C. R. Palevol xxx (2016) xxx–xxx

Contents lists available at ScienceDirect

Comptes Rendus Palevol

www.sciencedirect.com

Human Palaeontology and Prehistory

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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ARTICLE INFO

Article history:
Received 27 December 2015
Accepted after revision 25 March 2016
Available online xxx

Keywords:
Kromdraai
Evolution
Hominins
Paranthropus robustus
Paranthropus boisei
Robust australopiths

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.

Mots clés :
Kromdraai
Évolution
Homininés
Paranthropus robustus
Paranthropus boisei
Australopithèques robustes

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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http://dx.doi.org/10.1016/j.crpv.2016.03.003

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'hominiés 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

Please cite this article in press as:Braga, J., et al., Stretching the time span of hominin evolution at Kromdraai (Gauteng, South Africa): Recent discoveries. C. R. Palevol (2016), http://dx.doi.org/10.1016/j.crpv.2016.03.003