interpreted as indicative of taphonomically skewed samples with a higher proportion of small adults due to an increased predation level by carnivores (Grine et al., 2012) on a highly sexually dimorphic *P. robustus* species (Lockwood et al., 2007). While this tempting hypothesis has not been yet tested further with appropriate methods (e.g., measures of tooth-mark frequency and relative abundance of some anatomical elements), no alternative explanations of differences in size between hominin specimens have been explored.

Evolutionary trends for increasing body size along fossil hominin lineages may be difficult to demonstrate in the absence of appropriate dates and with limited sample sizes. In this context, Baker et al. (2016) used phylogenetic simulations to predict, after controlling for body size, the rate changes of molar crown area that may have occurred along the main branches of the primate phylogeny. They found one of the most exceptional shift with an increase of molar area relative to body size along the *Paranthropus* lineage (see fig. 5, in Baker et al., 2016). This result implies mainly that the relationship between molar area and body size (allometry) was not constant but instead, changed considerably along the *P. robustus* lineage. Therefore, molar size should be used with great caution for sex assessment, in particular in geologically younger *Paranthropus* sample with more disproportionate molar area. Given the biostratigraphic indices of an older age of Kromdraai Member 3, as compared to Swartkrans Member 1, Sterkfontein Member 5 and Drimolen, if molar area increased during this sequence along the *P. robustus* lineage as indicated by Baker et al. (2016), the hypothesis of an anagenetic trend for a proportionaly smaller increase of body size in *Paranthropus* from Kromdraai though Swartkrans/Drimolen would be interesting to test further.

The analysis of overall dental, cranial or postcranial size will not be sufficient to capture the morphological variation within and between South African fossil hominin samples and to test the hypothesis of the evolutionary uniqueness of at least some Kromdraai hominins. Deeper analyses of shape differences using 3D morphometric methods not contingent on sparsely selected landmarks (e.g., diffeomorphisms; see Durrleman et al., 2012, 2013) and formal measurements of phylogenetic signals combined with ancestral reconstructions (e.g., Braga et al., 2015), will allow us to test further our working hypothesis that the South African fossil hominin record, including the Kromdraai oldest specimens and individuals from Sterkfontein Member 4 attributed to *Au. prometheus* (Clarke, 2008), would contain an earliest member of the *P. robustus* lineage, probably somewhere in the southern Late Pliocene record.

A closer taxonomic and phylogenetic definition of the earliest Kromdraai hominins will not suffice to resolve the central question of *Paranthropus* monophyly. More detailed comparisons between the Kromdraai oldest hominins from Members 2 and 3 and pre-2.0 Ma *Paranthropus* specimens from eastern Africa will be useful to determine whether more generalized representatives of this genus in southern Africa predated the first appearance of *P. boisei* at 2.3 Ma in eastern Africa, gave rise to this latter species and survived the split to persist in South Africa as *P. robustus*. In this context, several craniodental features in which *P. robustus* and *P. boisei* differ significantly (e.g., the differential enlargement of lower molar entoconids and hypoconids) will merit close attention. Moreover, since little is known about the postcranial skeleton of *Paranthropus*, any newly discovered postcranial hominin specimens from Kromdraai might potentially be very information to document the locomotor repertoire of this genus.

6. Conclusive remarks and perspectives

Fieldwork undertaken since 2014 by the KRP, as well as laboratory work initiated on 2200 newly discovered fossils, demonstrate the much larger size of the Kromdraai site through the exposure of extensive and until then unexplored fossiliferous deposits, all tied in the earliest part of the stratigraphic sequence from Member 1 to Member 3 containing fossil hominins reported here for the first time. Our ongoing taxonomic, phylogenetic and taphonomic interpretations of these new dental, cranial and postcranial samples using computer-assisted imaging methods, recent advances in 3D morphometry and phylogenetic analyses, will help to determine whether Kromdraai hominins from Members 1 and 2 correspond to temporal and evolutionary events also represented in eastern Africa at the base of a presumptive *Paranthropus* monophyletic lineage between 2.6 and 2.3 Ma, or if they represent unique Plio-Pleistocene snapshots of hominin evolution in southern Africa with a transition from a local *Australopithecus* species (likely *Au. Prometheus* represented both at Sterkfontein Member 2 ancd 4, and Makapansgat) to a *Paranthropus* paraphyletic one.

Even if the interpretations presented here are only preliminary, we argue that a longer period of hominin evolution than previously thought is recorded at Kromdraai. This leads us to stretch the timeline of hominin at this site, with the discovery of hominin-bearing sediments older than Member 3 that might have registered a continuation from Sterkfontein Member 4 to the succeeding phases represented by Swartkrans Member 1 and Sterkfontein Member 5. Some Kromdraai deposits from Member 3 may correspond to the same period represented in Sterkfontein Member 5. Our working hypothesis is that the Kromdraai older sediments from both Members 1 and 2 illustrate significantly older temporal windows of hominin evolution, with an earliest member of the *P. robustus* lineage. Current analyses will help to determine the temporal depth, the nature and exact number of periods recorded in the Kromdraai older fossil-bearing sediments, as well as which ecological conditions prevailed at these times.

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References

Baker, J., Meade, A., Pagel, M., Venditti, C., 2016. Positive phenotypic selection inferred from phylogenies. 118, 95–115.

Balter, V., Blichert-Toft, J., Braga, J., Telouk, P., Thackeray, F., Albarède, F., 2008. U-Pb dating of fossil enamel from the Swartkrans Pleistocene hominid site, South Africa. Earth Planet. Sci. Lett. 267, 236–246.

Braga, J., 2016. The Kromdraai hominins revisited with an updated portray of differences between *Australopithecus africanus* and *Paranthropus robustus*. In: Braga, J., Thackeray, J.F. (Eds.), Kromdraai, a Birthplace of *Paranthropus* in the Cradle of Humankind. Sun Media Metro, Johannesburg (in press).

Braga, J., Thackeray, J.F., 2003. Early *Homo* at Kromdraai B: probabilistic and morphological analysis of the lower dentition. C. R. Palevol. 2, 269–279.

Braga, J., Thackeray, J.F., Dumoncel, J., Descouens, D., Bruxelles, L., Loubes, J.-M., Kahn, J.-L., Stampanoni, M., Bam, L., Hoffman, J., de Beer, F., Spoor, F., 2013. A new partial temporal bone of a juvenile hominin from the site of Kromdraai B (South Africa). J. Hum. Evol. 65, 447–456.

Braga, J., Loubes, J.-M., Descouens, D., Thackeray, J.F., Dumoncel, J., Kahn, J.-L., de Beer, F., Riberon, A., Hoffman, K., Balaresque, P., Gilissen, E.,

2015. Disproportionate cochlear length in genus *Homo* shows a high phylogenetic signal during apes' hearing evolution. PLoS One 10 (6), e0127780.

Brain, C.K., 1958. The Transvaal Ape-Man-Bearing Cave Deposits. Transvaal Museum Memoir No. 11. Transvaal Museum, Pretoria.

Brain, C.K., 1975. An interpretation of the bone assemblage from the Kromdraai australopithecine site, South Africa. In: Tutle, R.H. (Ed.), Palaeontology, Morphology and Palaeoecology. Mouton, The Hague, pp. 225–243.

Brain, C.K., 1978. Some aspects of the South African australopithecine sites and their bone accumulations. In: Jolly, C.J. (Ed.), African Hominidae of the Plio-Pleistocene. St. Martin's Press, New York, pp. 131–161.

Brain, C.K., 1981. The Hunters or the Hunted? An Introduction to African Cave Taphonomy. Chicago University Press, Chicago.

Broom, R., 1938a. The Pleistocene anthropoid apes of South Africa. Nature 142, 377–379.

Broom, R., 1938b. Further evidence on the structure of the South African Pleistocene Anthropoids. Nature 142, 897–899.

Broom, R., 1941. Structure of the Sterkfontein ape. Nature 147, 86.

Broom, R., 1942. The hand of the ape-man, *Paranthropus robustus*. Nature 149, 513–514.

Broom, R., 1943. An ankle-bone of the Ape-man, *Paranthropus robustus*. Nature 152, 689–690.

Broom, R., 1949. Another new type of fossil ape-man. Nature 163, 57.

Broom, R., 1950. The genera and species of the South African fossil ape-man. Am. J. Phys. Anthropol. 8, 1–13.

Broom, R., Schepers, G.W.H., 1946. The South African Fossil Ape-Men: the Australopithecinae. Transvaal Museum Memoir No. 2. Transvaal Museum, Pretoria.

Bruxelles, L., Maire, R., Couzens, R., Thackeray, F., Braga, J., 2016. A revised stratigraphy of Kromdraai. In: Braga, J., Thackeray, J.F. (Eds.), Kromdraai, a Birthplace of *Paranthropus* in the Cradle of Humankind. Sun Media Metro, Johannesburg (in press).

Chamberlain, A.T., Wood, B.A., 1985. A reappraisal of variation in hominid mandibular corpus dimensions. Am. J. Phys. Anthropol. 66, 399–405.

Clarke, R.J., 1988. A new *Australopithecus* cranium from Sterkfontein and its bearing on the ancestry of *Paranthropus*. In: Grine, F.E. (Ed.), Evolutionary History of the 'Robust' Australopithecines. Adline de Gruyter, New York, pp. 285–292.

Clarke, R.J., 2008. Latest information on Sterkfontein's *Australopithecus* skeleton and a new look at *Australopithecus*. S. Afr. J. Sci. 104, 443–449.

Day, M.H., 1978. Functional interpretations of the morphology of postcranial remains of early African hominids. In: Jolly, C.J. (Ed.), African Hominidae of the Plio-Pleistocene. St. Martin's Press, New York, pp. 311–345.

Day, M.H., Thornton, C.M.B., 1986. The extremity bones of *Paranthropus robustus* from Kromdraai B, East Formation Member 3, Republic of South Africa: a reappraisal. Anthropos (Brno) 23, 91–99.

de Ruiter, D.J., 2004. Undescribed hominin fossils from the Transvaal Museum faunal collections. Ann. Transv. Mus. 41, 29–40.

Durrleman, S., Pennec, X., Trouvé, A., Ayache, N., Braga, J., 2012. Comparison of the endocranial ontogenies between chimpanzees and bonobos via temporal regression and spatiotemporal registration. J. Hum. Evol. 62, 74–88.

Durrleman, S., Pennec, X., Trouvé, A., Braga, J., Gerig, G., Ayache, N., 2013. Toward a comprehensive framework for the spatiotemporal statistical analysis of longitudinal shape data. Int. J. Comput. Vis. 103, 22–59.

Fourvel, J.B., 2016. Some preliminary interpretations of the oldest faunal assemblage from Kromdraai. In: Braga, J., Thackeray, J.F. (Eds.), Kromdraai, a Birthplace of Paranthropus in the Cradle of Humankind. Sun Media Metro, Johannesburg (in press).

Freedman, L., Brain, C.K., 1972. Fossil cercopithecoid remains from the Kromdraai australopithecine site. Ann. Transv. Mus. 28, 1–16.

Gibbon, R.J., Pickering, T.R., Sutton, M.B., Heaton, J.L., Kuman, K., Clarke, R.J., Brain, C.K., Granger, D.E., 2014. Cosmogenic nuclide burial dating of hominin-bearing Pleistocene cave deposits at Swartkrans, South Africa. Quat. Geochronol. 24, 10–15.

Granger, D.E., Gibbon, R.J., Kuman, K., Clarke, R.J., Bruxelles, L., Caffee, M.W., 2015. New cosmogenic burial ages for Sterkfontein Member 2 *Australopithecus* and Member 5 Oldowan. Nature 522, 85–88.

Grine, F.E., 1982. A new juvenile hominid (Mammalia; Primates) from Member 3, Kromdraai Formation, Transvaal, South Africa. Ann. Transv. Mus. 33, 165–239.

Grine, F.E., 1985. Australopithecine evolution: The deciduous dental evidence. In: Delson, E. (Ed.), Ancestors: The Hard Evidence. Alan R. Liss, New York, pp. 153–167.

Grine, F.E., 1988. New craniodental fossils of *Paranthropus* from the Swartkrans Formation and their significance in "robust" australopithecine evolution. In: Grine, F.E. (Ed.), Evolutionary History of the 'Robust' Australopithecines. Adline de Gruyter, New York, pp. 223–243.

Grine, F.E., Daegling, D.J., 1993. New mandible of *Paranthropus robustus* from Member 1, Swartkrans Formation, South Africa. J. Hum. Evol. 24, 319–333.

Grine, F.E., Smith, H.F., Heesy, C.P., Smith, E.J., 2009. Phenetic affinities of Plio-Pleistocene *Homo* fossils from South Africa: Molar cusp proportions. In: Grine, F.E., Fleagle, J.G., Leakey, R.E. (Eds.), The First Humans. Origin and Early Evolution of the genus *Homo*. Springer, New York, pp. 49–62.

Grine, F.E., Jacobs, R.L., Reed, K.E., Plavcan, J.M., 2012. The enigmatic molar from Gondolin, South Africa: implications for *Paranthropus* paleobiology. J. Hum. Evol. 63, 597–609.

Heaton, J.L., (PhD thesis) 2006. Taxonomy of the Sterkfontein Fossil Cercopithecinae: The Papionini of Members 2 and 4 (Gauteng, South Africa). Indiana University, Bloomington.

Hendey, Q.B., 1973. Carnivore remains from the Kromdraai australopithecine site (Mammalia: Carnivora). Ann. Transv. Mus. 28, 99–112.

Herries, A., Curnoe, D., Adams, J., 2009. A multi-disciplinary seriation of early *Homo* and *Paranthropus* bearing palaeocaves in southern Africa. Quatern. Int. 202, 14–28.

Howell, F.C., 1978. Hominidae. In: Maglio, V.J., Cooke, H.B.S. (Eds.), Evolution of African Mammals. Harvard University Press, Cambridge, pp. 154–248.

Kaszycka, K.A., 2002. Status of Kromdraai: Cranial, Mandibular and Dental Morphology, Systematic Relationships, and Significance of the Kromdraai Hominids. Éditions du Cahiers de Paléoanthropologie, CNRS, Paris.

Keyser, A.W., Menter, C.G., Moggi-Cecchi, J., Pickering, T.R., Berger, L.R., 2000. Drimolen: a new hominid-bearing site in Gauteng, South Africa. S. Afr. J. Sci. 96, 193–197.

Kimbel, W.H., 2007. The species and diversity of australopiths. In: Henke, W., Tattersall, I. (Eds.), Handbook of Paleoanthropology. Springer, Berlin, pp. 1539–1573.

Kirsanow, K.O., (PhD thesis) 2009. Animal physiology, biomineral diagenesis, and the isotopic reconstruction of palaeoenvironment. Harvard University, Cambridge.

Kohn, M.J., Cerling, T.E., 2002. Stable isotope compositions of biological apatite. Phosphates Geochem. Geobiol. Mat. Import. 48, 455–488.

Kuman, K., Field, A., Thackeray, J.F., 1997. Discovery of new artefacts at Kromdraai. S. Afr. J. Sci. 93, 187–193.

Lockwood, C.A., Menter, C.G., Moggi-Cecchi, J., Keyser, A.W., 2007. Extended male growth in a fossil hominin species. Science 318, 1443–1446.

McHenry, H.M., 1974. How large were the australopithecines? Am. J. Phys. Anthropol. 40, 329–340.

McKee, J.K., Thackeray, J.F., Berger, L.R., 1995. Faunal seriation of Southern African Pliocene and Pleistocene fossil deposits. Am. J. Phys. Anthropol. 96, 235–250.

Moggi-Cecchi, J., Menter, C.G., Boccone, S., Keyser, A.W., 2010. Early hominin dental remains from the Plio-Pleistocene site of Drimolen, South Africa. J. Hum. Evol. 58, 374–405.

O'Regan, H.J., Cohen, B.F., Steininger, C.M., 2013. Mustelid and viverrid remains from the Pleistocene site of Cooper's D, Gauteng, South Africa. Palaeontol. Afr. 48, 19–23.

Partridge, T.C., 1978. Re-appraisal of lithostratigraphy of Sterkfontein hominid site. Nature 275, 282–287.

Partridge, T.C., 1982. Some preliminary observations on the stratigraphy and sedimentology of the Kromdraai B hominid site. In: Coetzee, J.A., Van Zinderen Bakker, E.M. (Eds.), Palaeoecology of Africa and the Surrounding Islands, vol. 15. CRC Press, Taylor & Francis Group, New York, pp. 3–12.

Pickering, R., Kramers, J.D., Hancox, P.J., de Ruiter, D.J., Woodhed, J.D., 2011. Contemporary flowstone development links early hominin bearing cave deposits in South Africa. Earth Planet. Sci. Lett. 306, 23–32.

Pickford, M., 2013. The diversity, age, biogeographic and phylogenetic relationships of Plio-Pleistocene suids from Kromdraai, South Africa. Ann. Ditsong Nat. Mus. Nat. Hist. 3, 11–32.

Robinson, J.T., 1954. The genera and species of the Australopithecinae. Am. J. Phys. Anthropol. 12, 181–200.

Robinson, J.T., 1972. Early Hominid Posture and Locomotion. The University of Chicago Press, Chicago.

Skinner, M.M., Kivell, T.L., Potze, S., Hublin, J.-J., 2013. Microtomographic archive of fossil hominin specimens from Kromdraai B, South Africa. J. Hum. Evol. 64, 434–447.

Sponheimer, M., Lee-Thorp, J.A., de Ruiter, D., Codron, D., Codron, J., Baugh, A.T., Thackeray, J.F., 2005. Hominins, sedges, and termites: New carbon isotope data from the Sterkfontein Valley and Kruger National Park. J. Hum. Evol. 48, 301–312.

Susman, R.L., de Ruiter, D., Brain, C.K., 2001. Recently identified postcranial remains of *Paranthropus* and early *Homo* from Swartkrans cave, South Africa. J. Hum. Evol. 41, 607–629.

Suwa, G., 1988. Evolution of the 'robust' australopithecines in the Omo succession: Evidence from mandibular premolar morphology. In: Grine, F.E. (Ed.), Evolutionary History of the 'Robust' Australopithecines. Aldine de Gruyter, New York, pp. 199–222.

Thackeray, J.F., Braga, J., Sénégas, F., Gommery, D., Potze, S., Senut, B., 2005. Discovery of a humerus shaft from Kromdraai B: Part of the skeleton of the type specimen of *Paranthropus robustus* (Broom, 1938)? Ann. Transv. Mus. 42, 92–93.

Thackeray, J.F., de Ruiter, D.J., Berger, L.R., van der Merwe, N.J., 2001. Hominid fossils from Kromdraai: A revised list of specimens discovered since 1938. Ann. Transv. Mus. 38, 43–56.

Thackeray, J.F., Kirschvink, J.L., Raub, T.D., 2002. Palaeomagnetic analyses of calcified deposits from the Plio-Pleistocene hominid site of Kromdraai, South Africa. S. Afr. J. Sci. 98, 537–540.

Tobias, P.V., 1988. Numerous apparently synapomorphic features in *Australopithecus robustus*, *Australopithecus boisei* and *Homo habilis*: Support for the Skelton-McHenry-Drawhorn hypothesis. In: Grine, F.E. (Ed.), Evolutionary History of the 'Robust' Australopithecines. Adline de Gruyter, New York, pp. 293–308.

Vrba, E., 1975. Some evidence of chronology and palaeoecology of Sterkfontein, Swartkrans and Kromdraai from the fossil bovidae. Nature 254, 301–304.

Vrba, E., 1981. The Kromdraai australopithecine site revisited in 1980: Recent investigations and results. Ann. Transv. Mus. 33, 17–60.

Vrba, E., Panagos, D.C., 1982. New perspectives on taphonomy, palaeoecology and chronology of the Kromdraai apeman. In: Coetzee, J.A., Van Zinderen Bakker, E.M. (Eds.), Palaeoecology of Africa and the Surrounding Islands, vol. 15. CRC Press, Taylor & Francis Group, New York, pp. 13–26.

Werdelin, L., Dehghani, R., 2011. Carnivora. In: Harrison, T. (Ed.), Paleontology and Geology of Laetoli: Human Evolution in Context. Volume 2: Fossil Hominins and the Associated Fauna. Springer, pp. 189–232.

Werdelin, L., Peigné, S., 2010. Carnivora. In: Werdelin, L., Sanders, W.J. (Eds.), Cenozoic Mammals of Africa. University of California Press, pp. 603–657.

Wood, B., 1991. Koobi Fora Research Project: Hominid Cranial Remains. Clarendon Press.

Wood, B., Boyle, E.K., 2016. Hominin taxic diversity: fact or fantasy? Yearb. Phys. Anthropol. 159, S37–S78.