Quaternary Science Reviews 190 (2018) 81–97

Contents lists available at ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

Taphonomic interpretations of a new Plio-Pleistocene hominin-bearing assemblage at Kromdraai (Gauteng, South Africa)

Jean-Baptiste Fourvel [a, *], John Francis Thackeray [b], James S. Brink [c, d], Hannah O'Regan [e], José Braga [b, f]

[a] UMR5608 CNRS TRACES, Université de Toulouse-Jean Jaurès, Toulouse, France
[b] Evolutionary Studies Institute and School of Geosciences, University of the Witwatersrand, PO WITS, Johannesburg, 2050, South Africa
[c] Florisbad Quaternary Research, National Museum, P.O. Box 266, Bloemfontein, 9300, South Africa
[d] Centre for Environmental Management, University of the Free State, Bloemfontein, South Africa
[e] Department of Archaeology, Humanities Building, University Park, University of Nottingham, Nottingham, NG7 2RD, United Kingdom
[f] Computer-assisted Palaeoanthropology Team, UMR 5288 CNRS-Université de Toulouse, Paul Sabatier, France

ARTICLE INFO

Article history:
Received 1 September 2017
Received in revised form
28 March 2018
Accepted 20 April 2018

Keywords:
Kromdraai
South Africa
Plio-Pleistocene
Taphonomy
Hominin-carnivore interactions
Palaeoecology

ABSTRACT

Within the past 80 years, the Kromdraai site in South Africa has provided a diverse Early Pleistocene fauna (notably bovids, carnivores, primates, large rodents, birds, proboscidea). Since 2014, the Kromdraai bone accumulation has been the focus of intensive fieldwork that demonstrated that the site is much larger than previously recognised. In the present taphonomic study of a new and large faunal sample including more than 2400 remains, stratigraphically controlled, we aim to test previous interpretations of the Kromdraai assemblage as representing a death trap or a carnivore lair. In particular, we aim to discuss the relationships between faunal communities in the context of carnivores, either predator-prey or predator-predator interactions. We investigate the relative abundance of anatomical elements and their fragmentation, the mortality profiles and tooth-mark frequency. We conclude that carnivores (particularly felids and hyenids) played a major role in the accumulation of fauna from Member 2, which (thus far) is the oldest depositional period investigated at Kromdraai. However, the high species diversity suggests that the secondary predators (scavengers) could have modified the bone deposit produced by the primary predators. The presence of hominin remains is also questioned. Our results shed new light on the palaeoecology of the Kromdraai Member 2 hominins, in terms of opportunistic predators and/or prey of large carnivores.

1. Introduction

Our understanding of the ecological and physical conditions under which animal remains and artefacts accumulated in early hominin-bearing sites, and the degree to which potential bias operated until the present time, are particularly important not only to reconstruct past behaviors, but also to accurately assess differences within and between fossil species. The main South African Plio-Pleistocene faunal assemblages described thus far have been taphonomically interpreted in different ways that led not only to distinct reconstructions of hominin behaviors (e.g., Brain, 1981; Vrba, 1975, 1981; Blumenschine et al., 1994, 2003; Pickering et al., 2004; Domínguez-Rodrigo, 2002) but also to uncertainties in terms of assessments of body size variation (and any potentially associated morphological variability) within some hominin taxa, particularly *Paranthropus* in South Africa. For instance, the predominance of small-sized hominins in most South African Plio-Pleistocene assemblages has often been interpreted as indicative of taphonomically skewed samples with a higher proportion of juveniles or small adults due to an increased predation level by carnivores (mainly felids), showing a "smaller prey adaptation" (Vrba, 1975; Grine et al., 2012) in a highly sexually dimorphic *P. robustus* species (Lockwood et al., 2007).

However, until now, no systematic comparisons have been made of taphonomic indicators (e.g., mortality profiles, bone fragmentation, tooth marks) within and between *Paranthropus*-bearing

* Corresponding author. UMR5608 CNRS TRACES, Université de Toulouse-Jean Jaurès, Toulouse, France.
E-mail addresses: jbfourvel@yahoo.com (J.-B. Fourvel), francis.thackeray@wits.ac.za (J.F. Thackeray), jbrink@nasmus.co.za (J.S. Brink), hannah.oregan@nottingham.ac.uk (H. O'Regan), jose.braga@univ-tlse3.fr (J. Braga).

https://doi.org/10.1016/j.quascirev.2018.04.018
0277-3791/

assemblages in South Afric. Such approaches have the potential to provide insights into potential differences in taphonomic bias. It is necessary to examine the sampling of females and small males within a single *P. robustus* species (Keyser et al., 2000; Moggi-Cecchi et al., 2010) with a high but yet unknown range of body size. It is also necessary to examine the sampling of distinct *Paranthropus* morphs (Broom, 1949; Howell, 1978; Grine, 1982, 1984, 1985, 1988, 1993; Jungers and Grine, 1986) with differences in body sizes, possibly representing temporally (Braga et al., 2013, 2017) or ecologically distinct assemblages.

Taphonomic analyses of faunal remains have suggested that Plio-Pleistocene hominins with a significant proportion of meat in their diet had either primary (e.g., Domínguez-Rodrigo, 2002) or secondary (e.g., Blumenschine et al., 1994, 2003) access to carcasses. In addition, relatively carnivores probably played a role in the accumulation of faunal remains of large animals (Brain, 1975; Vrba, 1975; Pickering et al., 2004). However, since *Paranthropus* in South Africa was probably a specialist relying more on plants than on than meat (see Balter et al., 2012) it was not responsible for the accumulation of some bone assemblages from various Sterkfontein Valley cave sites. Moreover, based on its presence in the main southern African *Paranthropus*-bearing deposits (Swartkrans Members 1 to 3; Sterkfontein Member 5; Kromdraai Member 3; Kromdraai Member 2, this study), it was suggested that leopards (*Panthera pardus*) was largely responsible for the accumulation of a majority of the size class 1 and 2 animal remains in these assemblages (e.g., Brain, 1981; De Ruiter and Berger, 2000).

Previous taphonomic interpretations of faunal assemblages from Kromdraai should be considered with great caution because they have been hampered by the absence of temporally or stratigraphically seriated assemblages from this site (Braga et al., 2017; Table 1). Indeed, as detailed by Braga et al. (2017), the Kromdraai B faunal sample recovered before 2014 represents a mixing of distinct assemblages, from different time periods and presumably, distinct accumulation processes. Therefore, new data from Kromdraai should be evaluated separately before any comparison is made with other *Paranthropus*-bearing assemblages from the same geographic area.

Since 2014, new fieldwork undertaken at Kromdraai demonstrates the much larger size of this site through the exposure of extensive and unexplored fossiliferous deposits (Braga et al., 2017) characterized by extremely rich bone accumulations and a high faunal diversity (Fourvel et al., 2016). New cranial, dental and postcranial hominin specimens, as well as more than 2400 other diagnostic faunal remains (related to both micro and macro-fauna) were discovered at Kromdraai, a site now regarded to represent "a single stratigraphic succession, with no distinction between KA, KB and KE localities" (Braga et al., 2017: 7). Member 2, as recognized by Bruxelles et al. (2016), corresponds to the "pink breccias" described by Brain (1958), as well as to Member 2 recognized by Partridge (1982).

The present study represents the first attempt to evaluate the taphonomic processes involved in the accumulation of a temporally homogenous faunal assemblage at Kromdraai. We aim to explore the view as to whether the Kromdraai Member 2 assemblage was associated with a hominin opportunistic scavenger or hunter, or with a natural death trap, or with a carnivore lair. We use a conceptual framework to discuss the relationships between the various animal communities, with either predator-prey or predator-predator interactions. From the combined study of several indicators (e.g., measures of tooth-mark frequency, relative abundance of some anatomical elements, fragmentation, mortality profiles) and some newly proposed taphonomic criteria, we assess the role of carnivores in the accumulations processes. We describe and use taphonomic criteria that relate to the behavior of various species of carnivores, as reflected by distinct damage to bone. For instance, we focus on differences between the damage and tooth marks associated with felids, and the high degree of fragmentation associated with hyenids (Fourvel et al., 2012, 2014). Our taphonomic approach, combined with a species-specific conceptual framework presented here, allows us to address the central question regarding the palaeoecological status of the Kromdraai Member 2 hominins as opportunistic predators and/or prey of large carnivores.

2. Materials and methods

During the 2014/2016 period, the Kromdraai Research Project field seasons (Braga and Thackeray, 2016; Braga et al., 2017) have produced more than 2400 faunal remains (including hominins) derived mainly from Member 2, an assemblage with a high species diversity that includes birds, mammals and reptiles (Fourvel et al., 2016; Fourvel, 2017a).Within that sample, 197 specimens relate to carnivores (including coprolites). 1127 specimens are attributed to ungulates, 284 to non-hominin primates, 415 to birds. 114 specimens are attributed to rodents and lagomorphs. 284 specimens could not be identified at a species level, and/or anatomically identified. The percentage of identification is very high (more than 80% considering the macromammalian remains). The entire bone sample has been considered for identification. Considering general morphology or size of the bone remains, some have been referred to a family and a size class (e.g., small-sized bovid) while the smallest pieces remain generally unidentified and have been classified within the undetermined remains. Several groups are excluded from this taphonomic analysis. Birds are not considered since they probably nested around the site (Fourvel et al., 2016).

Table 1
Synthesis of the various interpretations of archaeological/palaeontological deposits, Kromdraai localities.

Kromdraai A		
Reference	***Archaeological observation***	***Hypothesis/Interpretation***
Brain 1981	Tooth marks + Coprolithes	Carnivore lair
Vrba 1975	Bovid age / size class	Carnivore lair
Kromdraai B		
Reference	***Archaeological observation***	***Hypothesis/Interpretation***
Brain 1975	Extreme bone fragmentation	Hominin involvement ?
Brain 1981	Carnivore/Bovid ratio	Carnivore involvement
Vrba 1975	Bovid age / size class + Hominin	Hominin involvement ?
Kromdraai B East Member 3		
Reference	***Archaeological observation***	***Hypothesis/Interpretation***
Vrba 1981	Skeletal part + Bovid scarcity	Natural trap / feeding place
Vrba and Panagos 1982	Skeletal part + Bovid scarcity	Natural trap / feeding place