Final permit report
Excavation of the **Kromdraai, in the Cradle of Humankind World Heritage Site**

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PermitID: 2036

Validity of the permit: from 01/07/2015 to 01/07/2018

Report due before 1st of July 2018.

Attachments/Notes in pdf format: book and papers published (copies) during the validity of the permit

The Kromdraai site in October 2016

Report Contents

Published book: Braga and Thackeray (2016) &
Published papers resulting from the excavation at Kromdraai during the validity of the permit.

1. INTRODUCTION: THE KROMDRAAI RESEARCH PROJECT

The Plio-Pleistocene Kromdraai Heritage Site is located in the "Cradle of Humankind" (26°00'41"S, 27°44'60"E) in the Gauteng Province (Figure 1), approximately 2 km east of Sterkfontein Caves, on the southern side of the Blaauwbank stream. It is an unroofed dolomite cave partially shaped by the erosional surface and filled with fossil-bearing deposits (Figure 2). It has long been considered as two main and distinct localities – Kromdraai A (KA) and Kromdraai B (KB) – of relatively limited extent.

The KB locality has yielded the type specimen of *Paranthropus robustus* (Broom, 1938a,b, 1942, 1943), as well as 27 additional fossil hominin craniodental and postcranial specimens (with a minimum number of 17 individuals) discovered from 1938 to 2009 (Braga and Thackeray, 2003; Braga et al., 2013; Thackeray et al., 2001). 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 published thus far.
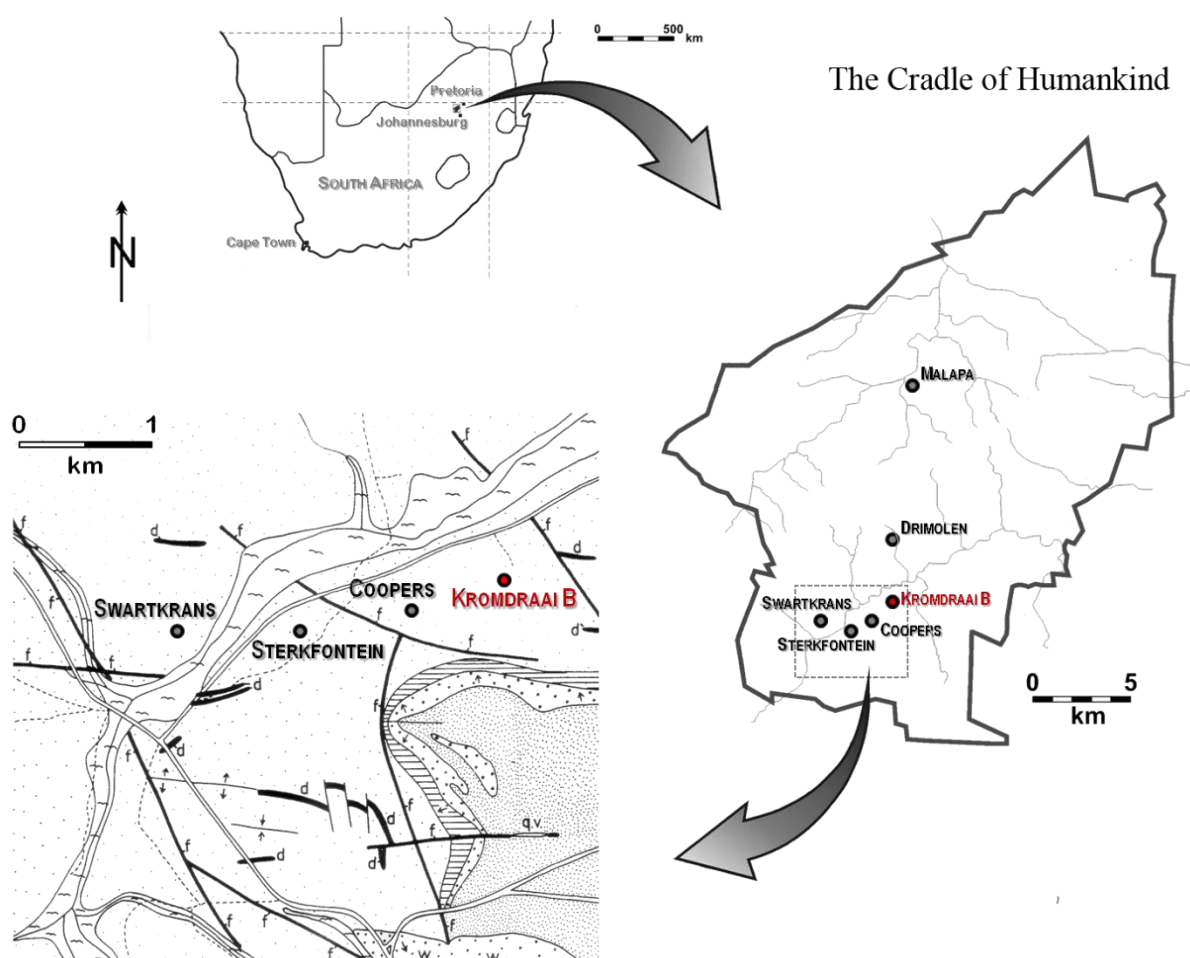

Figure 1. Location of the Plio-Pleistocene Kromdraai National Heritage Site (Gauteng, South Africa).

Figure 2. Aerial view of the Kromdraai site in March 2015 with locations of KA (left part of the view) and KB (ongoing excavation) localities.

1.1. Rationale

The KB *P. robustus* hominins have been considered by some as distinct from their congenerics from the nearby site of Swartkrans. Indeed, 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). Whereas the initial specific distinction has been supported by 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.

Moreover, 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). The morphological 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 are in 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 million years ago (Ma) eastern African *P. boisei* (Suwa, 1988). Therefore, 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."

The working hypothesis of the Kromdraai Research Project (KRP) is that the previously unrealized (before 2014) **and older hominin-bearing sediments at Kromdraai** (i.e., Members 1 and 2, see below) **illustrate an as yet undocumented temporal window of the earliest evolution of both *P. robustus* and early *Homo* lineages in South Africa**. Our ongoing field studies and further analyses help not only to test this hypothesis, but also 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.

After the discovery of additional fossil material at KB in 2002 (Thackeray et al., 2005), the Kromdraai Research Project (KRP) was established.

1.2. Management of the Kromdraai site and its excavation

The Kromdraai Research (KR) team has been working at the site at intervals from February 2016 to November 2017. Before and after this period, in 2014 and in 2018, the KR team has conducted 2 field seasons each year (2 months in total).

From February 2016 to November 2017, the KR Project (KRP) has employed five technicians at the Kromdraai site (R 13 196,67 and R. 14 120.41 respectively for months in 2016 and 2017). All of the five technicians are members of the nearby local communities: M. Moleko Monyama and M. Levy Modise (previously unemployed), M. Sipho Makhele, M. Shadrack Molefe and M Clopus Seshoene (partly employed at the nearby site of Sterkfontein). Moreover, M Andrew Phaswana was employed on a half-time basis in months from February 2016 to December 2016.

1.2.1. Protection of the site

The relationship between the KRP team and Mr Riaan Lotz, the landowner of the Kromdraai site is excellent (the KR team was invited to Mr Lotz's farm for a lovely braai in October 2017). At the request of Mr Lotz, in late June 2017, J Braga had a meeting at the site with him. Mr Lotz expressed his satisfaction for the work that has been done at the site since 2014. He also considered necessary and extremely important the urgent need to fence off the

excavations and the caves nearby. The distance around the excavations and the caves was measured and it was decided that the KRP will cover the costs of 550 metres of fences (R 39 900) on its own budget. Mr Lotz kindly agreed to supervise the project at no additional cost. Therefore, **in order to improve the protection of the Kromdraai site, a 550 m long fence was erected in August 2017 using steel poles and y-standards which were concreted into the ground. A gate was welded and secured to a long steel pole in order to prevent theft**.

1.2.2.   Equipment of the site

In 2016, the permit holders submitted an application to SAHRA for approval for the erection and installation of a container at the site. With the approval of the landowner, the KRP aimed to utilise a concrete slab laid down by a previous excavator, likely between 1950 and 1977. After approval from SAHRA, the KRP erected the container for site equipment, on disturbed and decalcified sediments. In terms of sieving, the KR team preferred wet sieving over dry sieving. Indeed, when we tested wet sieving in April 2014, we noted an increasing number of discoveries of very small fossils, including hominin and non-hominin deciduous teeth. Therefore, we opted for wet sieving even if access to water was not possible at the site. Until recently, the decalcified sediments were wet sieved at Swartkrans, but this has now ceased. In early 2018, we designed **a new system for wet sieving at Kromdraai itself**. **It consists of a removable sieving station (after each field season) in which we recycle water that runs in a recirculating system (with one pump and two small setting tanks)** (Figure 3). This system has no impact on the surrounding area.
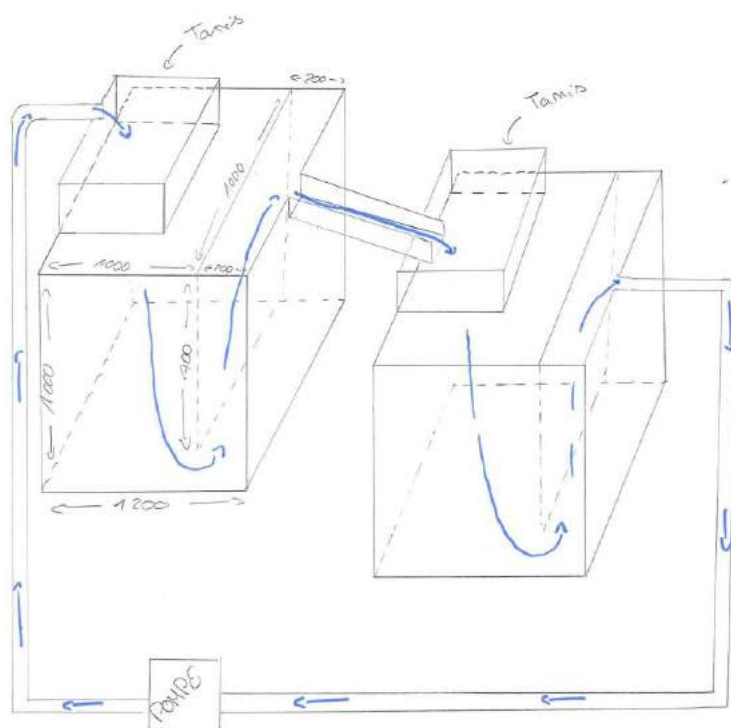

Figure 3. Sketch of the removable sieving station used at the Kromdraai site.

1.2.3. Security, site maintenance and erosion control measures

In 2016, the KR team organized First Aid training (at least one team member with a Level 3 certification) for M. Moleko Monyama. Moreover, when some parts of the excavation reached a depth of 2 metres, it has been decided to establish safety rules during the excavation. Visible clothing and hard hats are utilised by the team in the deep excavations. Whenever possible, we reduce decalcified walls to 1.5m or less. However, when this is not possible, especially on the southernmost part of the excavation, near the dolomitic wall, we also use safety ropes and harnesses. Moreover, during the off season, in order to implement erosion control and site protection measures to conserve it for future research, we use sand bags to cap the edges of the excavation, as well as tarp at the bottom of the depressions and on excavation profiles (Figure 4). We also use rock packing to shore up some edges of the excavation, to decrease the height of some excavated walls and to delineate paths within the excavation areas.

Figure 4. During the off season, the site is conserved for future research with the use of sand bags to cap the edges of the excavation, and tarp at the bottom of the depressions.

1.2.4. Site and excavation recording

At least once per week during each field season, the KR team regularly updates the site plan via land and aerial photogrammetry. A South African PhD student Ms Nonkululeko Mantombi Ngoloyi (currently supervised at the University of Toulouse (France) under the supervision of J Braga) is in charge of the three dimensional (3D) visualisation of geological and archaeological features from Kromdraai. It allows site preservation and also enables in-depth analyses. Digital photogrammetric methods have been applied as mapping tools in

archaeology to visualise archaeological objects, record their geometry, size, texture and other attributes in 3D. These provide 3D vector and point cloud data enabling the generation of 3D surface models. The 3D approach used by the KRP is therefore a reliable method for recording the Kromdraai site and visualizing it in post excavation analyses, hence increasing overall productivity and convenience (Figure 5).

As detailed in the book co-edited by Braga and Thackeray (2016), **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 combine this approach with 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 also 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 visualization of the better-preserved fossil specimens (particularly, the articulated bones) within their sedimentary units.

Figure 5. Hotspot Analysis showing zones of high fossil density in Member 2.

2. RESULTS

2.1. The fossil discoveries

Since 2014, we excavated the earliest known infilling of the Kromdraai cave system in a previously unexplored area where sediments from Members 1 and 2 have accumulated. **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.**

During field seasons from April 2014 to May 2018, we recovered 4804 identifiable fossils (including 43 hominin specimens), mainly from Members 1 and 2, the two oldest

sedimentary units from the Kromdraai site that were previously considered as nearly sterile (Braga and Thackeray 2016). These fossil discoveries confirm that the Kromdraai site is at least six times larger than previously thought (in 2014) and particularly rich in macrofauna (including fossil hominins).

All the newly discovered fossil specimens from Kromdraai are curated at the Evolutionary Studies Institute of the University of the Witwatersrand in Johannesburg, and are accessioned using the catalogue system with the 'KW' prefix (numbered from KW 6068 to KW 10891, in the present stage of the excavation). The former distinction between KA and KB is no longer justified because the KA locality contains sediments also represented at KB (Braga and Thackeray, 2016). We therefore use in all publications (as well as in the present report) the new prefix 'KW' that corresponds to a single stratigraphic succession, with no distinction between KA and KB localities.

At this stage, the KRP has been presented in one paper in which some preliminary results have been published (Braga et al. 2017). The book entitled *Kromdraai: A birthplace of* Paranthropus *in the Cradle of Humankind, a South African heritage site*, was co-edited by J Braga and F Thackeray and published by SUN PReSS (AFRICAN SUN MeDIA) in 2016 after peer review. Important results were presented in this book by an international team (French, South African, Italian and German) to report on the latest developments of research and fieldwork at Kromdraai at this time. An important outcome presented throughout the book is that the Kromdraai hominins and the associated fauna do not represent one single temporal period. Until recently, the chronological interpretations of the Kromdraai hominin-bearing deposits have been based essentially on the unsubstantiated combination of three sets of assemblages (successively collected by Robert Broom, Bob Brain and Elisabeth Vrba) into Partridge's Member 3.

Recently, the first taphonomic interpretations of the Kromdraai Member 2 assemblage (more than 2 400 remains) have been published by Fourvel et al. (2018). In this paper, we concluded that carnivores (particularly felids and hyenids) played a major role in the accumulation of fauna from Member 2. The high species diversity suggests that the secondary predators (scavengers) could have modified the bone deposit produced by the primary predators. We also questioned the presence of hominin remains in the Kromdraai Member 2 assemblage. 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.

While we write this document for SAHRA, two extensive papers reporting important results obtained from the newly discovered hominins from Kromdraai are being prepared under the supervision of J Braga. The first study will be submitted for publication at the end of 2018, the second one will follow and may be submitted at the end of 2019. In November 2017, an extremely important fossil hominin discovery was made in Kromdraai Member 1, the oldest sedimentary unit yet known from this site. This discovery will require considerable attention before it can be submitted for publication.

More details about our published results on the fossil discoveries at Kromdraai can be found in the book co-edited by Braga and Thackeray (2016).

1.2. The geological studies

The revised stratigraphy of Kromdraai has been published by Bruxelles et al. (2016). Since this first step of geological investigations at Kromdraai, the KRP has conducted important research which is briefly presented here, and which is to be submitted for publication before the end of 2018 by Dr B. Lans and Professor J.L. Schneider.

Samples of decalcified sediments have been collected since June 2016 at the excavation site for preliminary and exploratory sedimentological studies. These studies aimed mainly to define precisely the characteristics of the deposits of the excavated area in order to distinguish various facies in coarse deposits that are apparently homogeneous. In some areas, the sedimentary deposits are very complex, with big blocks of dolomite enclosed within a soft breccia that contains clasts (mainly dolomite) of various sizes with a fine-grained matrix. In other areas of the excavation, deposits are more clearly recognizable, with superimposed layers. Figure 6 displays a vertical view of the excavations with the location of the various deposits sampled for the preliminary and exploratory sedimentological studies. The samples have been investigated along vertical sections. These sections are referred herein as G1, G2, G3, G4, G6 and G8 (see Figure 6 for locations). For comparison, samples have been collected 2 m south of the calcified flowstone below a pebble-rich horizon (G5; Figure 6) and 3 m west of a stalagmite in a layer that has yielded hyena coprolites (G7; Figure 6).
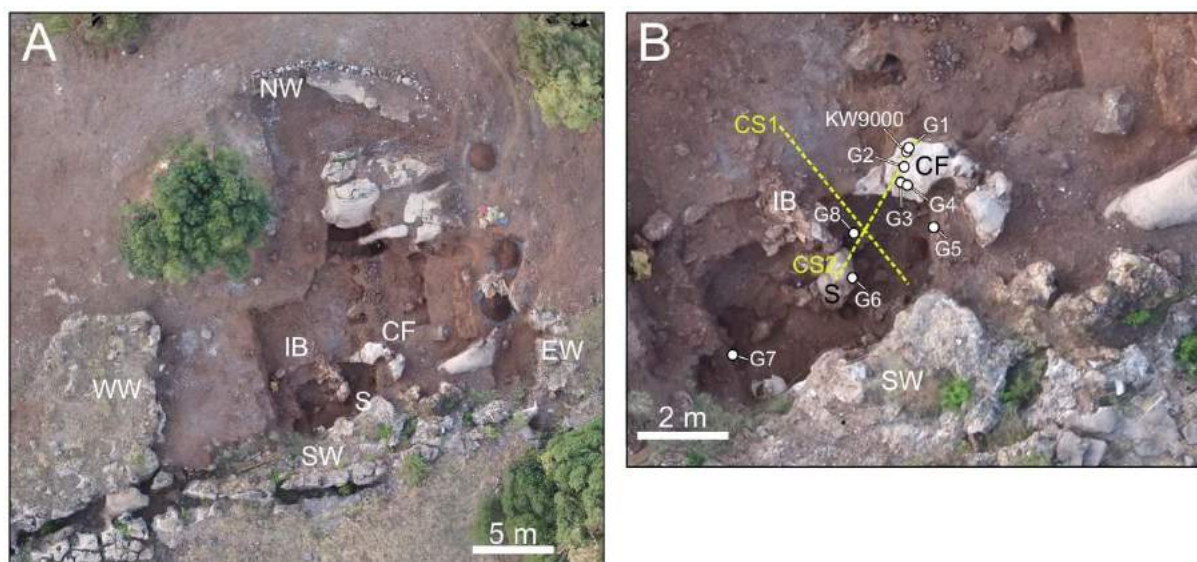

Figure 6. **A**. Aerial orthophotography of the Kromdraai excavation site (orthophotography computed by R. Hautefort and B. Lans; May 2016). **B**. Location of the sedimentary deposits investigated. The dashed yellow lines indicate the location of the cross sections (CS1 and CS2) presented in **Figures 7 and 8**. CF: calcified flowstone; EW, NW, SW, WW: eastern,

northern, southern, western walls of the excavation (former cave's edges); IB: indurated breccia; S: stalagmite.

The sediments have been analyzed using three independent methods: (1) magnetic susceptibility, (2) grain size analysis of the fine-grained matrix of the deposits and (3) morphometry of the lithic clasts. The magnetic susceptibility K is the "term" relating the inducing magnetic field (H) applied to a sample, and the induced, or resulting, magnetization (M) according to the following relation: M = K.H. The magnetic susceptibility (MS) is related to the magnetic (ferri-, ferro-, para- and diamagnetic) minerals content of the sediment. Grain-size distributions measurements have been limited to the fine-grained matrix of the deposits (fraction < 1250 μm) to allow comparisons between heterometric deposits. Samples have been collected along 6 vertical sections with 1 cm sampling intervals. Morphometric analyses of clasts present in the sediment have been performed to quantify their flatness, dissymmetry and roundness ratios. Data are available on request to J.-L. Schneider.
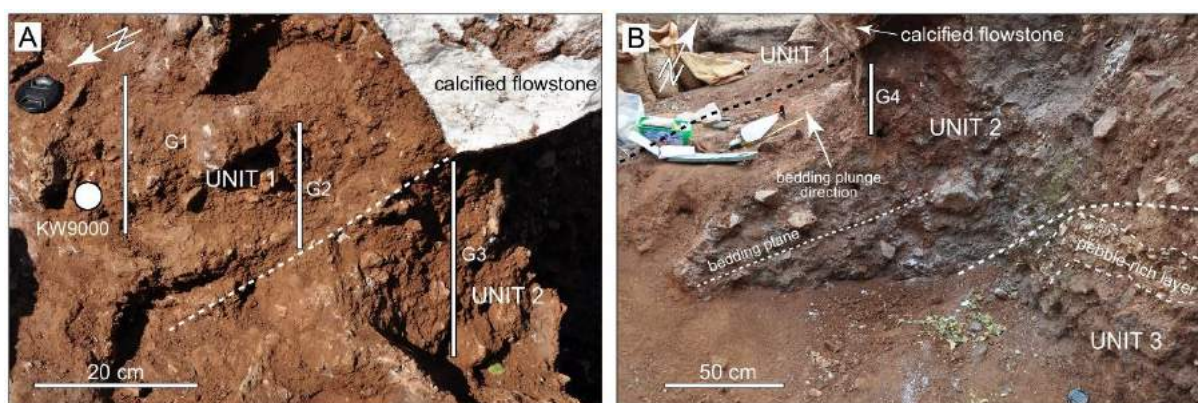

Figure 7. Outcrops at Kromdraai. **A**. The location of the G1, G2 and G3 profiles. Note the NNW dipping of the basal bedding plane. **B**. The sedimentary interval below the calcified flowstone (CF) and location of profile G4. Note the NNW feature of the basal bedding plane (dashed white line). Three sedimentary units can be distinguished. The pebble-rich layer belongs to sedimentary unit 3.
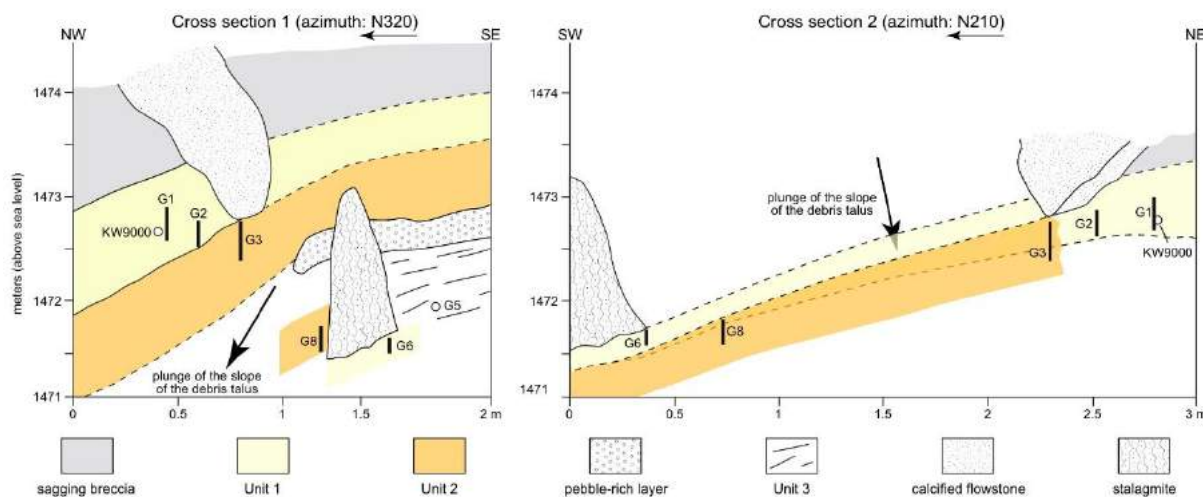
Figure 8. Stratigraphic cross sections of the deposits with location of some of the studied profiles. Location of the cross sections is indicated in Figure **6**.

In summary, the main conclusions reached thus far are:

✓ An important part of the Kromdraai Member 2 assemblage has accumulated over a debris talus that has formed well before the collapse of the cave's roof. The deposits display a macroscopic layering and discrete bedding identified with the grain size distribution data that dip towards the NNW. The identified talus slope serves to confirm that an entrance of the cave was open toward the SSE.

✓ SM data suggest that all the depositional intervals have similar magnetic characteristics that differ from other close depositional intervals of the cave's sedimentary infill.

✓ **Three superimposed sedimentary units have been identified within Member 2. It shows that the stratigraphy of Kromdraai is more complex than previously considered**. Grain size distribution data allow us to group deposits of profiles G1, G2 and G6 (sedimentary unit 1) and of profiles G3, G4 and G8 (sedimentary unit 2) in two separated sedimentary units. Geometric relationships between both units indicate that the sedimentary unit 1 was deposited over the sedimentary unit 2 and is consequently younger. The sedimentary unit 3 is the lowest. The stalagmite directly overlies the deposits (profile G6) of the sedimentary unit 1.

1.3. Future studies

26 bone tools have been found in Member 2. Dr. Lucinda Blackwell has examined some of them. Dr Francesco d'Errico has accepted an invitation to study these tools. It is recognized that a temporary export permit will be necessary for this study from SAHRA because it will require the use of a confocal microscope (located in Bordeaux, France).

The team is also hoping to export 6 small samples of flowstones for U-Pb dating by Professor Troy Rasbury, at the Department of Geosciences, Stony Brook University (USA). We will soon apply for an export permit.

3. TRAINING OF STUDENTS

Since 2013, the KRP has welcomed a large number of students for training during the excavations at Kromdraai. These Master and PhD students were not only from South Africa, but also from Europe and China.

This training has been supported within the framework of an important partnership called "A European and South African Partnership on Heritage and Past (AESOP)". The AESOP multidisciplinary and intersectorial Erasmus Mundus consortium is co-managed by the University Paul Sabatier-Toulouse 3 (France) and the University of the Western Cape (South Africa). The coordinator is J Braga. It is composed of 11 European and 9 South African university partners, as well as four additional associate members. AESOP involves eight thematic fields and encourages the collaboration between different sectors. It aims to contribute to the development of educational/academic networking and new skilled human resources in South Africa through academic training and through the use of cultural and natural heritage as vectors for sustainable partnership. The AESOP Steering Committee organizes and supports 250 fellowships (6 or 10 months for Masters, 6, 18 or 36 months for PhDs, 10 months for post-doctorate and 1 month for staff) by encouraging double-degree programmes between European and South African members (in order to prevent "brain-drain"). Through staff mobilities, AESOP also explores opportunities to draft a future European and South African training and research unit for the study, promoting the awareness of European and South African heritage.

4. PROPOSED FUTURE MANAGEMENT ACTIONS FOR THE KROMDRAAI NATIONAL HERITAGE SITE

With the permission of the landowner and SAHRA, we hope to erect a small laboratory at the site. This could be used during visits to the site to show certain replicas (casts) of fossils to the public. Moreover, we could use this laboratory for some preliminary manual preparation and restoration of fossils for the Kromdraai material discovered during the excavation.

We also plan to recruit one permanent site manager that will be a member of one of the nearby local communities.

5. ACKNOWLEDGEMENTS

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J. Braga and J.F. Thackeray

In 1999, the United Nations Educational, Scientific and Cultural Organization (UNESCO) officially listed the first three South African World Heritage sites – a truly historic national moment.

The 'Cradle of Humankind', an area in the Gauteng Province considered to represent an invaluable record of the early stages in the evolution of humanity, was listed along with Robben Island and the Greater St Lucia Wetland Park. During the same year, the South African Heritage Resources Authority established the National Heritage Resources Act No. 25 to introduce an integrated and interactive system for the identification, assessment and management of the South African heritage resources; to establish the South African Heritage Resources Agency (SARHA), and together with its council to coordinate and promote the management of heritage resources at national level.

According to the South African Government Brief 14 of 2012, the South African heritage is "characterised by peoples' identification with particular spaces and places shaped by historical events and collective memory" (www.gcis.gov.za). The South African national and provincial authorities have designated the South African heritage as one of the major domains to develop new strategies in order to balance the need for business development and the creation of jobs, with the need to maximise the benefits for the education of as many people as possible. Arising from these opportunities, the South African heritage, maintained in the present and restored for the benefit of future generations, represents an increasingly important educational/ economic resource that generates substantial public interest from local and international visitors.

It is also through international scientific relationships that South Africa shares the technological skills and expertise needed to achieve greater understanding of the value that its heritage has for the world. The multidisciplinary and intersectorial 'Erasmus Mundus' programmes of the European Union are designed to contribute to the development of new professional profiles to face rapid changes in practices and to use South African national symbols, cultural and natural heritage as vectors for sustainable partnership. Within the 'Erasmus Mundus' framework, European and South African joint efforts through collaborations between universities, public and private companies, management authorities of tourism lead to innovative ideas in the knowledge triangle of education-research industry.

This book is dedicated to one of the most well-known heritage sites of the 'Cradle of Humankind' – Kromdraai – the birthplace of one of our distant relatives called *Paranthropus* (www.kromdraai-origins.org). In addition to the ongoing academic research in this area, the Kromdraai Research Project is associated with two 'Erasmus Mundus' collaborative networks, AESOP and AESOP+ ('A European and South African Partnership on Heritage and Past'), and composed of 21 South African and European universities, as well as six associated partners. They organise mobilities for masters, PhD, post-doctoral fellows and academic staff in several fields including sciences and humanities in order to meet employment needs and to facilitate intercultural exchanges and mutual enrichment of European and South African societies. These actions promote the South African natural and cultural heritage and enhance the expertise and capability of teachers, students and researchers to assimilate new technical developments.

The scientific results presented in this book would not have been obtained without the early support of the South African National Research Foundation (NRF), the Department of Science and Technology (DST) of South Africa, the Centre National de la Recherche Scientifique (CNRS, France), the French Ministry of Foreign Affairs, the French Embassy in Pretoria, the Institut des Déserts et des Steppes in Paris (France) and the Andrew Mellon Foundation.

It is a pleasure to present this volume and we hope that it shows how the study of our common past can bring people together.

When Francis Thackeray brought me a copy of the text of this remarkable book, I was delighted to see the great detail in which he and his French colleagues were undertaking their research at the Kromdraai fossil site in the Sterkfontein valley. It was here, in 1938 that a 15-year-old schoolboy, Gert Terblanche found the first fossil of a robust ape-man weathering out of a block of cave-breccia on the dolomite hillside of Kromdraai, about 2 km east of the Sterkfontein Cave where Dr. Robert Broom had described a fossil of the first adult ape-man, *Australopithecus africanus* in 1936. Gert Terblanche used to work as a guide for visitors to the Sterkfontein Cave on Sundays and he showed his Kromdraai fossil to the site manager who immediately bought it from him and passed it on to Dr. Broom who then visited the Kromdraai site with Gert and obtained more pieces of this beautifully preserved skull.

For over fifty years I have been involved in excavations at the Swartkrans Cave. Close to Sterkfontein, this cave-filling has proved to be a rich source of fossils of the robust ape-men with remains of over 80 individuals coming from there. Here, we also have evidence of the co-existence of the robust ape-men with early humans who continued to evolve after the extinction of the robust ape-men. The Swartkrans cave showed me that the hominids – our ancestors and the robust ape-men – were constantly being preyed upon by predators, by leopards and sabre-toothed cats – who consumed their prey at the cave entrance, the scraps of which found their way into the fossilisation site below. My work at the Swartkrans Cave also showed us just how complicated the stratigraphy of a dolomite cave filling is likely to be. When I started work at Swartkrans I had assumed that the oldest part of a cave filling would be at the bottom with the youngest parts at the top. This proved to be wrong, with parts of the oldest calcified filling adhering to the north wall undercut by much younger infillings lying beneath them. This was because of successive cycles of erosion and deposition in the cave with some parts being carried away and some parts remaining intact. It now seems likely that these events were linked to the worldwide cycles of glacial and interglacial climatic change that have characterised the last few million years.

The ongoing investigations at Kromdraai described in this book will reveal the complexity of the fossil-bearing sediments there, and I am delighted and impressed at the quality of the work. Congratulations to the authors and may they stimulate many up-coming students to do the same. Good luck!

Evolutionary, chrono-cultural and palaeoenvironmental backgrounds to the Kromdraai site: A regional perspective

José Braga, Jean-Baptiste Fourvel, Benjamin Lans, Laurent Bruxelles and John Francis Thackeray

INTRODUCTION

The Plio-Pleistocene site of Kromdraai (26°00′41″S, 27°44′60″E) in Gauteng Province, South Africa is situated approximately 2 km east of Sterkfontein Caves, on the southern side of the Blaauwbank stream (Figure 1.1). It is an unroofed dolomite cave partially shaped by the erosional surface and filled with fossil-bearing deposits and has long been considered as two main and distinct localities – Kromdraai A (KA) and Kromdraai B (KB) – of relatively limited extent. The Kromdraai C (KC) locality is less important as no fossils of artefacts have been previously reported from this area (Figure 1.2).

Before 2014, the older Kromdraai B locality yielded the type specimen of *Paranthropus robustus* (TM 1517), the only partial skeleton of this species known thus far (Broom 1938a, 1938b, 1942, 1943, as well as other fossil hominin individuals (Thackeray *et al.* 2001; Braga *et al.* 2013) (see Chapter 4) and is referred to as the 'hominin site'. The KB sedimentary deposits fill an east-west deep fissure of about 46 m formed by the dissolution of limestone by water and occur on either side of a rib of 'dolomitic bridge' located near the western end of the KB site (Figure 1.2). Vrba (1981) and Partridge (1982) have named these two fillings, 'KB East' and 'KB West' formations.

The younger KA locality, situated about 30 m to the west of KB (Figure 1.2), has not yielded hominin fossils yet and is therefore called the 'faunal site'. Only the easternmost part of KB yielded a single Oldowan stone tool (a polyhedral core), whereas circa 100 artefacts associated with the early Acheulean or developed Oldowan were found at KA (Kuman *et al.* 1997). The presence of cultural material at KA also 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). Interestingly enough, KB has been considered as 'nearly contemporaneous' with the Member 5 (a 'member' is a stratigraphic layer) deposits at Sterkfontein (McKee *et al.* 1995:244). These deposits mark the appearance of the earliest lower Oldowan tools in South Africa, currently dated at 2.18 +/- 0.21 millions of years ago (Ma) (Granger *et al.* 2015).

As discussed in this chapter, the current KB faunal and archaeological samples are primarily derived from at least three distinct depositional phases securely tied in a stratigraphic context and often incorrectly mixed into one single sample in several studies. Previous reports published by scientists involved in excavations at Kromdraai clearly indicated that the site was "far from containing a temporally homogeneous breccia" (Vrba 1981:19; Vrba & Panagos 1982:21) because, first, its faunal assemblage was not recovered from a single stratigraphic unit, and second, most of its sample (discovered before the 1970s) is of unknown stratigraphic origin (Brain 1981) (see details below and in Chapter 4). Therefore, even though some
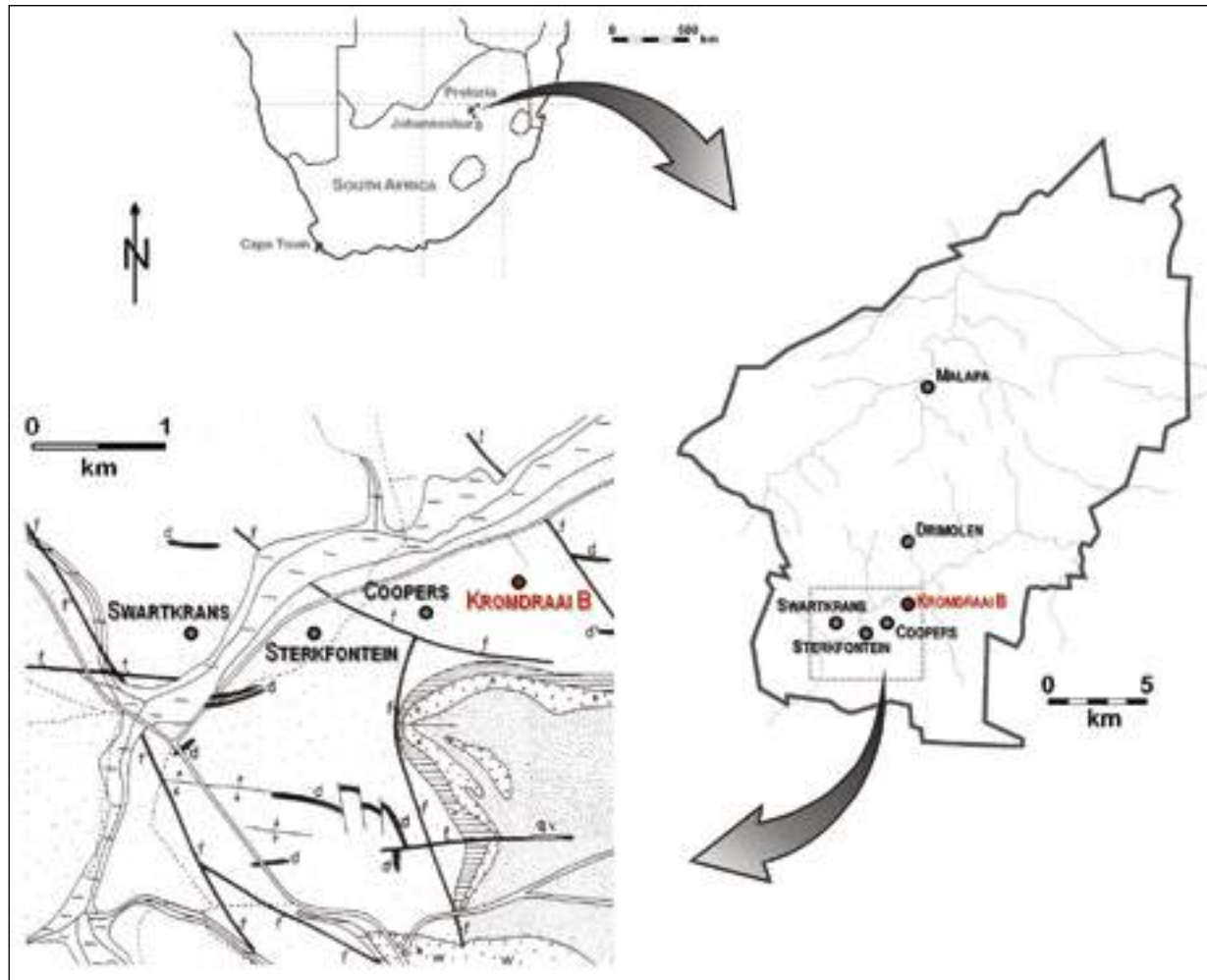
Figure 1.1 *Map showing the location of the site of Kromdraai (Gauteng, South Africa)*

KB deposits may correspond to the same period represented in Sterkfontein Member 5, other cultural and faunal evidence from KB may well illustrate significantly younger or older temporal windows of human evolution. From the current lithostratigraphic framework first established by Vrba (1981) and Partridge (1982), we cannot determine the temporal depth, the nature and exact number of periods recorded in the KB fossil-bearing sediments (see Chapter 3). It is not clear whether some of the KB hominins found in *ex situ* breccia blocks or in decalcified breccias (see Chapter 4) are distributed across distinct periods and which ecological conditions prevailed at these times. Moreover, we do not know whether these periods correspond to temporal events also represented in other parts of Africa, or if they represent unique Plio-Pleistocene snapshots in southern Africa.

No consensus has been reached on the chronology and palaeoenvironments of the Kromdraai site or the taxonomy and phylogenetic status of the KB fossil hominins (Grine 1982, 1988; Vrba & Panagos 1982; Tobias 1988; Thackeray *et al.* 2001; Kaszycka 2002; Braga & Thackeray 2003; Lacruz 2007; Braga *et al.* 2013, 2016). Until recent excavations started in 2014, the large majority of the KB fossils have been found from *ex situ* breccia blocks (Broom 1938a, 1938b, 1942, 1943), or from decalcified breccias with no ascertained stratigraphic context (Brain 1981). Moreover, as discussed in Braga *et al.* (2013, 2016), despite several previous published reports (e.g., Vrba 1981:19; Vrba & Panagos 1982:21), it is disappointing that most studies treat the Kromdraai fossils (including its hominin sample) as a temporally homogeneous sample (e.g., Kaszycka 2002; Herries *et al.* 2009; Skinner *et al.* 2013;). The age estimate for the KB fossil assemblage is set via biochronological dating (Vrba 1981; Vrba & Panagos 1982; McKee

et al. 1995) and paleomagnetism (Thackeray *et al.* 2002) to postdate the boundary between the Pliocene and Pleistocene (set at 2.6 Ma), and is generally taken as close to 2.0 Ma. However, we cannot consider the current biochronological estimates from the KB temporally heterogeneous fossil sample as primary in taxonomic or phylogenetic interpretations of the KB fauna (including hominins) unless a firm morphological basis is first demonstrated.

Our view of the phylogenetic status of the KB hominins has been greatly influenced by the difficulties in obtaining 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 *Australopithecus africanus* hypodigm (from Makapansgat, Sterkfontein, Taung and Gladysvale). Moreover, the taxonomic interpretations of the KB hominins have been obscured by the lack of studies on the morphological variability within and between *A. africanus* and *P. robustus*. More Kromdraai fossil hominins are needed to obtain a better evolutionary scenario and paleobiological portrayal of the southern African 'robust' hominins, often referred to as *Paranthropus* or paranthropines (see Chapter 4 for a definition). As briefly described here, it has already been demonstrated that the KB fossil hominins display a unique total morphological pattern (see more details in Chapter 4). In addition to new fossil discoveries, the use of advanced imaging techniques, computer-aided morphometry and formal statistical methods will help to clarify the distinctive features of the southern African paranthropines, among them the Kromdraai hominins, and their phylogenetic relationships with their eastern African equivalent (*P. boisei*) as well as with *Australopithecus* and early *Homo* from both East and South Africa.
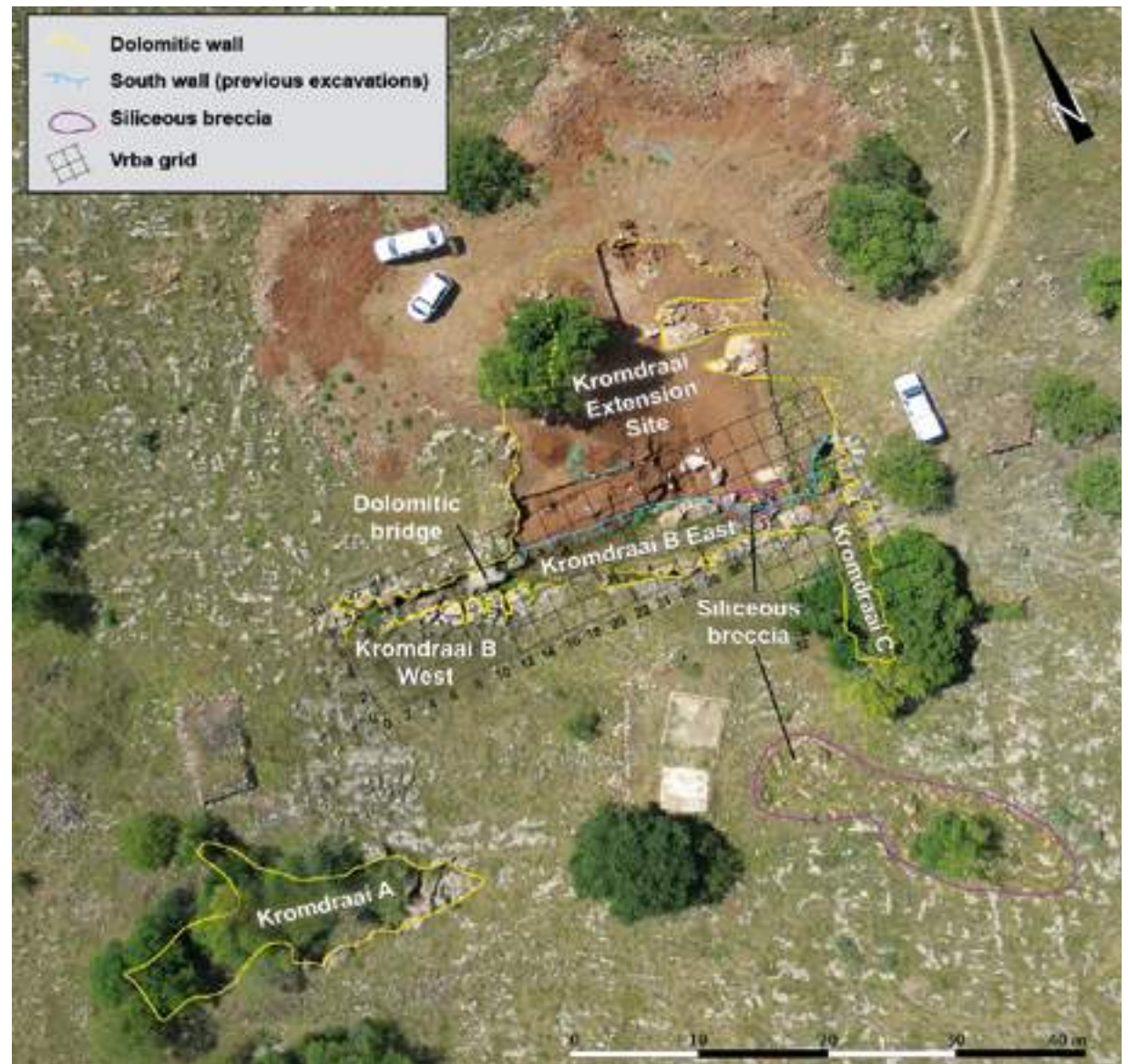

Figure 1.2   *Aerial view of the Kromdraai site with locations of its main features*

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 – *P. 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. 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.

Since only one KB hominin specimen has been allocated to the genus *Homo* (Braga & Thackeray 2003; but see Grine *et al.* 2009), more evidence for the occurrence of early *Homo* at Kromdraai is needed, not only to unambiguously confirm the co-existence of two species of hominins – *P. robustus* and early *Homo* – in this site during the Plio-Pleistocene (in addition to the two nearby sites of Swartkrans and Drimolen), but also to portray most of the as yet unknown juvenile and adult skeletal features of the earliest humans in South Africa during this period.

Indeed, even though the recently reported large fossil hominin assemblage from the Dinaledi Chamber of the Rising Star cave system (Gauteng, South Africa) have been attributed to a new and primitive species of the genus *Homo* – *H. naledi* (Berger *et al.* 2015) – in the absence of both biochronological evidence and absolute dates, it remains to be established whether these important specimens portray the ealiest humans in South Africa. Moreover, the most fundamental differential diagnostic features for early *Homo* are still difficult to distinguish because they often appear as not reliable to separate our own genus from the australopiths (e.g., Berger *et al.* 2010; Wood & Baker 2011). Therfore, further hominin discoveries at KB are needed to establish the relative abundance of *P. robustus* and early *Homo* across the distinct periods represented in this site as well as to understand their associated environmental and evolutionary contexts.

AIMS OF THIS VOLUME

This volume presents detailed results obtained during the fieldwork undertaken at Kromdraai since 2002 by the Kromdraai Research Project (KRP) as well as laboratory work on newly and previously discovered KB fossils. As first reported in Braga *et al.* (2016), all these studies have (i) demonstrated the much larger size of KB than previously thought, through the exposure of extensive and until then unexplored fossiliferous deposits situated in an area called 'Kromdraai extension' locality to the north of the previous KB excavations (see below and Figure 1.2), but close to the exploratory fieldwork undertaken by Brain in 1955 and 1956 (see Chapter 2); (ii) opened up the excavation of the soft breccias of the Kromdraai extension (KE) locality (Figure 1.2) and recovered as yet (until February 2016) more than 2 200 identifiable macrovertebrate fossils (including 22 hominin

specimens) precisely tied in the stratigraphy; (iii) revised the previous stratigraphic interpretation of Kromdraai into a minimum number of five breccia stratigraphic units (i.e. members; see below) (Partridge 1982) and established relative chronological relationships between KA and KB (see Chapter 3); and (iv) initiated a revised taxonomic and phylogenetic interpretation of the KB fossil hominins by taking into account the context of their discovery (i.e. stratigraphic provenience or not) within the framework of a detailed comparison with the Swartkrans and Sterkfontein hominins using computer-assisted 3D imaging methods and recent advances in 3D morphometry (see Chapter 4).

AIMS OF THIS CHAPTER

To frame what comes later in this volume, the aims of the present chapter are 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. We comment our current knowledge about Kromdraai within an integrated regional context. In particular, we discuss how recent data gathered by the KRP will help to understand how environmental and geological changes over time may have influenced the evolutionary processes and taphonomic agents observed at Kromdraai, and the variation seen among its fossil-bearing deposits, faunal and hominin samples.

The construction of the Kromdraai B fossil and archaeological assemblages

The KB fossil assemblage found before 2014 comprises 6 067 specimens, all stored at the Ditsong National Museum of Natural History (formerly Transvaal Museum) in Pretoria and accessioned into the catalogue system with the KB prefix. Among the

last published KB fossils is a partial temporal bone of a juvenile hominin (KB 6067; Braga *et al.* 2013). These KB fossils and cultural artefacts were recovered during five distinct periods: 1938–44 (Broom 1938a, 1938b, 1942, 1943; Broom & Schepers 1946), 1955–56 (Brain 1958, 1975, 1978, 1981), 1977–80 (Vrba 1981; Grine 1982, 1988; Partridge 1982; Vrba & Panagos 1982), 1993–2002 (Berger *et al.* 1994) and 2002 onwards (Thackeray *et al.* 2001, 2002, 2003, 2005; Braga *et al.* 2003, 2013, 2016).

Broom's excavations (1938–44)

The exact circumstances of the discovery of the holotype of *Paranthropus 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, 1938b; 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 (TM1517c), no mention was unambiguously made as to whether these specimens have been found *in situ* or in a loose block (Broom 1938a). In this paper, Broom also reported 'faunas associated with the apes', including '*Parapapio coronatus'* (Broom & Robinson 1950; reviewed by Freedman 1957) now recognised as belonging to *Papio angusticeps* (two mandibular fragments – KB 94 and 104 – formerly numbered KA 196 and 197), and *Cercopithecoides williamsi* (a calvaria – KB 122 – previously numbered KA 195) (Freedman & Brain 1972). A few weeks after the first publication, Broom (1938b) reported the discovery of the distal end of the right humerus (TM 1517g), part of the proximal end of the right ulna (TM 1517e), and a manual distal phalanx from rays II to V (Day 1978; TM 1517o, possibly of a baboon (see Skinner *et al.* 2013), which he assigned to the

same individual as TM 1517a, b and c. These three additional specimens were reported to come from "the same matrix as the skull and within a few feet of the spot where it was found" (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 that are now identified as cercopithecoid specimens (TM 1517h, i, j, l, m, n; see for more details Broom & Schepers 1946; Day 1978; Day & Thornton 1986; Skinner *et al.* 2013). A year later, Broom reported the discovery of "the most important part of the right talus" (TM1517d) from the same "block of matrix" from which other numbered TM 1517 fossils came (1943:689). Further work or visits at KB produced more remains attributed to *P. robustus*, including the mandible of a child (TM 1536 in 1941) found "within four feet of the place where the type skull lay" (Broom & Schepers 1946:109–110), and according to Brain, in "a small pocket of breccia within two yards of the spot where the original block had been found" (1958:90). Finally, the crown (with no developed roots) of a left upper third molar (M³) assigned to the TM 1517 individual (TM 1603, in 1944) was found on the "tailings from the Kromdraai skull site" (Broom & Schepers 1946:98–99).

Brain's excavations (1955–56)

The large majority of the KB fossil sample known thus far was found during the 1955–56 fieldwork leaded by Brain (Brain 1958, 1975, 1978, 1981; Freedman & Brain 1972; Hendey 1973). Despite previous fossil finds in the same area, almost nothing about the geology of KB was available in the literature 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 Vrba's grid system) (Figure 1.2) to a maximum depth of about 5 m. Brain 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" (1975:226).

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 emphasised by Brain (1958) himself, contrary to several subsequent and unsubstantiated statements (including in the recent literature), the horizontal delineation of decalcified deposits had "little meaning". As emphasised (Brain 1981; Vrba 1981; Vrba & Panagos 1982;), Brain's KB fossil sample (including five hominin specimens discovered *in situ*; see Table 4.1) could not be tied precisely to any of the five successive breccia members of the KB East and West Formations later defined in detail by Partridge (1982) (see below).

Importantly, Brain's excavations led to the first discoveries of cultural material at KB. This material consisted mainly of several blocks and pebbles of quartzite, and at least one unquestionable flake of chert, that were all interpreted as possibly "artificially introduced" (Brain 1958).

Vrba's excavations (1977–80)

During the 1977–80 fieldwork leaded by Vrba, a grid system (shown in Figure 1.2) was established for the first time at KB (Vrba 1981; Grine 1982; Vrba & Panagos 1982). The KB East Formation was interpreted to represent a single debris cone, which

initial geometry was assessed by extrapolating the inclinations of the interfaces (either observed on the surface or probed by drilling of boreholes) 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 (Vrba 1981:22; Partridge 1982).

The vast majority of the macrovertebrate sample recovered during Vrba's excavation (1977–80) was found in Member 3 (corresponding to Members 3 and 4 as defined in Chapter 3), on the central part of the KB East Formation, between E–W coordinates 22 and 30 m (Figure 1.2), 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 microfaunal remains, and a couple of isolated broken baboon teeth' were discovered from Member 1, with Member 2 breccias appearing sterile (Vrba 1981).

Thackeray's excavations (1993–2002)

In September 1993, Thackeray started new excavations at KB with a 100 m² eastern extension of Vrba's grid system (Berger *et al.* 1994). This fieldwork was focused on an area 30–40 m north and 0–10 m east of Vrba's datum point (see Figure 2 in Kuman *et al.* 1997). Fossil bones discoveries (beginning with the number KB 5500) were reported, including one fossil hominin (KB 5503). Notably, this excavation led to the discovery of the only provenanced Oldowan polyhedral core from KB (KB 5501; from the decalcified breccia) 1.5 m below datum (Kuman *et al.* 1997). A revised list of the KB hominins (Thackeray *et al.* 2001)

and palaeomagnetic analyses of a capping flowstone (Thackeray *et al.* 2002) were also published. This later flowstone revealed an interval of reversed polarity interpreted as older than the normal Olduvai Event (between 1.95 and 1.78 Ma).

The Kromdraai Research Project (since 2002)

The Kromdraai Research Project was established after the discovery of additional fossil material at KB in 2002 (Thackeray *et al.* 2005) and before devising new systematic excavations at this site.

The KRP aimed to (i) define more precisely the extension of the Kromdraai cave deposits; (ii) revise the site's stratigraphy accordingly; (iii) identify flowstones securely placed in this stratigraphy in order to obtain reliable radiometric dates and palaeoclimatic records; and (iv) obtain and compare distinct fossil samples precisely tied to each of the stratigraphic units, in order to interpret them in terms of biochronology, palaeoenvironments and evolutionary history.

We therefore started a careful cleaning of the KB solid breccias with acetic acid (10%) and a high-pressure cleaner in order to expose the texture of the solid breccias and to be able the analyse their geometry. From this step and from the analysis of aerial photographs, we reached the main conclusion that the Kromdraai site had a larger extension toward the north than previously thought. We inferred that this extension, shown at Figure 1.2, represented the decalcified part of the earliest known infilling of a single Kromdraai cave system (which has lost its roof through erosion) accessible from the surface, with around 600 m² of exposed fossiliferous deposits.

We conducted test pits and sections in this purported extension of the Kromdraai site ('Kromdraai extension' locality, or KE, Figure 1.2). This fieldwork revealed that approximately the first top metre of the deposits (below the natural surface of the soil) was affected by pedogenesis, which led to the formation of a ferruginous soil characterised by iron oxidation. This pedogenic process was associated with a severe decalcification in which only pieces of weathered cherts and gravels remained in place. The dolomite, calcite and fossil bones were totally dissolved. Moreover, the top 20 to 30 cm of this ferruginous soil was eroded by 'residualisation' – a process whereby the thinner sediments were washed away by erosion. Only the heavier blocks of more or less weathered cherts and gravels were left in place by erosion and protected the bottom part of the reddish ferruginous soil. This 'residualised' top layer can be regarded as colluviums. Therefore, no paleontological remains could be found in the first top metre of 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 metre of the soil on a surface of approximately 300 m². The main geological features (dolomitic walls, flowstones, …) were recorded by creating a topographical database generated by a total station theodolite (TST) instead of a grid system. We then obtained a continually updated computer-assisted map of Kromdraai using our geographic information system (GIS) to process the data collected daily during the excavation (Figure 1.3). Not even a single bone was found during this phase of the excavation of the top 'residualised' layer of KE. Moreover, when the sediments became darker, less than one unidentifiable bone fragment per m² was found between a depth of approximately 1.0 and 1.2 m.

As also indicated by some pieces of flowstones and weathered dolomitic blocs found associated with these fragments, we reached the levels not affected by the pedogenetic process at a depth of 1.2 m.

We also started cleaning the bottom and the sections of Brain's excavation conducted along the wall that he interpreted as the northern side of KB. We started finding numerous macrovertebrate fossils (including two fossil hominin specimens), not only at the level of Brain's exploratory excavation conducted in the 1950s, but also to the north (KE) at a minimal depth of 1.2 m below the datum point where both soft and solid breccias were preserved.

Since April 2014, over a period of almost two years and seven field seasons, we recovered more than 2 200 identifiable fossils in the KE site, all precisely tied in the revised stratigraphy of Kromdraai (Braga *et al*. 2016). These new fossil discoveries at KE confirm that the Kromdraai site is at least six times larger than previously thought and particularly rich in macrofauna (including fossil hominins). All these newly discovered fossils 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). Indeed, the former distinction between KA and KB (and the use of these prefixes) is now not justified because the KA locality contains sediments also represented at KB (as described in Chapter 3). We therefore use the new prefix KW that corresponds to a single stratigraphic succession, with no distinction between KA, KB and KE localities. The KE locality is also interesting because it preserves important geological features, including a large stalagmite (more than 2.0 m in
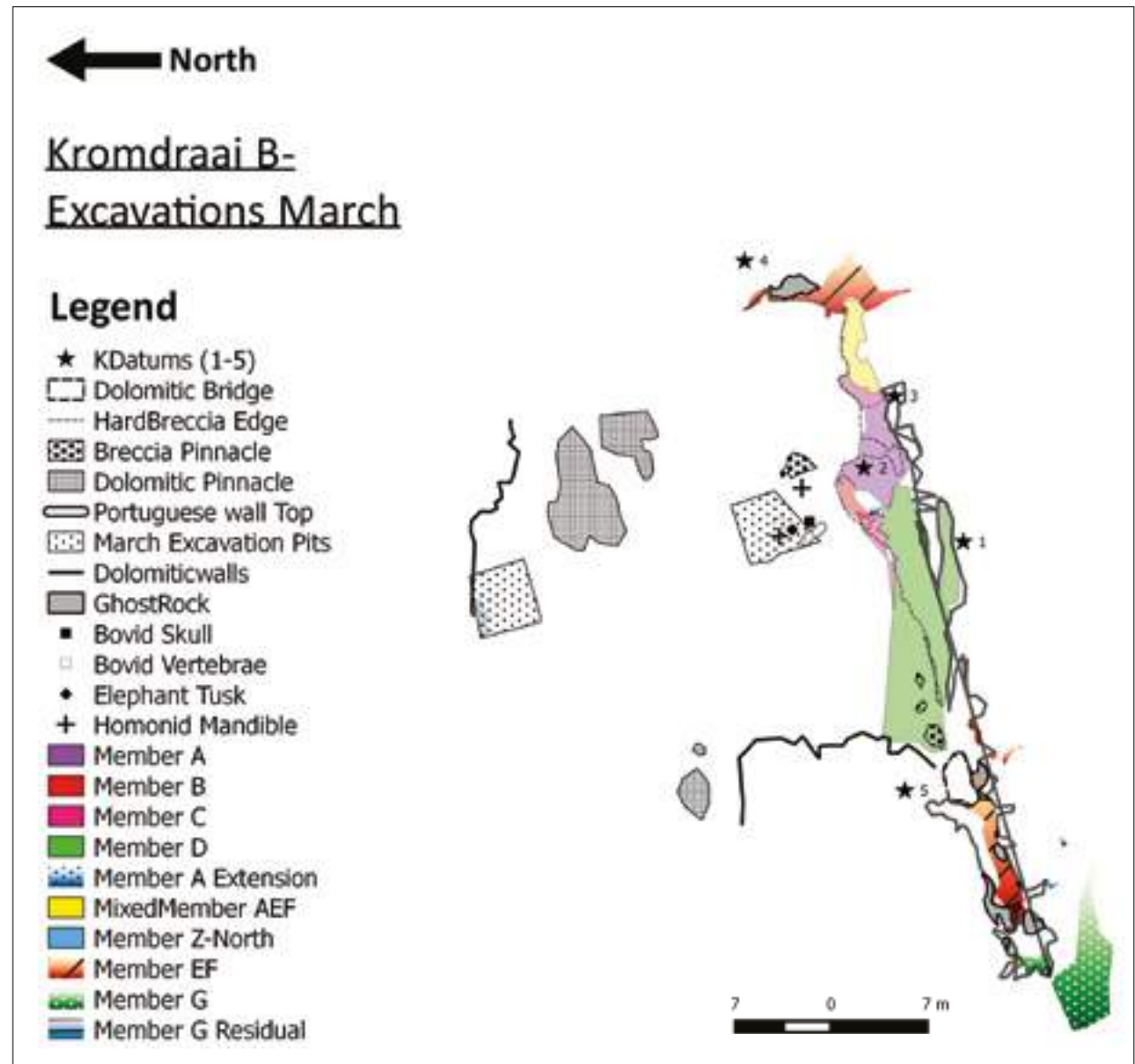

Figure 1.3   *GIS map of the Kromdraai extension site*

THE KROMDRAAI LITHO- AND BIO-STRATIGRAPHY

The localities of KA, KB and KE correspond to a single unroofed cave that is part of a huge network of galleries formed during the Miocene-Pliocene period and partially cut by the erosional surface, due to the deepening of the valley. The deposits formed polygenic talus cones interbedded with flowstones that filled nearly all the voids around the entrances. The detailed lithostratigraphy of Kromdraai indicates the succession of deposits, mineralisations, demineralisations and declogging by the karst and subsumes a complex succession of more than a single time period. Chapter 3 gives a detailed account of the new stratigraphic interpretation of Kromdraai. Here, we very briefly summarise the lithostratigraphic interpretation first proposed by Partridge (1982).

Partridge's stratigraphic interpretation of KB

First of all, it is interesting to note that throughout the succession of the KB five members reported by Partridge, all the upper contacts were considered as eroded and disconformable. Moreover, the occurrence of macrovertebrate fossils across the stratigraphic succession was considered as very heterogeneous within breccias "generally less calcified than that at Sterkfontein … 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, than is indicated at any other Transvaal australopithecine site or is evident on present dolomite hillsides in the area" (Partridge 1982:11). At this stage, this observation is not interpreted in terms of palaeoenvironments even if a "significantly more humid climate" than the present climatic regime may be an explanation (Partridge 1982:12).

Member 1 was reported at the eastern end of KB ('KB East Formation') (Figure 1.2) to consist of about 7.0–13.0 m of dark reddish-brown breccias containing abundant, slightly weathered, subangular 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 of this unit was considered to form a pyrolusite-rich layer representing a depositional hiatus. Importantly, the top surface of Member 2 bears a beautifully preserved stalagmite (Figure 2.6, Chapter 2) currently under study for absolute datings. Member 3 was considered as localised to the west of Member 2 where it thickened in this direction to reach about 3.7 m. Its light reddish-brown breccias was reported as very fossiliferous and indeed led to the discovery of numerous macrovertebrate fossils during Vrba's excavations. Members 4 and 5 were described to the west of the Member 3 outcrops with respectively 2.5–3.0 m and 1.0 m of reddish breccias containing rare fossils.

Only a minority of the KB fossils (including the fossil hominin sample) can be unambiguously assigned to the single and relatively homogenous period represented by the calcified Member 3 deposits (Brain 1981; Vrba 1981; Vrba & Panagos 1982; Thackeray et al. 2005).

THE KROMDRAAI BIOSTRATIGRAPHY

Previous biochronological assessments of the KB faunal assemblage (e.g., McKee et al. 1995; Heaton 2006) 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. Therefore, previous 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 2 versus Member 3), or from various circumstances of discovery (i.e., ex situ versus in situ, or unknown). Chapter 4 gives an example of the variety of these distinct samples for the KB fossil hominins (see Table 4.1).

The KB animal bones collected from in situ Member 3 breccias include a predominance of cercopithecoid monkeys (approximately 75% of the faunal sample), including leaf-eating forms (colobinae), whose presence suggests relatively wooded and moist surroundings. The KB cercopithecinae sample is taxonomically diverse and includes several papionins; one of the most suitable biogeographical models to provide indirect evidence about early hominin adaptations and dispersal because of their hypothesised similar ecological niche on the Plio-Pleistocene African woodland mosaic or savannah environments. Along with an extinct and large-bodied subspecies of the contemporaneous *Papio hamadryas*

(*P. h. robinsoni*) this sample includes two other extinct papionin species: the large and unusual *Gorgopithecus major* and the smaller *Papio angusticeps* (or *P. izodi angusticeps*), either regarded as indistinguishable from *P. izodi* (Werdelin & Sanders 2010) or considered as endemic to Kromdraai (Heaton 2006). Interestingly enough, small-bodied papionins occur exclusively in the oldest faunal assemblages of the Plio-Pleistocene in South Africa (e.g., Makapansgat, Taung and Sterkfontein Member 4). After a detailed comparison of the South African Plio-Pleistocene cercopithecinae, 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. Another large-bodied papionin species – *Dinopithecus ingens* – that may have migrated from East to South Africa between 2.5 and 1.5 Ma could also represent a good biostratigraphic indicator. This species is not represented at KB, but instead is found at Swartkrans Member 1. The absence of *D. ingens* at KB may represent an additional indice of its older age as compared to Swartkrans Member 1, Sterkfontein Member 5 or Drimolen.

Faunal seriation using macromammal groups other 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 (Reed 1996), the low-lying fossiliferous breccias at Sterkfontein represented by Member 2 (Clarke 2006) and Jacovec Cavern (Partridge *et al.* 2003). Indeed, Pickford

assigned a single tooth recovered from the lowermost decalcified breccia layer during Brain's KB excavation (1958) (KB 3276, an isolated unworn right upper molar previously identified as *Phacochoerus modestus* by Cooke 1993) to *Potamochoeroides hypsodon* 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)" (Pickford 2013:30).

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 and 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 Ma (Werdelin & 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 & 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. Kromdraai A 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. From the cercopithecoid evidence and the fact that *Dinofelis piveteaui* of KA is regarded as an evolutionary descendent of *D. barlowi*, known from Swartkrans Member 1 and earlier sites (Cooke 1991), the later deposits may be bracketed between the older KB and the younger KA.

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 the two sites' 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 (Ortega *et al.* 2005). This may have an as yet unknown impact on the absolute dates. Taking this into account, we hope to obtain in the near future, U-Pb dates for both the top Member 2 stalagmite and the recently discovered large stalagmite from the KE locality (see above).

U-Pb dates are available for the nearby site of Swartkrans (Pickering *et al.* 2011; Gibbon *et al.* 2014). The oldest *P. robustus* specimens from Swartkrans Member 1 may represent either a relatively short period averaging 1.99 ± 0.19 Ma or 1.8 Ma, or rather a duration of deposition from 2.19 ± 0.08 Ma to 1.80 ± 0.09 Ma (Pickering *et al.* 2011; Gibbon *et al.* 2014). When considering previous faunal seriations on 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 +/– 0.21 Ma (Granger *et al.* 2015).

Interpretations of the temporal relation between KB and the nearby Swartkrans and Sterkfontein sites are in accordance with both the dental and cranial morphology of the KB hominins from Member 3 that was shown to be more plesiomorphic than that of the Swartkrans Member 1 sample (Grine 1988; Kaszycka 2002; Braga *et al.* 2013).

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 & 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, Herries *et al.* (2009) miscorrelated Thackeray *et al.*'s (2002) paleomagnetic data and ignored the KB stratigraphy.

A PRELIMINARY SKETCH OF THE KB FOSSIL HOMININS

The KB hominin sample published as yet comprises 28 postcranial and cranio-dental specimens, with a minimum number of 17 individuals (Thackeray *et al.* 2001; Braga *et al.* 2013, 2016) (Table 4.1, see Chapter 4) attributed to *P. robustus* (Broom 1938a,b; Vrba 1981; Thackeray *et al.* 2001) and early *Homo* (Braga & Thackeray 2003; but see Grine *et al.* 2009). The KB hominin sample contains only three non-dental diagnostic cranial remains: the geologically younger

type specimen of *P. robustus* (TM 1517; Broom, 1938a, 1938b, 1942, 1943), the unprovenanced TM 1602 adult palate (Brain 1981) and a significantly older isolated temporal bone (KB 6067) (Braga *et al.* 2013). Moreover, only a few hominin post-cranial specimens have been thus far recovered at KB.

Only three small KB hominin samples can be precisely tied to *in situ* deposits (Table 4.1, see Chapter 4) and are spread across the succession of distinct time periods (Braga *et al.* 2013) separated by lengthy time-lapse unconformities (see Chapter 3). The calcified and soft breccia deposits of Member 2 currently excavated represent the oldest of these time periods (see Chapter 3).

The KB hominin sample found before 2014 falls into five groups (Table 4.1, see Chapter 4): (i) only 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 or Submember 4.1 (see Chapter 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 authors, Francis Thackaray (FT) and José Braga (JB) (since 2002) on the easternmost part of KB East (circa 36 m east of datum point); (iii) one specimen (KW 6087a,b) found *in situ* (since 2014) in one of the two oldest fossiliferous deposits yet identified (Member 2 soft breccia; see Chapter 3) and newly reported here; (iv) four specimens from Brain's excavation that cannot be securely tied in the stratigraphy; and (v) all the other KB hominins are unprovenienced (including TM 1517) and were recovered either by Broom between 1938 and 1944

(Broom 1938a, 1938b; 1942; 1943), by one 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 in Braga *et al.* (2016), 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 have not yet provided fossil hominins. The newly discovered Kromdraai hominin cranial, dental and postcranial material will be reported in detail when more comparisons are be made. In 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.

THE HALLMARK OF THE KB HOMININ SAMPLE

In a number of cranial and dental morphological features, the states shown by at least some hominins from KB indicate that they may represent the primitive condition for the *P. robustus* lineage. Several dental features observed on *P. robustus* at KB contrast to the more derived conditions displayed not only by South African conspecifics sampled thus far in other sites in South Africa (Grine 1988; Kaszycka 2002), but also by the post-2.3 Ma Eastern *P. boisei* (Suwa 1988) (see Wood & Constantino 2007 for a definition). For example, both KB deciduous and permanent teeth resemble more closely those of *A. africanus* than the more specialised *P. robustus* ones from Swartkrans – a finding suggesting that some KB hominins may

lie very close to the root of the *Paranthropus* lineage (Grine 1988). As suggested by Tobias, "the population represented by the Kromdraai hominid may throw light on the nature of the cladogenetic trans-specific change from the postulated 'derived *A. africanu*' [as represented by the Taung child] to the earliest 'robust' australopithecine sensu stricto" (1988:305). Cranial features displayed by the KB fossil hominins are also shared with some specimens from Sterkfontein Member 4, either attributed to *A. africanus* or with uncertain affinities (Braga *et al.* 2013). In this context, as discussed later in Chapter 4, more detailed morphological evidence obtained from micro-computed tomography (*μ*-CT) and computer-aided morphometry may help to determine whether at least some KB hominin represent an old occurrence of *Paranthropus* in southern Africa.

From the currently published maxillo-facial, basicranial and postcranial evidence, small size represents an important hallmark of the KB hominins (Braga *et al.* 2016), even though the very limited size of the sample prevents us from any further interpretation. 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) (even though the roots of its M_3s are not fully formed) 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) (Wood 1991; Grine & Daegling 1993). Another and more complete adult mandible from Kromdraai Member 3 (KW 6220), first reported in Braga *et al.* (2016), 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 mm and 24.2 mm). Differences in mandibular corpus dimensions within *Paranthropus* species may reflect patterns of sexual dimophism rather than dietary adaptations (Chamberlain & 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. An example is here given with the inner ear. In cochlea and oval window size, two proxies of body size (Braga *et al.* 2015), 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 obtained for *P. robustus* adult specimens from Swartkrans, or falls well below them (for cochlear length), being 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*] that was ancestral to and directly on the lineage of *Paranthropus*" (Clarke, 1988:291). The small size of KB 6067 can therefore be interpreted either as

indicative of a small body size for an adult *P. robustus* or as closer affinities with some Sterkfontein Member 4 specimens. Finally, a last example of small size in the KB hominins can be found on the postcranial remains presumed to be associated with the partial cranium of TM 1517, the 'type specimen' of *P. robustus*: a right talus (TM 1517d), a right proximal ulnar fragment (TM 1517e) and a right distal humerus (TM 1517g) (see Table 4.1, Chapter 4). Among the handful of lower 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 to 40 kg female range for this species (depending on the formula used) (McHenry 1974; Susman *et al.* 2001). Moreover, as already noted by McHenry, if the three postcranial bone fragments attributed to TM 1517 belong indeed 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 (McHenry 1974:335–336).

THE TAPHONOMY AND PALEO-ENVIRONMENTS AT KROMDRAAI B

The accumulative agents at KB

Brain has noticed an extreme fragmentation of the KB bone found during his fieldwork in decalcified breccias mainly (Brain 1975; but see Vrba 1981). He interpreted this pattern of fragmentation as an indication of food remains of hominins. Another interpretation was given by Vrba who considered the fragmentation of the KB bones as a result of the decalcification process with "initial softening and disintegration in water, and subsequent trampling and overburden pressure on the weakened bone" (1981:1). In addition to the noticeable absence of

stone artefacts in the Member 3 solid and soft breccias (corresponding to Member 3 and Submember 4.1, see Chapter 3), Vrba has noticed "the anatomical association of fragments, the virtual absence of bovids, the good representation of cercopithecoids and large carnivores" (1981:21). She interpreted the Member 3 assemblage as of largely, or entirely autopod origin (i.e., the arrival on the animals' own feet) and the result of "a place part shelter to some, like the baboons and perhaps the apeman [*P. robustus*], part deathtrap [in steep shafts], and part feeding-place of opportunist carnivores" (Vrba 1981:49). 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. In particular, hyenas were likely active inside the Kromdraai cave used as a shelter, as indicated by several coprolithes recently found in the base of Member 2 (see Chapter 5).

Paleoenvironments at KB

The gradual replacements of woodland environments by open savannah grassland between 3.0 and 2.0 Ma in sub-Saharan Africa is demonstrated by carbon isotope records from both soil carbonates (Levin *et al.* 2004; Wynn 2004; Segalen *et al.* 2007) and biomarkers extracted from deep-sea sediments (Feakins *et al.* 2005). This general climatic trend was associated with the onset of Plio-Pleistocene ice ages, between a marked cooling step at 2.73 Ma and the first major glaciation at 2.15 Ma (Haug & Tiedemann 1998; Rohling *et al.* 2014). These climatic changes leaded to a northern and/or southern compression of the African Intertropical Convergence Zone and caused periods of climate variability characterised by the development of large deep lakes or by extreme aridity in the East

African Rift Valley. Such environmental changes likely did not occur at the same time and in the same way in eastern and southern Africa. The isotopic analysis of a large stalagmite newly discovered *in situ* in KE may help to clarify this issue in the future.

Speciation and/or extinction faunal events have been tied to large-scale or more local environmental changes even. However, it is often argued that faunal assemblages exert a significant time-averaging effect that decreases the temporal resolution of palaeoenvironmental reconstructions. Moreover, the number, periods and extent of faunal movements between eastern and southern Africa in the Plio-Pleistocene is clearly not known. Turner and Wood (1993) concluded to reasonable degree of contact and movement between the two regions in the early Pleistocene. Interestingly, they observed that the macromammal groups fell between two extremes in terms of dispersion between eastern and southern Africa. The bovidae appeared highly regional in their distributions at one end, and the papionin monkey appeared as one of the most dispersed group at the other extreme.

Faunal evidence

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 greater than 30% of the total bovid population in areas with considerable tree and bush cover ('closed' habitats), but always greater than 60% in areas with high grass cover but few trees and bushes ('open' habitats). Based on this AAC criterion she argued for a major African faunal turnover at about 2.4 to 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 KB Member 3 (Member 3 and Submember 4.1, see Chapter 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 abovementioned 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 (see Chapter 5) will lead to a better understanding of the paleoecological conditions that prevailed at this time, well before the deposition of KB Member 3 excavated by Vrba (see above).

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 (^{13}C values) in the fossil tooth enamel carbonate (Kohn & Cerling 2002). The comparisons between karstic hominin site paleoenvironmental contexts based on ^{13}C values have been used to decide whether the observed differences were due to long-term or short-term shifts in habitats, or instead were caused by adaptations and versatility of dietary behaviours.

Data have been gathered from the main South African hominin-bearing sites, including Makapansgat (Sponheimer & Lee-Thorp 1999), Sterkfontein (van der Merwe *et al.* 2003), Swartkrans (Lee-Thorp *et al.* 1994; Sponheimer *et al.* 2006), Kromdraai (Sponheimer

et al. 2005; Kirsanow 2009) and Malapa (Henry *et al*. 2012). 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). As regards fossil hominins, a single *P. robustus* tooth (the lower second permanent molar of TM 1600) has been measured for its ^{13}C value (−7.9‰, Sponheimer *et al*. 2005) with no evaluation of potential intra-tooth variability and post-depositional (diagenetic) interactions with groundwater and alterations (dissolutions and re-precipitations). This single measurement made on a KB hominin tooth not precisely tied in the lithostratigraphy (see above) revealed no significant difference with those obtained on *P. robustus* specimens from the nearby site of Swartkrans (Lee-Thorp *et al*. 1994, 2000; Sponheimer *et al*. 2005, 2006).

The ^{13}C values obtained for secondary carbonates (attached breccia or calcite inclusions in fossil samples) (Schwarcz 1986) sampled in South African Plio-Pleistocene sites revealed a clear trend towards more positive values when they compared Makapansgat Member 3 to later accumulations in Sterkfontein Members 4 and 5. This was interpreted as an increasing contribution over time of C4 plant biomass on secondary carbonates in karst systems (Lee-Thorp *et al*. 2007). The same trend was observed when using ^{13}C values obtained for fossil enamel (Lee-Thorp *et al* 2007; Sponheimer and Lee-Thorp 2009). These measurements revealed a sharp increase of C4 feeders during the period of accumulation of Swartkrans Member 1 and Sterkfontein Member 5, suggesting greater grass cover at this time.

PRELIMINARY CONCLUSIONS: A REGIONAL PERSPECTIVE

Under the caveat that only a handful of hominin specimens were found *in situ* from the KB deposits before 2014, and that a very limited part of the faunal sample (including the hominins) could be precisely tied in the lithostratigraphy, the interpretations presented in this short review are only preliminary. 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, from our current biochronological evidence (Fourvel, pers. obs.), we consider that the KB Members 1 to 3 accumulated before the first appearance of the Oldowan in South Africa. Therefore, ongoing fieldwork at Kromdraai may help to portray the early co-evolution of the southern 'robust' australopith lineage with early *Homo*, and its paleoenvironmental conditions in the Late Pliocene or early Pleistocene.

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CHAPTER 2

A computer-guided 3D multiscale reconstruction of the Kromdraai site

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INTRODUCTION

A large range of methods is increasingly used for heritage purposes, particularly in archaeology. Several techniques can be employed, depending on the complexity in size, shape and level of detail of objects (Pavlidis *et al*. 2007). Long-range scanners are used to record buildings (Allen *et al*. 2004; Craciun *et al*. 2012) or archaeological excavations (Doneus & Neubauer 2005; Rüther *et al*. 2009; Subsol *et al*. 2015). Long-range scanning methods may be associated with photogrammetry (Lambers *et al*. 2007; Yastikli 2007; Rüther *et al*. 2012). Digitisation is often used to document the cultural heritage, in particular to generate and visualise 3D reconstructions and to record the 3D geometry of archaeological materials (Kuzminsky & Gardiner 2012) and individual items.

Very few excavation sites are fully scanned (Nigro *et al*. 2003), yet many methods exist and require very long post-treatment. An accurate digitisation requires multi-scale devices and the information collected must be fused for a complete reconstruction and appropriate use. The exact spatial position of fossils is an important element for understanding the taphonomy of a site (Brain 1993). In addition to the taphonomic context, it is also important to record spatially the stratigraphic information available in the cave deposits (Bruxelles *et al*. 2014).

Since 2010, we gathered high quality survey data of the Kromdraai fossiliferous area, including Kromdraai B (KB) for its 3D modeling at various scales, from an Unmanned Aerial System (UAS) (at a km scale) to micro-computed tomography (µCT) (at a micrometre – µm – scale) (Figure 2.1). These methods not only reduce the time spent on the site when compared with traditional direct survey methods (e.g., mapping with an electronic Total station to create a digital elevation model), but also produce a range of information, such as orthographic images, elevation drawings and sections of the land surface.

We mainly combined three methods to gather 3D data at Kromdraai. First, we used multi-image photogrammetry to capture high-resolution 3D surfaces with complete texture at two different scales, from a few kilometres (Figure 2.2) to a few metres (Figure 2.6), with respectively centimetre and sub-centimetre accuracies. Second, we used terrestrial and close-range laser scanning for the detailed recording of the KB site (Figures 2.3-2.4) at a sub-
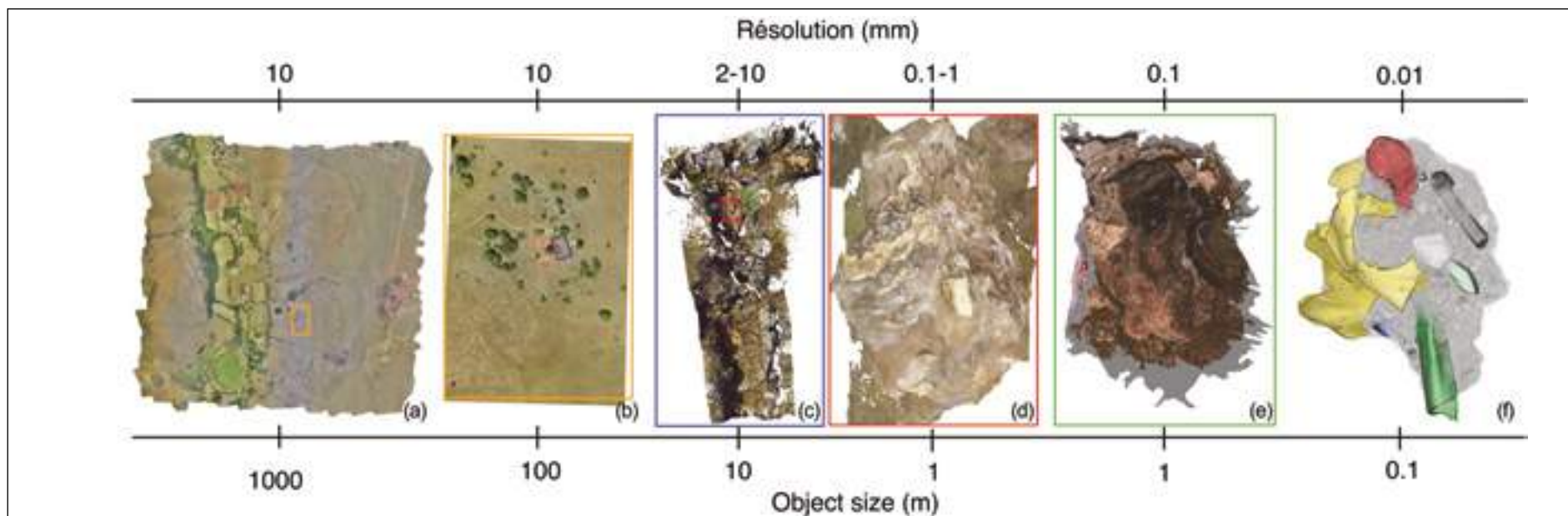
Figure 2.1 *3D modeling of Kromdraai B at various scales. From top to bottom: (a) and (b) UAS photogrammetry; (c) long-range laser scanning; (d) photogrammetry; (e) portable laser scanning; (f) micro-computed tomography.*

centimetre scale as well as to record objects (e.g., fossils) during the excavation and some aspects of the ground surface (e.g., contacts between breccias and flowstones). Finally, we exploited μCT (Figure 2.1) to observe, before their mechanical preparation and cleaning, the fossils that have been preserved inside plasters caps during the excavation for their safe removal from the site.

This chapter aims to present the 3D multiscale data from KB through several examples. We show how we captured our 3D multiscale data at Kromdraai for monitoring purposes, in particular: (i) to propose a visit of the site in a 3D virtual environment (with the use of computer graphics) that will help the reader

and the KRP team to understand better the geological and depositional contexts of this site, (ii) to record the diggings over the successive excavations and to assess the changes of the site related to these archaeological activities, and (iii) to allow a precise location and visualisation of the better-preserved fossil specimens (particularly, the articulated bones) within their sedimentary units.

DATA ACQUISITION AND PROCESSING

Multiresolution data constitute the common basis for building representations of a geometric shape at different levels of details. We used three methods to digitise the site: μCT, terrestrial and close-range

laser scanning, and multi-image terrestrial and aerial photogrammetry.

The μCT approach was explored to create the cross-section through plasters caps containing significant fossil remains, mostly articulated skeletal parts or fragile decalcified portions of skulls. We could then create virtual 3D models of the fossils specimens still embedded in plaster in order to plan their subsequent mechanical preparation in a more efficient way.

Terrestrial and close-range laser scanning involved the use of a laser beam. Data provided are represented by a triangular mesh – a set of three dimensional points connected by their common edges to represent
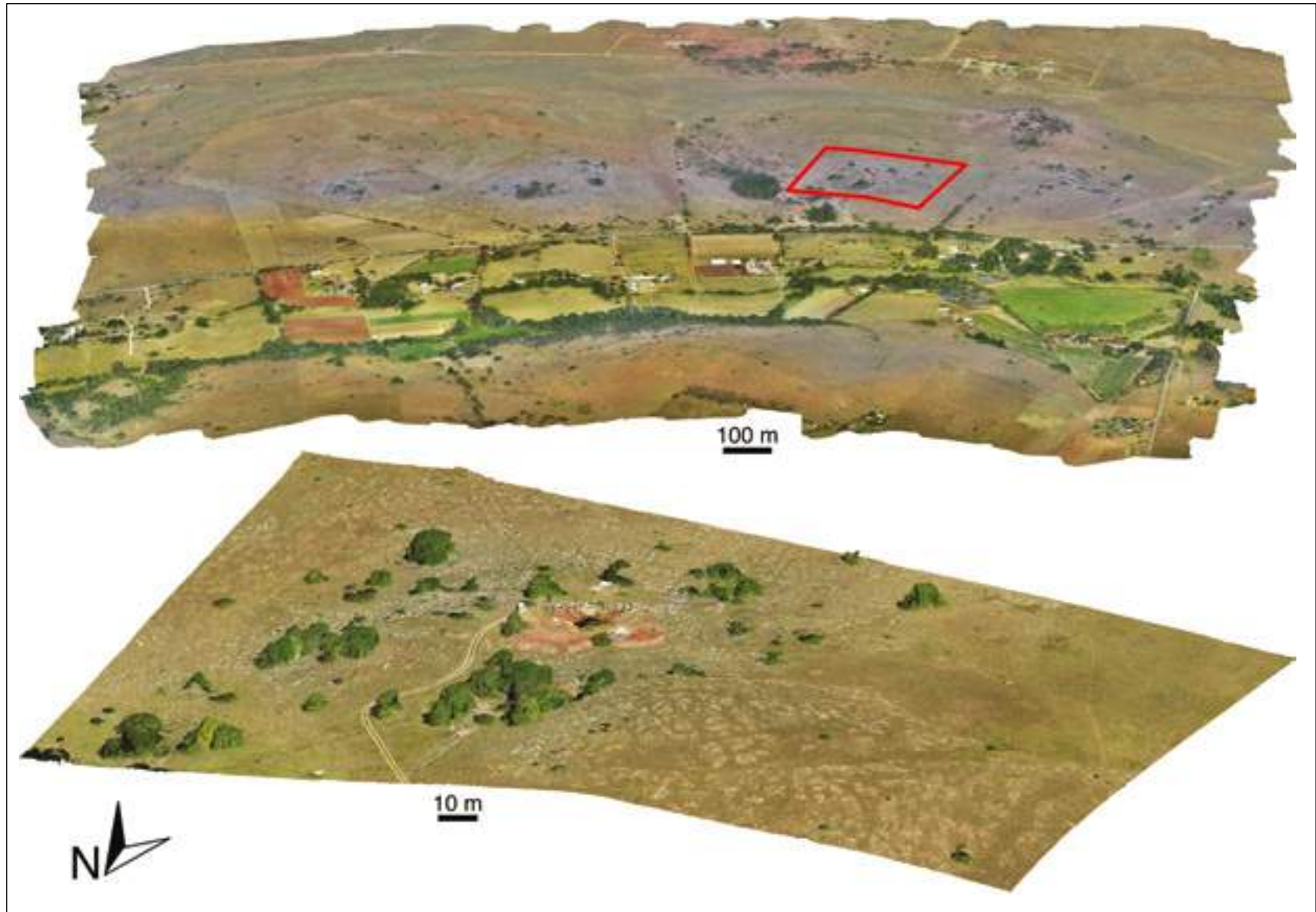
Figure 2.2 *UAS photogrammetry of the landscape around Kromdraai.*

mathematically the surface of an object. This method was useful to produce a reference template (i.e., a mesh) of the KB excavation that could be subsequently used to plot geological features and fossil remains (Figure 2.3). This template was also useful to draw profiles across surface features and to infer predictions on aspects of the ground surface (e.g., contacts between breccias and flowstones).

Multi-image terrestrial and aerial photogrammetry is a rapid and cost-effective technique able to produce results similar to those of laser scanning with the use of computing power and professional photogrammetric software, but with much lower overheads. We used both land and UAS multi-image photogrammetry to produce a georeferenced 3D model of the landscape on a vast area (between 26° 1′ 19″ S, 27° 44′ 43″ E and 25° 59′ 38″ S, 27° 45′ 40″ E – WSG84) (Figure 2.2) to assess the quantities and locations of the soil removed from the site during each fieldwork season as well as the overall spatial distribution of important geological features.

In situ 3D reconstruction

Terrestrial laser scanning

We combined two different laser scanners, a FARO Focus 3D (www.faro.com) and a Creaform Handyscan VIUscan (www.creaform3d.com), both of which are widely used for cultural heritage applications. The KB site was scanned using a Faro Focus 3D, a 360 degrees scanner with an accuracy varying between 2 and 10 mm, and with a resolution of 40 megapixel
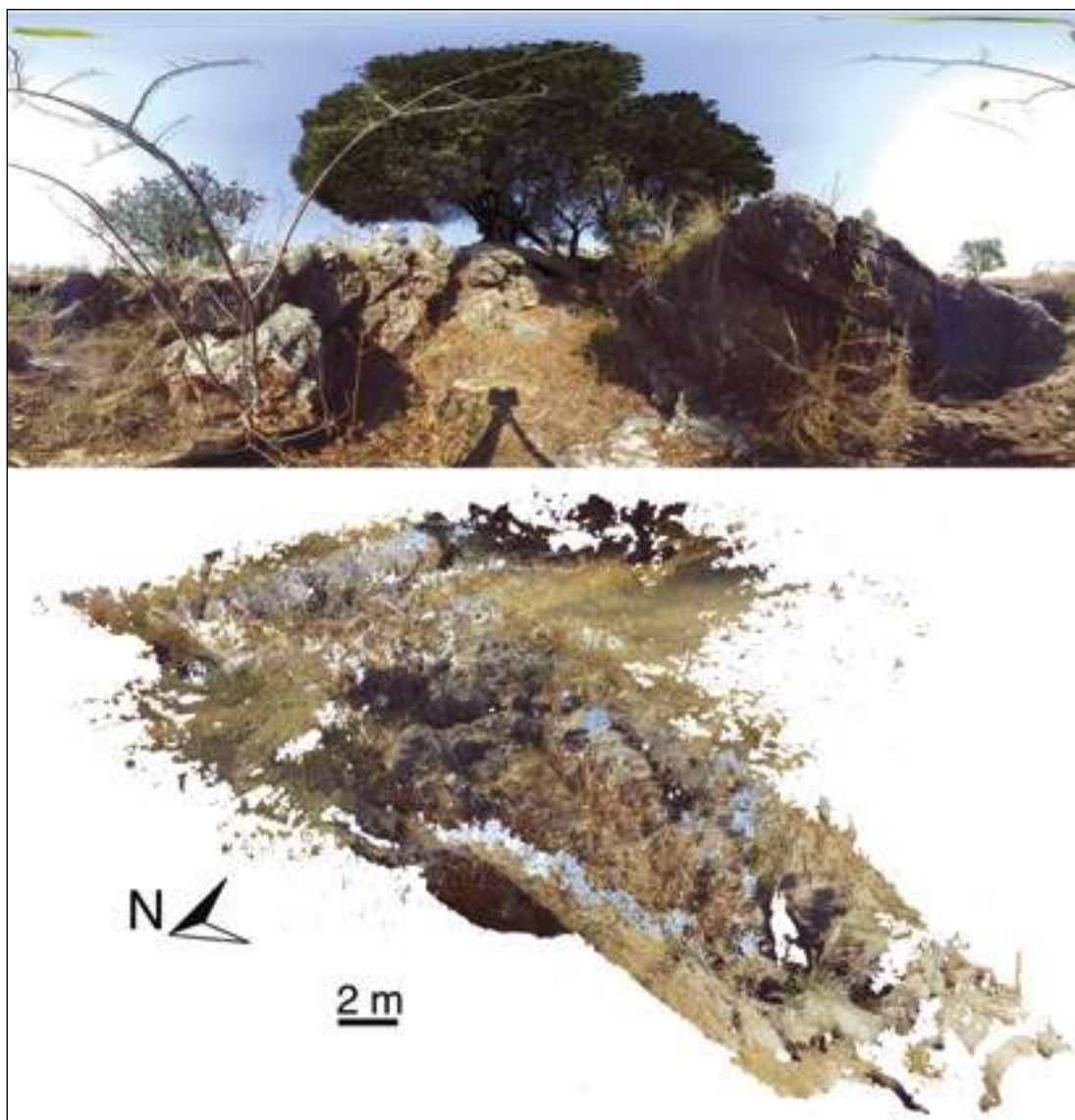

Figure 2.3 *Laser scan of the site with the FARO Focus 3D scanner showing a picture taken from the location of the FARO Focus 3D scanner in-situ (top, see the shadow of the scanner) and the resulting 3D point cloud (bottom).*

Table 2.1   *Description of long-range laser scanner acquisitions.*

Method used	Acquisition			Post-processing			
	Date	Number of scans	Number of vertices/faces (in millions)	Number of vertices/faces (in millions)	Dimensions (m)	Color points	Texture
FARO Focus 3D	May 2012	27	800/1000	240/400	20 x 10	Yes	No
Creaform Handyscan VIUscan	May 2012	5	0.3/0.7	0.3/0.7	1.8 x 0.8	Yes	Yes

for the colour and a range from 0.6 m up to 120 m (Table 2.1).

To avoid (as far as possible) the laser occultations, we scanned the same areas using different points of view, resulting in a large amount of data. We performed twenty-seven scans in order to cover the whole site of KB (Figure 2.3). The first step in the post-processing was to align the scans (a process also called 'registration') and to delimit an area of interest. We did this with the Faro Scene laser scanner software (www. faro.com). For the registration, we used spheres that were positioned, scanned and then detected by the Faro Scene software. The alignment of the scans was computed based on the position of the spheres. We then defined a region of interest in order to remove areas that were not relevant (e.g., vegetation). We obtained a mesh with 330 millions of vertices and 580 millions of faces. The last step was to merge the overlapping areas. Changes in resolution, noise due to scan outdoor conditions, as well as registration errors may disturb the fusion process. An automatic processing was then developed using several filters of MeshLab software (www.meshlab.sourceforge. net) to reconstruct the 3D model. In order to simplify the dataset, we chose to work on subdivisions of the mesh. Accordingly, we divided the mesh along the x- and y-axes with a set of blocks, each of 500 mm

side length and width with an overlap of 50% between adjacent blocks. The workflow (Figure 2.4) has been automatised with MATLAB (www.mathworks.com) using MeshLab filter scripts as follows for each block:

- Merging. Data located inside the block were concatenated in a single file.

- Surface reconstruction. A surface reconstruction 'Poisson' filter (with an octree depth of 11) was applied. We chose this filter because it smooths the noisy data and manages possible registration errors (Kazhdan *et al*. 2006). The result is a mesh generated from a set of surface samples.

- Colour transfer. As the light was not constant during the acquisitions, there was no homogeneity of colours between meshes. We chose to keep the colours of the best represented area and to apply them to the reconstructed surface. Therefore, we assigned a colour to each point of the reconstructed surface using the mesh that contained the larger number of triangles inside the block and using a distance criterion (less than 10 mm). Then, we used the same criteria to assign a colour to the remaining uncoloured point using the other meshes. This step allowed us to remove extrapolated and uncoloured faces created by the Poisson surface reconstruction.

- Cleaning up and cropping. We removed the isolated pieces (less than 30 faces) and the unreferenced points. Finally, we removed the overlapping areas between blocks by reducing the length and width by 100 mm in order to avoid side effects.

The final mesh comprised 240 millions of points and 400 millions of triangles (or faces). We developed a user interface in MATLAB to allow the user to select and to view areas of interest. The user can select any area on a zenithal view and the program generates the corresponding mesh. Some holes were visible due to laser occultations, but the fossiliferous breccias were generally well covered.

Portable laser scanner

We used a Creaform Handyscan VIUscan (with a resolution and an accuracy of 0.10 and 0.05 mm, respectively) to record a specific area of KB with more realistic textures, but also to scan objects during the excavation as well as some extracted blocks. This device produces a white light during the scanning to ensure the recording of a uniform texture. At the same time, laser lines are projected onto the surface to be recorded. The final result is a 3D point cloud, which is transformed into a polygonal mesh. A texture recorded during the scanning is then mapped onto that mesh (Figure 2.1).

Blocks overlapping the region of interest

Surface reconstruction → Color transfert → Block reduction

Bounding box of the block

Original mesh — Post-processed mesh

1 m
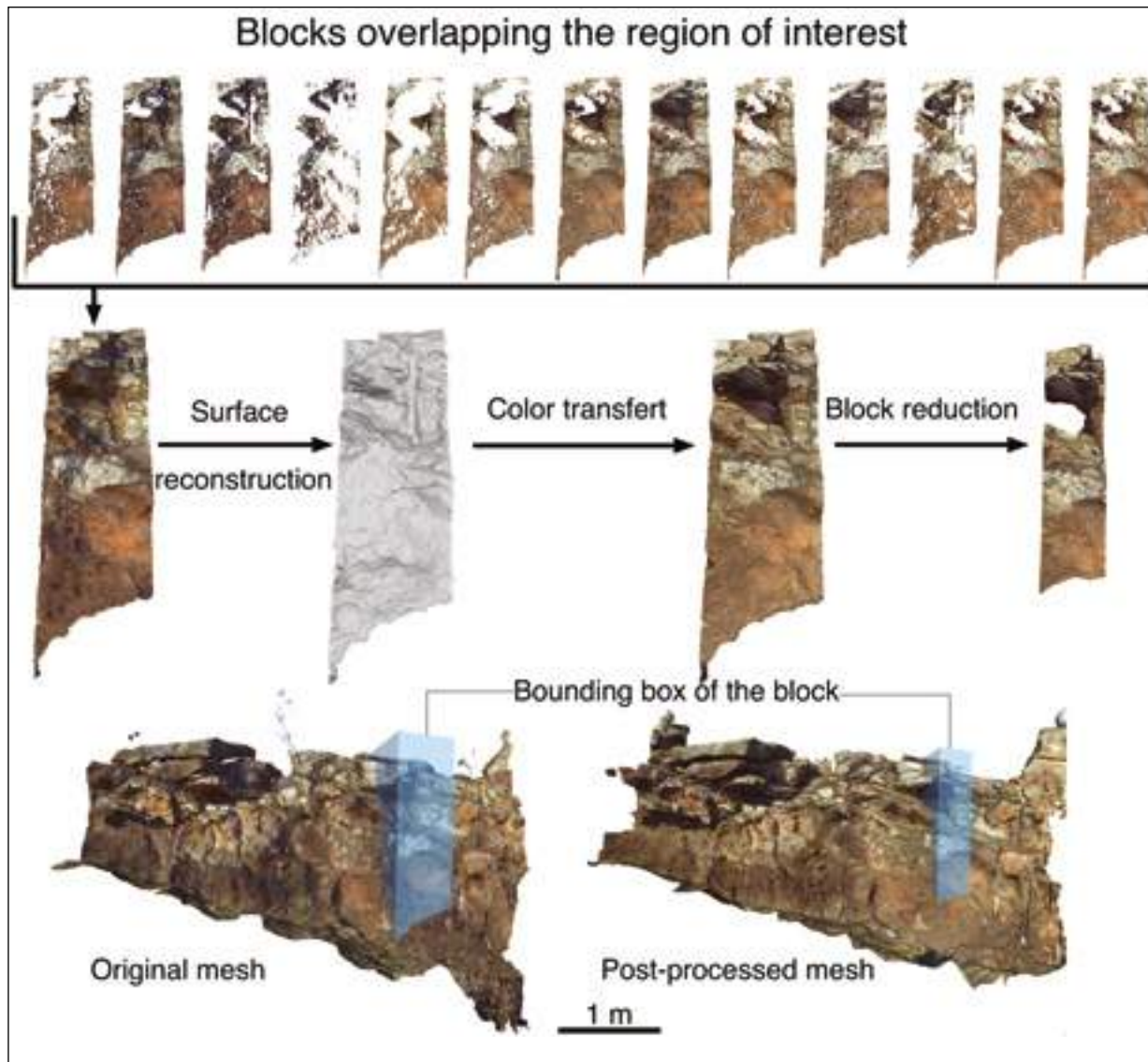
Figure 2.4 *Workflow applied on data provided by the Faro Focus.*

Photos-based 3D reconstructions

By using several images of the same scene, photogrammetry allows the reconstruction of a 3D point cloud from at least two photographic views. The method of 'structure from motion' (SFM) (Ullman 1979) reconstructs a three-dimensional representation of a dense point cloud of the scene. The initial data are simple photographs of the scene under various angles with some overlapping areas. The SFM method finds correspondence points between photographs and connects them to calculate the positions in 3D of these points and to generate a 3D structure of the scene. A complementary approach of dense multi-view stereo can be used to interpolate the surface generated from the point cloud. We then obtain a cloud of dense points on which a 3D triangular mesh is approximated. The colours of points are directly defined according to the photos. A texture can therefore be applied to the 3D model to obtain a photo-realistic 3D model expressed in a local system of coordinate.

Several tools compute 3D data from 2D images with the use of SFM algorithm. We chose the PhotoScan software (professional edition; www.agisoft.com), which proposes a user-friendly interface. Its workflow can be followed by non-experts in computer science, and it offers several useful exportation tools (e.g., orthophoto, digital elevation model). This workflow consists in three steps: (i) aligning the photos by detecting the successive positions of the camera processed and by matching homologous points to generate a 3D point cloud; (ii) generating a triangle mesh with a colour given to each vertex; and (iii) mapping a texture onto the mesh by mixing the photos. Some post-processing has been done to clean the mesh by removing isolated pieces (less than 50 faces) and by decimating the mesh.

UAS photogrammetry

We used UAS photogrammetry with a SenseFly eBee drone (www.sensefly.com) (Table 2.2), which is an appropriate device for the acquisition of a set of photographs of a scene under various points of view (Nex & Remondino 2014). We then generated a 3D model with the method described above. In this case, time-stamped GPS data were recorded during the flight. The Photoscan software could generate a geo-referenced 3D model using GPS data. The advantage of an automatic alignment is the avoidance of human manipulation and potential errors. We chose relatively large areas to produce an easily exploitable 3D model with a reduced number of points (Table 2.2). We also selected more focused areas with higher resolution 3D models, depending on our needs.

Table 2.2 *Description of photogrammetry acquisitions.*

| Method used | Acquisition | | | Post-processing | | | |
	Date	Number of photos	Camera	Number of vertices/ faces (millions)	Dimensions (m)	Colour points	Texture
Drone photogrammetry	March 2015	43	Canon IXUS 127 HS	0.5/1	200 x 300	Yes	Yes
Drone photogrammetry	March 2015	918	Canon IXUS 127 HS	0.5/1	2 600 x 2 400	Yes	Yes
Land photogrammetry	June 2015	68	Sony DSC-TX10	0.4/0.8	3 x 3	Yes	Yes
Land photogrammetry	June 2015	225	Nikon D3300	0.4/0.8	10 x 10	Yes	Yes
Land photogrammetry	December 2014	209	Sony DSC-TX10	0.5/1	25 x 27	Yes	Yes
Land photogrammetry	September 2014	139	Sony DSC-TX10	0.5/1	19 x 18	Yes	Yes
Land photogrammetry	April 2014	47	Sony DSC-TX10	0.6/1.2	13 x 13	Yes	Yes

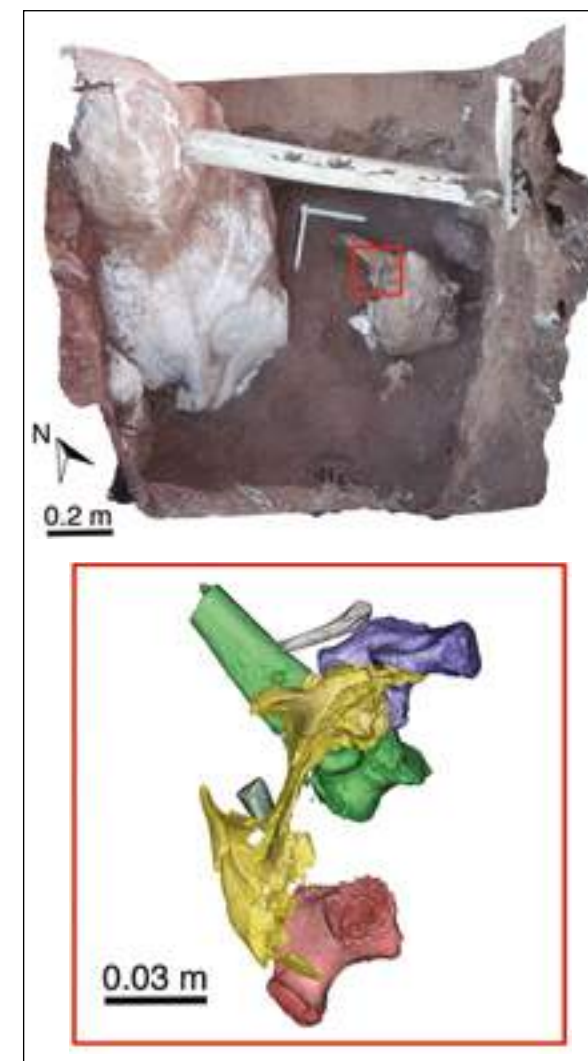**Figure 2.5** *3D photogrammetry of a block during the excavation (top) and computer-aided virtual extraction of fossils specimens (including the partial skull of a large monkey in yellow) from the same block (bottom).*
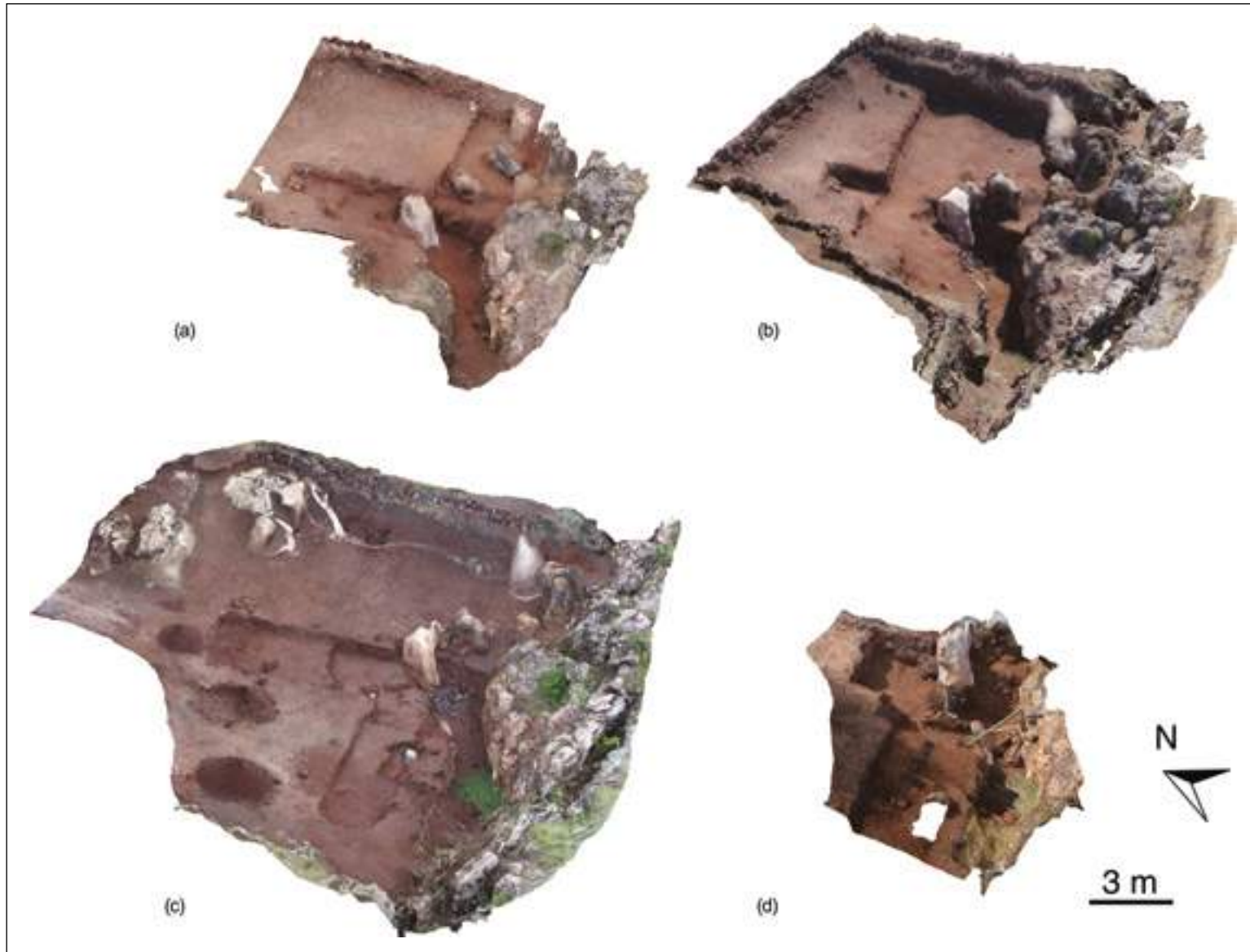
Figure 2.6 *3D photogrammetry model describing the excavation of the Kromdraai extension site at different times: (a) April 2014; (b) September 2014; (c) December 2014; (d) June 2015.*

Fusing different data

The fusion of data from distinct sources was not automatic because the spatial references and the scales of the various devices differed. Furthermore, each dataset includes unstructured points connected by triangulated meshes. Therefore, it was necessary to align these datasets by matching corresponding points or by minimising the distances between meshes.

As the UAS photogrammetry data was geo-referenced, we used them as the reference to align the KB 3D model reconstructed from the Faro scan. All the other 3D models were then aligned on the KB 3D model. We performed the alignments using the Photoscan or the MeshLab software. With Photoscan, five ground control points were manually placed in each model (KB 3D model made with Faro and UAS photogrammetry). Then, the best alignment between the models was computed. The 3D surface reconstruction of a block of fossiliferous breccia obtained from μCT (described in greater detail in Chapter 5) was aligned using the same method (Figure 2.5). The MeshLab tool consists of an automatic alignment with matching pair of points and an iterative closest point algorithm. Whenever possible, we tried to adjust the model by using an iterative closest point method, but it was not always possible since the topology of the excavation changes over the different excavation periods.

CONCLUSIONS

The methods presented in this chapter contribute to demonstrate how the study of the Kromdraai site was enhanced by the use of technical methods at different levels by creating accurate 3D registered models and data. We computed a 3D model of the Kromdraai site for which the geometry of the breccias

was very well recorded and reconstructed in 3D. This model is of interest for various fields of research (e.g., geomorphology, archaeology). Since an excavation is also a destructive process, our duty was to develop methods allowing us to archive the context of the fossil discoveries (Figure 2.5) as well as the main phases of the excavation, and with the best possible accuracy (Figure 2.6). In the future, the precise position of the newly discovered fossils will help us to understand better the taphonomy of the site. The combined use of photogrammetry and tomography will also provide more robust protocols and data.

Another scale level has been added to the existing model in the view of improving our field observations at Kromdraai and, more widely, in the Blaauwbank valley. Indeed, we also used a UAS and low-altitude flights to investigate more precisely the Kromdraai site location, its immediate environment and its topographical relationship with adjacent sites. In order to produce 3D models with high levels of accuracies that can be useful for detailed geomorphologic interpretations, we will need to combine more systematically our photogrammetric survey using a UAS with topographic measurements of ground control points

Recent developments in photogrammetry, laser scanning and micro-tomography represent the last frontiers to produce large quantities of 3D information with a major scientific value. These 3D data allow interpretations not previously possible in bi-dimensional view. The combination of photogrammetry, laser scanning and μCT for 3D modeling has proven to be particularly efficient and flexible. Different levels of resolution and different viewing angles of the three recording systems

allowed us to produce 3D models according to the specific requirements of the archaeological and geomorphologic analyses.

The digital data produced by the KRP will also be used to disseminate information to the general public that are not easily accessible at museum exhibitions, at conferences or on websites.

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CHAPTER 3

A revised stratigraphy of Kromdraai

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INTRODUCTION

The unroofed dolomitic cave of KB is part of a huge network of galleries formed during the Miocene-Pliocene period and partially cut by the erosional surface due to the deepening of the valley. Until 2014, the KB site was only 1 to 3 m wide at the ends and visible over a length of about 40 m (KB West and East at Figure 3.1). It had a rectilinear layout and an east-west alignment. The southern dolomitic wall of this paleo-cavity is clearly visible and was cleared by the successive excavations. On the other hand, the northern wall is only identifiable in the western part of the site. It then disappears and the northern edge of

the site only really corresponds to an excavation limit, and by no means marks the real gallery wall.

To the east, the gallery ends abruptly at the intersection with a north-south oriented passage, also initially filled with breccia and calcite (KC). At the other end, the west termination is more diffuse and the passage seems to narrow out progressively, with the breccia outcrops intersected by *in situ* dolomite partitions. Figure 3.1 shows that, unlike what was written earlier (Partridge 1982), these are not rises in the dolomitic substratum forming limits, but truncated roof pendants now preserved as rocky bridges. The cavity roof dips progressively towards the west below an irregular dolomitic vault. This is represented by a clear

constriction of the walls and a 'dotted' end, where the vault remains still in place alternate with 'windows' onto the brecciated infill clogging up the gallery.

In the central part of KB (Figure 3.1), a particular breccia corresponds to a heritage of the geological history. It is a vertical yellowish body of siliceous breccia of 3 to 4 m in diameter, which seems to fill an old vertical pit. Composed of siliceous angular chert fragments, the presence of twins of cubic iron oxide, which corresponds to pseudomorphosis of previous pyrite, could have an ancient hydrothermal origin. This siliceous breccia played an important role in the evolution of the cave and also in its fillings, splitting the deposits in two parts.
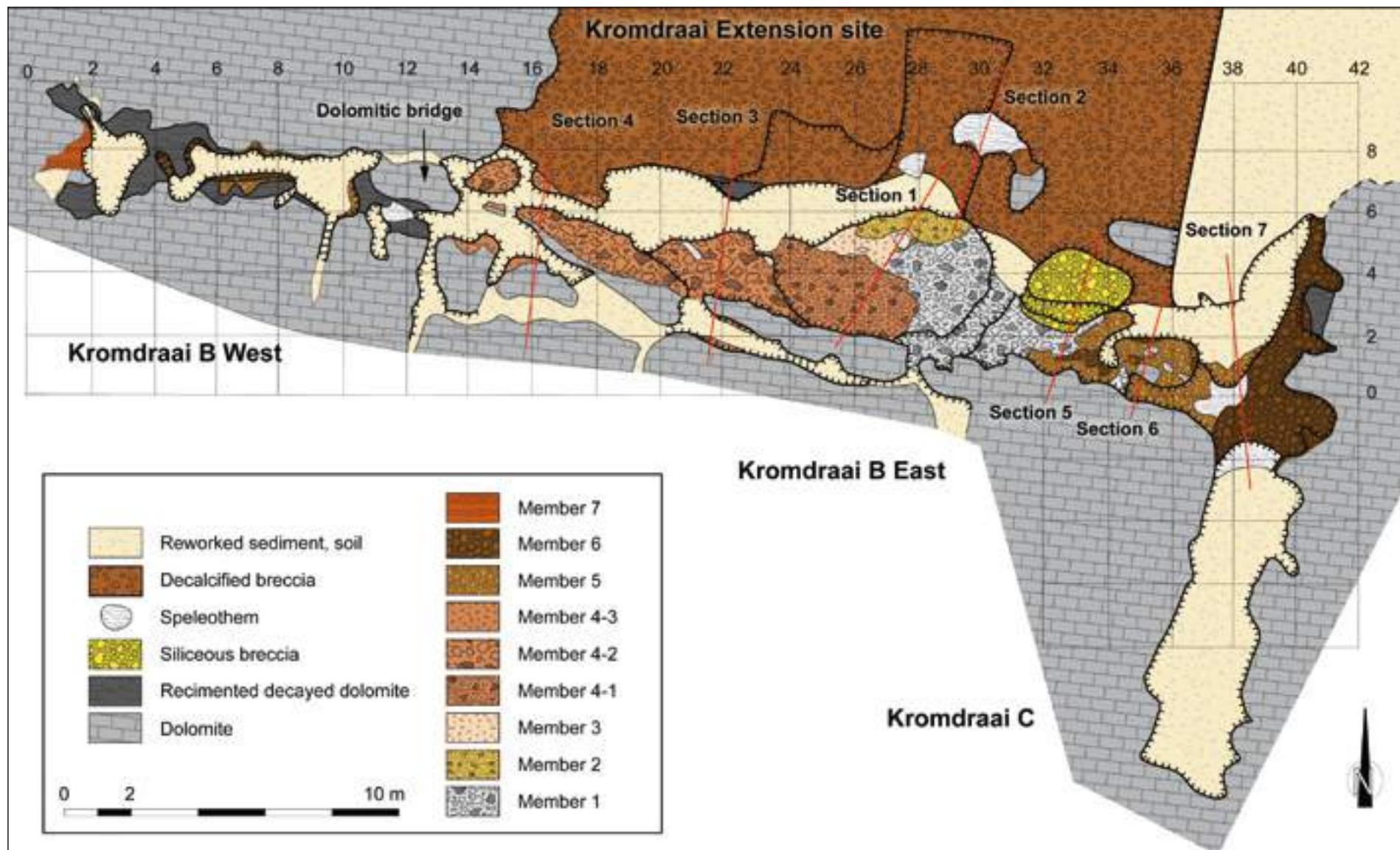
Figure 3.1 *Map of Kromdraai B formations*

DESCRIPTION OF THE SITE

Three sections can be discerned along this gallery from east to west, here demarcated using the reference grid system established by Vrba (1981): from the eastern end to the siliceous breccia, from the siliceous breccia to the first dolomitic bridge, and from the first dolomitic bridge to the western extremity.

From the eastern end to the siliceous breccia (33 to 42 m)

The breccias making up the infill of the paleo-cavity appear suddenly, after the junction with a perpendicular gallery partially emptied by miners (KC, Figure 3.1). The remains of stony breccia and fine breccia are visible along the eastern cavity wall. From the surface, the east-west gallery seems to thrust into this junction. However, the general orthogonal grid geometry of the networks and the exploration of other cavities in the sector suggest that the cavity continues towards the east, but probably a little deeper down. In addition, there are several breccia outcrops about 10 m further east, in the same alignment.

In this part of the site, between 33 and 42 m, the south dolomitic wall is clearly identifiable. On the other hand, the north wall is made up of breccia and it appears obvious that the cavity extends well beyond the excavation limit towards the north.

The infilling of this area is rather complex (cf. *infra*) and we observe the nesting of several different breccias. A good example of this is an area where the discovery of the *P. robustus* type specimen (TM 1517, see Chapter 1) was relocated (Thackeray *et al.* 2003)

(hereinafter called 'holotype block'). Nonetheless, large and consistently strongly sloping siliceous slabs underline the existence of a stony talus with an east-facing dip. This ancient talus, visibly made up of stony breccia with altered chert fragments, seems to begin above of the siliceous breccia and unconformably covers the other nested brecciated formations.

Large flowstones are still visible on the ground at the junction between KB and KC. It was these calcite formations that first attracted lime miners who proceeded to clear the eastern part of the site. However, the links between the flowstones and the breccias are complex and some of them clearly predate the breccias as they are partially dismantled by them.

From the siliceous breccia to the dolomitic bridge (33 to 12 m)

The southern wall of the paleo-gallery follows on throughout the whole of this section. It is partially concealed by breccia slabs up to the highest points. As for the previous section, there is no dolomite along the northern wall here. This artificial wall marking the limit of early excavations is made up of a silty-stony formation, with blocks of chert, altered dolomite and concretions. It is a karstic filling, which shows that this zone still corresponds to a karstic infill. The gallery widens here considerably and the breccia outcrop extends towards the north. Clearing with a mechanical digger, the ongoing excavation enabled us to confirm that this is an ancient underground chamber that we could recognise for more than 20 m towards the north. The discovery of an *in situ* stalagmite and a large calcite flowstone confirm that this is an ancient cave gallery, now decapitated by erosion.

Where the gallery widens, the infill covering these concretions is a decalcified breccia. Several breccia remnants are still present in places within the loose formation, generally protected by dolomite or calcite blocks ('geochemical umbrella'). The orientation and the dip of the elongated blocks (hereinafter called 'fabric') underlines the initial geometry of the deposit and confirms that this zone is on the side of a debris talus, also deriving from the siliceous breccia sector. It develops in a cone shape towards the north and the west. The other more recent breccias highlight the permanence of this geometry and indicate that all the breccias come from this area, around the siliceous breccia.

Towards the west, the talus terminates against a dolomitic block located between 11 and 14 m (Figure 3.1). This dolomitic uplift block is located in the middle of the gallery axis and has been interpreted as a rise in the dolomitic substratum (Partridge 1982). In earlier works on the site, a dolomitic partition starting at a depth of over 10 m was used to explain the presence of this dolomite. Yet the core drilling (B3) described in Vrba (1981) cut into more than 10 m of deposits just beside this partition.

We interpret this dolomite as a rocky bridge. This dolomitic block is in lithological and structural coherence with the walls (the interbeds follow on from each other, the dip is the same) and is consequently clearly in place. But in contrast to a rise in the substratum, which we have never observed in cavities in the sector, this could be the gallery vault. Vaults are often very irregular and are cut into by dolomitic vault pendants several metres to several tens of metres high (cf. the vault pendants

in Milner Hall, Sterkfontein). The lowering of the vault would be perfectly coherent with the sudden convergence of the walls at the western end of the chamber. Lastly, calcite, but also dolomite altered *in situ* (ghost rock), which are generally preserved in the higher parts of cavities, are conserved between the dolomitic uplift block and the south wall. Thus, the depth of the dolomitic substratum identified by the core drilling, the general irregularity of the limestone vaults and the presence of calcite and ghost rock imply that this block is more surely a rocky bridge. In this way, the initial gallery and the infilling deposits should pass below it and continue towards the west. This dolomitic bridge does not correspond to a partition of the lowest Members of breccias, but it stopped the upper ones that were accumulated against it.

From the dolomitic bridge to the western extremity (12 to 0 m)

The part of the site stretching from the dolomitic bridge to the western extremity (12 to 0 m) presents a different morphology. Whereas the first two sections are really only the southern part of a former chamber filled with breccia, here the dolomitic walls contract suddenly at 15 m (Figure 3.1). From this point onwards, the width of the gallery does not exceed 4 m and narrows progressively towards the west.

The initial height of the passage also seems to decrease, as shown by the presence of the dolomitic bridge. But other elements also corroborate this. Classically, galleries close in progressively towards the top, which is coherent with the narrowness of all of this section. In addition, the presence of ghost rock still positioned against the dolomitic walls is a characteristic feature of high zones in passages where these very fragile weathered rocks are only residually preserved. This can be explained by the fact that erosional dynamics are weakest in these areas, but also that they were secondarily indurated by calcite brought by saturated infiltrations from the surface. The presence of these ghost rock remains, forming bridges in places, indicates that this zone is not far from the initial passage vault. They are also associated with and partly indurated by very white calcite concretions.

At the western end of the site, breccia can only be perceived through 'windows' in the ghost rocks. These perforations are much more recent and are linked to crypto-corrosion below the pedologic soil, which perforated the ghost rocks and thereby shows that the brecciated infill extends further towards the west.

These observations also show that the end of the surface site does not by any means correspond to the end of the gallery. From the rocky bridge, we can follow the progressive westward dip of the infill roof. At the same time, the walls constrict and ghost rocks become more abundant. This lateral variation simply shows that the gallery roof gradually drops in keeping with the slope. It thus very probably continues towards the west, below the present dolomitic lapiaz.

A NEW PROPOSED STRATIGRAPHIC DESCRIPTION OF THE KROMDRAAI B KARST FILLINGS

Axial and transversal section recording, the characterisation of the different breccias and the analysis of their contacts enable us to propose a new interpretation of the stratigraphy of the KB deposits. In this section we will often refer to Table 3.1 as to allow the reader to easily establish a correspondence between our revised stratigraphy and the one previously published by Brain (1958) and Partridge (1982). We have shown that the overall pattern corresponds to a dissymmetrical cone with an apex located in the siliceous breccias, directly below the initial entrance. In this description, we will treat the west and east sides of this talus separately. This is essential as these two parts of the cave do not record the same stratigraphic sequence. However, they are complementary and enable us to construct the general history of the site.

From the siliciclastic breccia to the western end of Kromdraai B West

Member 1 – First breccia level, formation of the main talus

Member 1 is the oldest infill identified up until now and is only visible in KB East, where it lies all around the siliciclastic breccia (Figure 3.1). It is made up of a breccia including altered and non-altered blocks of chert, several dolomite and ghost rock fragments, all covered in a grey, indurated, rather abundant matrix. The calcitic infill is dominant where the blocks are largest (interstitial residual voids); elsewhere, the matrix is pale as a consequence of the high calcite content, and calcite crystals and lattice are visible. The rest of the matrix is made up of dark grey particles mainly corresponding to reworked altered dolomite rich in manganese and iron.

When we measure the fabric of the chert slab elements throughout the member, we clearly perceive the existence of a system of radiating slopes with dips reaching 35 to 45°, which is in keeping with the scree slopes generally observed underground. The system of slopes and dips runs: (i) towards the southwest,

between the siliceous breccia until the southern wall – here, the breccia is coarse and rapidly runs against the southern wall; (ii) towards the west, in the axis of the gallery, mostly truncated by the subsequent evolution of the cavity, and (iii) towards the north, perceptible in the indurated breccia.

This stony cone system corresponds to the high part of a talus, formed by the collapse of decayed dolomite around the siliceous breccia. The core drills first described in Vrba (1981) indicate that this complex is 16 m thick. The geometry of this talus is markedly dissymmetric, with a short dip towards the south (as the wall is nearby) and a long dip towards the north. This indicates that the supply zone is not located in the middle of the gallery, but quite near the southern wall, which is relatively common in the region and perfectly in keeping with the general northern dip of the dolomite.

Most of this member could correspond to internal cavity collapse, before any direct communication with the surface (cf. Member 1 in Sterkfontein). The weakness zone, formed by contact between the dolomite and the siliceous breccia (differential permeability, former alteration), could have favoured the formation of a swallow hole. For this reason, the first talus developed all around these breccia, beneath a more fragile vault zone. The fabric of the elements composing this breccia, combined with the presence of fragments of siliceous breccia and cubic iron (pseudomorphosis of pyrite cubes), confirms that the zone located near the siliceous breccia is indeed the zone from which the material accumulated in the cavity derives. As the vault was at its highest here, the entrance logically formed here when the topographic surface cut into the cavity. Moreover, this phenomenon is visible for another cavity located about 50 m southeast of KB.

Member 2 – First breccia level of the secondary slope

A stony breccia capping the south and the western part of Member 1 seals a clear discordance (Figure 3.2). The contact outlines a slight westward slope, but it drops more clearly towards the north and becomes subvertical. This contact is not easy to see as only a residual, much altered, breccia plating remains. However, it clearly differs from Member 1 as it presents very regular bedding, dipping about 30 degrees in a
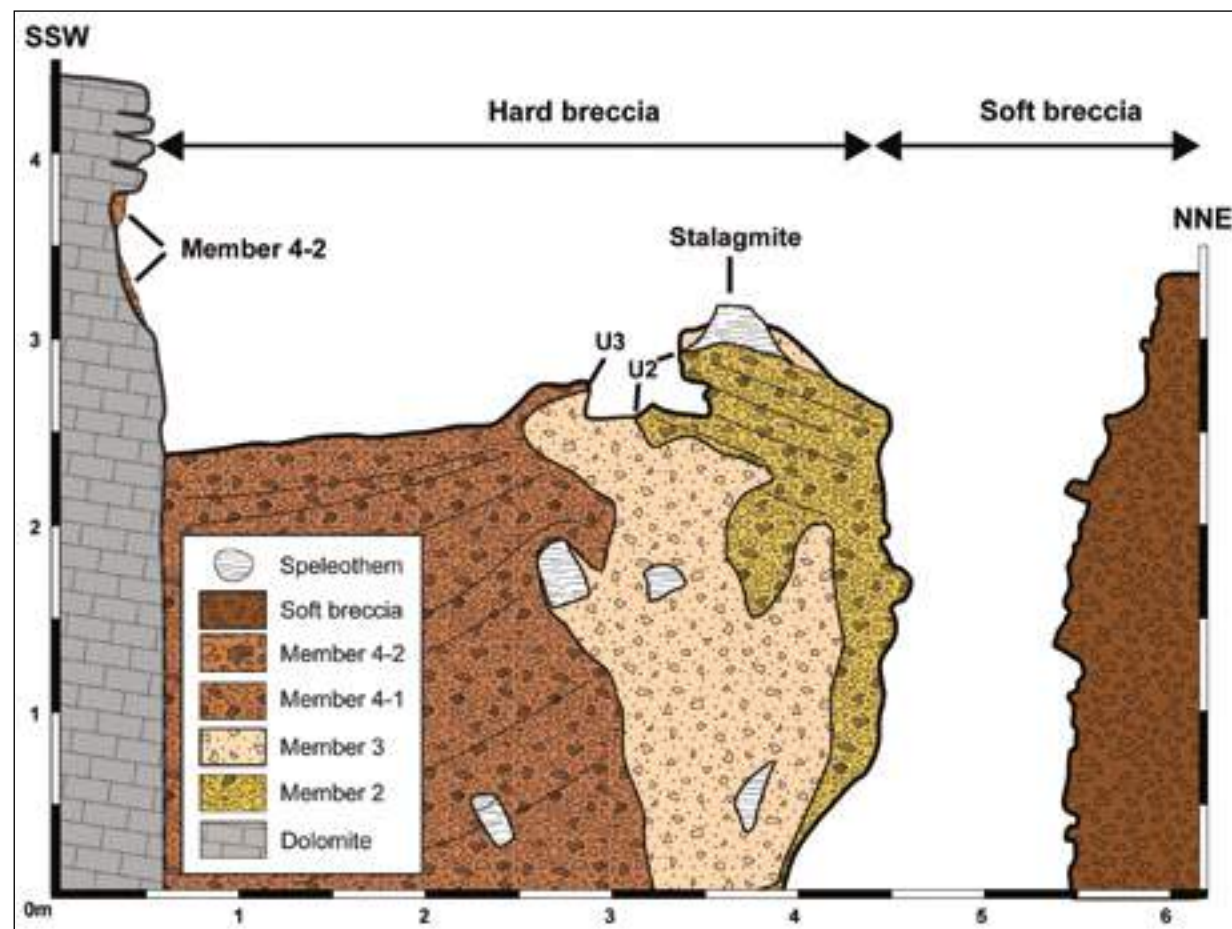

Figure 3.2 *Cross section 1 located in the central part of KB West. The near vertical contacts correspond to important unconformities in the cave deposits.*

northern and north-western direction. It is rich in gravels with an abundant matrix. Lastly, the rather considerable calcitic cementation gives this level good coherence and a whitish colour where calcite impregnations stand out.

The large majority of the coarse elements are made up of angular to blunted dolomite and chert fragments, but we can also identify siliceous elements derived from the siliciclastic breccia, as well as purplish ferruginous elements. Several fine zones, with more matrix, alternate with the chert slab alignments.

Member 2 corresponds to the development of a second slope that covers the rest of Member 1 and seals the truncations (unconformity U1). The western part of Member 1 was thus first recarved by renewed karstification (decalcification and suffosion). However, a large quantity remains in the central part of KB, around the siliceous breccia. Member 2 then seals the subvertical truncation that affects the breccia of Member 1. They form a new north- and west-facing slope, where the rest of the cave was still partially empty.

This breccia is only residually preserved and now only forms a plating against Member 1. However, towards the north, it continues as a brown silty-sandy formation with gravel and sparse blocks. The detailed drawing (Figure 3.3) enabled us to follow the transition from the breccia to the soft formation. In spite of the perturbations linked to bioturbation (burrows), we found a comparable fabric and the same proportion of coarse elements (stones and blocks) in a rather abundant matrix. This is thus the decalcified facies of Member 2. The geometry of the elements in this facies highlights the extension of the talus towards

the north. This formation seals a stalagmite, which reaches a diameter of nearly one metre and also embedded a large sloped and broken speleothem.

Member 3 – Pinkish sandstone with broken speleothems

The fine brecciated Member 3 is rather original. It is pinkish in colour and preserved vertically between Members 2 and 4. For a long time we hesitated before placing it here as these two latter breccias are similar in composition and organisation. Member 3 could have been 'intrusive', sealing a narrow karstified channel in the same older breccia. However, detailed observations and the analysis of thin sections enabled us to collect several convergent markers indicating that these three breccias make up distinct and successive sedimentary cycles (Figure 3.2). Member 3 is discordant with Member 2, which contains clearly truncated stratified levels. This signifies that a new phase of alteration and erosion evacuated all the western part of the talus of Member 2 (unconformity U2). This could even have affected Member 1 in places and it is possible that Member 3 lies directly on Member 1 deeper down.

This discordance represents a relatively long period of time as, after the deposition of Member 2 and its cementation by calcite, a phase of alteration and suffosion evacuated all the western part of the talus of Member 2. A stalagmite developed at the top of what is left the Member 2 (Figure 3.2). It seals the stratified facies with cherts, sloping towards the west, and underlies the U2 unconformity. The small calcite flowstone that extends out from this stalagmite also highlights this unconformity between Member 2 and Member 3. The stalagmite and the little flowstone are, in turn, covered by the pinkish sandstones from the

following member (3) with no sedimentary structure. In this exact sector, just around the stalagmite, this discordance is not necessarily angular. It extends towards the northwest as a blackened, ferro manganic (pyrolusite) surface, which also underlines the discordance. In addition, several calcite laminae are still visible in places. This concretion is currently being dated as it would enable us to chronologically position this discordance and thus obtain *de facto* minimum ages for ms 1 and 2.

In Member 3, the stratification is hard to discern and the composition of this breccia is rather original, which makes it possible to distinguish the other members. It has high matrix content and can be defined as coarse sandstone in which we observe several more or less detrital but completely disorganised zones, or even clusters. Clasts are rare, made up of angular chert fragments and more or less altered pieces of dolomite. But it is the presence of numerous fragments of white, very crystallised calcite concretions that distinguishes this member the most. They are in reworked position and correspond to the dismantling of the flowstone or concretions a little higher up. However, we did not observe a high proportion of dolomitic blocks, which would tend to point towards more generalised dismantling of the vault.

Given the small outcropping surface, it is not easy to establish the formation conditions of this fine breccia (here we will refer rather to coarse thick sandstone). However, the importance of the surrounding matrix and the absence of clear structuration could suggest mass input, perhaps as a mud flow. The gravel and the clayey-silty matrix covering the calcite block samples higher up could have abruptly sealed a channel cut into Members 1 and 2.

Another important element concerning the sedimentation mode is that these pinkish sandstones fossilise the stalagmite. And the latter shows no sign of renewed growth. This could indicate that the formation of this pink breccia was rather rapid, or even abrupt, as although the water supply from the vault must have continued, we cannot perceive any further flowstone development downstream of and following on from the stalagmite, which could signify sedimentation stoppages in this member. In addition, the presence of sparse concretion blocks in all sorts of positions (one of them is vertical), could result from mass formation. They are not laid out following the talus slope, but in bulk in the matrix. It is even possible that these concretions were broken by the sudden accumulation of this mud flow.

These coarse sandstones contain calcite veinlets that correspond to fractures in the breccia, subsequently filled in with beige calcite. In the upper part, these veinlets connect with a fine calcite flow, marking the contact here between Members 3 and 4. The upper surface of this small flowstone is well rounded and undulating in places and could resemble a capping flowstone. But it divides into two parts in places, as if it was both sides of a filling flowstone. The lower surface moulds the breccia irregularities, but its upper surface is less clear. Here we observe the extreme complexity of the links between calcite flowstones and breccias (Bruxelles *et al.* 2014). Once again, this calls for caution in using concretions too hastily for the chronological setting of sites.

Member 4 – Stratified breccia and gravelly talus
A marked discordance truncates these coarse sandstones (U3, Figure 3.2) and the contact with the lower member is undulating or even subvertical in places.

The largest clasts from Member 3, and in particular pieces of calcite, remained in relief due to alteration and differential erosion. This discordance is moulded by a stratified breccia with alternating gravelly levels including sparse large blocks and relatively coarse sandstone levels.

This formation is visible over a thickness of at least 5 m. It drops progressively towards the west (former talus, Figure 3.4), then disappears deeper down at the level marking the limit between KB East and KB West, represented by the dolomitic bridge joining both walls of the gallery. We do not yet know the extension of this formation deeper towards the north. Future excavation campaigns will enable us to identify whether this talus also forms a cone or whether these deposits are contingent on the contact with the southern wall of the paleo-cavity.

The beds dip approximately 30 degrees towards the west (Figure 3.4). In detail, this member is made up of a sequence of levels of conglomerates with chert gravel, fragments of siliceous breccia, dolomite and more rarely of calcite. There are also several sparsely distributed larger decimetric chert or dolomite blocks. Lastly, microfauna and macrofauna from Member 4 have been published (Member 3; Vrba 1981; Partridge 1982; Vrba & Panagos 1982; Braga *et al.* 2013).

Three facies (Submembers) can be discerned in Member 4 (Figure 3.4 and Figure 3.5, Sections 3 and 4):

■ Submember 4.1 is nearly 2 m thick. Irregular thicknesses of sandstone and conglomerate beds alternate. The facies of these beds also varies laterally and more and more blocks appear in the distal part of the former talus. This part is thus

nearer to the lower part of the talus where the largest elements accumulated. They are made up of blocks of chert, fragments of dolomite and pieces of flowstones. Small calcite layers are interstratified in some levels. These could be used for U/Pb dates, but they could contain a considerable detrital load.

■ Above Submember 4.1, Submember 4.2 is about 5 m thick. Without any noticeable discordance, the sandstone becomes pinkish, more homogeneous, and with less visible stratification. However, this member is not very visible in the proximal part as it was almost totally excavated by Vrba in 1977. As in Submember 4.1, the facies becomes laterally coarser towards the west. This very coarse conglomerate consists of large blocks of dolomite, chert, ghost rocks and siliceous breccia, ranging from several tens of centimetres to over a metre, embedded in a pinkish sandstone matrix, comparable to the sandstones identified in the proximal part of the talus. They all present a very clear fabric towards the west. Bones are present in the sandstone proximal part and in the distal part with blocks. The upper part of 4.2 contains less large blocks and more matrix, but we can still identify the petrographic composition of this member, with abundant chert blocks and especially pieces of dolomite and calcite.

■ During the aggradation of Member 4, the space between the vault and the slope decreased. The first point of contact between the talus and the roof of the cave was the dolomitic bridge. The presence of such pendant illustrates the irregular lowering of the vault towards the west. The detrital sequence then becomes richer in sandy matrix as it constitutes the terminus for water run-off from the surface (Submember 4.3). It

nonetheless covers sparse pluridecimetric blocks of dolomite, chert and calcite. They show that this zone is still at the base of the talus and that several elements descend until here. The petrographic composition of the coarse elements is the same as that observed throughout Member 4.

Member 5 – Fine pinkish sandstones with ferruginous fragments, calcite blocks and ghost rock clusters

In KB East, on the other side of the rocky bridge, things are very different and we do not observe any of the preceding members described in KB West. It appears that we have here a major unconformity (U4), which could cover a long period of time (see after). As the breccias described above are the oldest of the site, and that the ones described below the youngest, we decided to name them with the last letters of the alphabet. This allows us to insert new members, which will undoubtedly be found during the next steps of excavation.

Several metres to the east of the dolomite bridge, a sandstone formation with no stratification is only preserved against the southern wall. It is orangey-brown in colour and composed exclusively of small fragments of rounded cherts and small cubic ferruginous elements. The latter are not, or only very rarely present in the pinkish breccias in Members 3 and 4, thereby allowing for the differentiation of this member. But the most distinguishing criterion is the absence of dolomite fragments, which are however relatively abundant in the breccia further east. This formation fills a fissure aligned ESE, leading onto the southern wall of the paleo-gallery (Figure 3.1). It is present as a plating on the southern wall and it then extends towards the west, on the other side of the dolomitic bridge.

From this bridge onwards, the space between the two gallery walls decreases and oscillates around 2 m. Remains of non-stratified sandstones are preserved as residual plaques against the walls. In the upper part, these sandstones cover blocks of fine black sandstone with abundant white calcite partitions. These are ghost rock fragments, indurated by calcite and reworked into this formation. However, it is important to note that they are very abundant at the top of this member, probably highlighting the contact between the sandstones and the gallery vault. Elsewhere, more and more *in situ* ghost rocks are visible on both sides of the gallery and even form 'bridges' between the walls (Figure 3.1). Lastly, we observe the presence of *in situ* calcite concretions, developed against the dolomite or the ghost rock. All these morphological and sedimentary elements indicate that this is the gallery vault and that it drops very gradually towards the west.

The orangey sandstones thus fill the high part of this paleo-gallery. A rather rough dip is visible 4 m to the
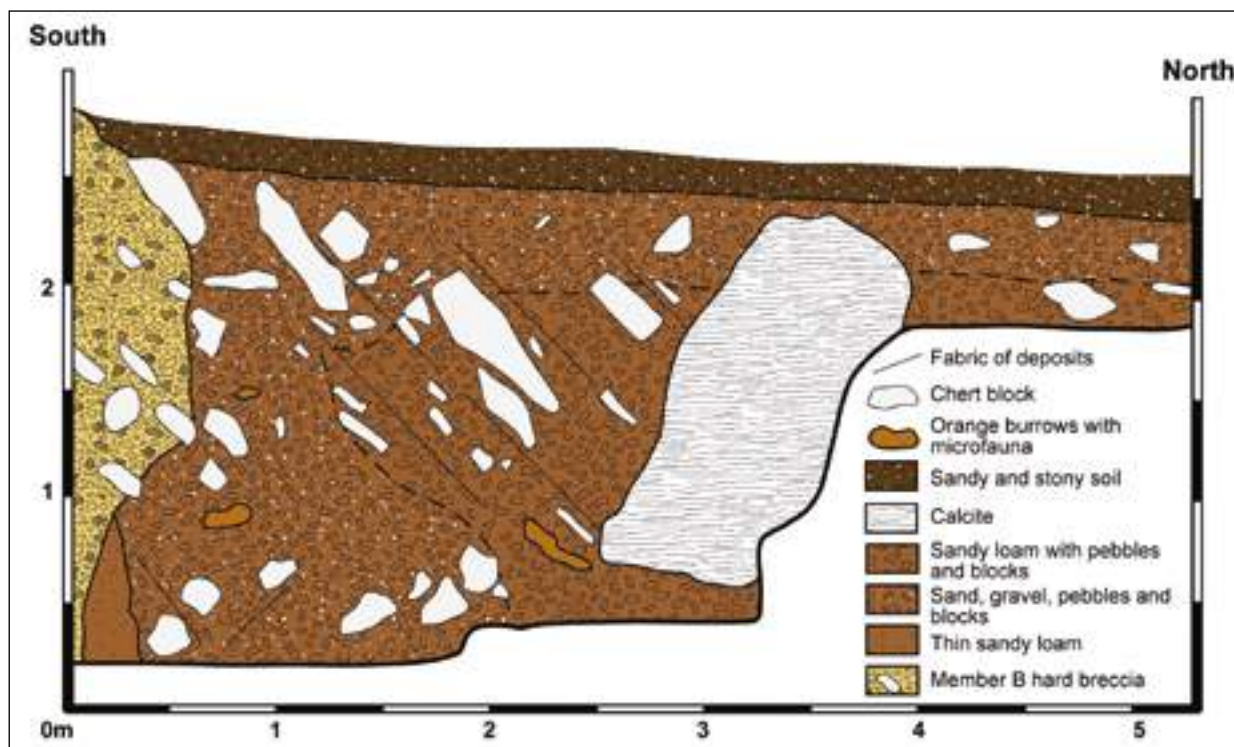
Figure 3.3 *Cross section 2, between the Member 2 hard breccia and the decalcified breccia found in 2014.*

west of the dolomitic 'bridge'. It is west-facing and indicates permanent transit towards the western part of the cavity. The deposition of these sandstones occurred by run-off or mud flows and the latter contributed to the dismantling of the concretions and the ghost rocks that were preserved at the vault. For this reason, this member contains more clusters of reworked ghost rocks and fragments of concretions than all the other older deposits. In places, this breccia

appears to have been injected into the ghost rock still in place.

Member 6 – Orangey breccia with blocks of chert and goethite cubes

In this same sector, an original breccia stands out from all the others observed up until now. The coarse detrital part is exclusively made up of rounded

chert fragments with a yellowish white patina. We also observe the presence of heaps of ferruginous cubes, in much higher proportions than in the other members. This is the pseudomorphosis of pyrite cubes into goethite or hematite. These heaps derive from siliciclastic breccias that were then reworked in the superficial formations. With the cherts, they make up a stock of insoluble material that often forms a paving at the soil surface. The high concentration
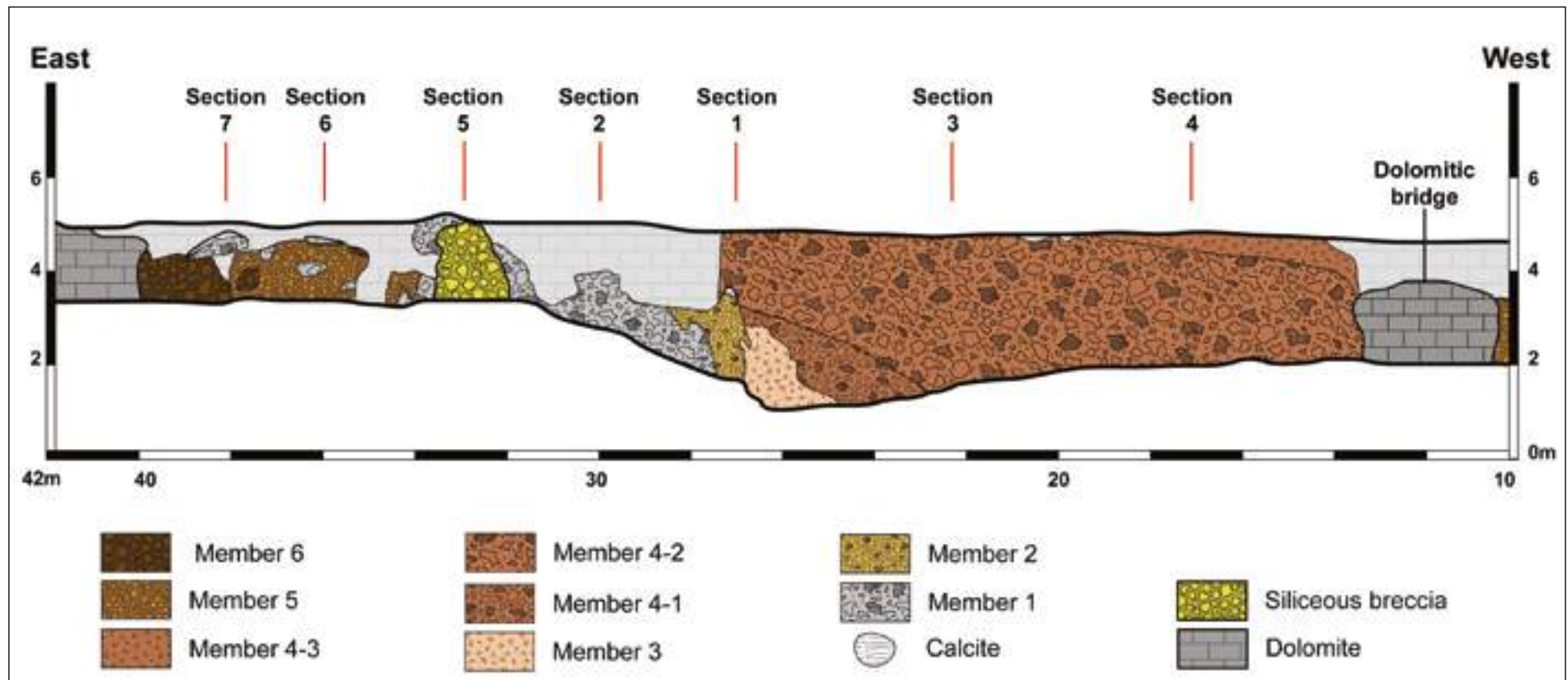
Figure 3.4 *Cross section along KB East formations. We can recognise the main talus in the central part of KB West (Members 1 to 4). The distal parts of the paleocave were filled by the latest Members (5 to 7).*

of these heaps, combined with the total absence of calcite and dolomite, could indicate that this formation consists of materials mostly derived from the surface (colluviums), having undergone marked pedological alteration.

In the western end of the site, this breccia dips progressively in depth and disappears beneath the residual ghost rock. The surface corrosion morphologies (lapies) cut into it in places and show that it extends more and more deeply towards the west.

The stratigraphic associations between Members 5 and 6 are complex, and contacts are extremely irregular when they can be observed. Member 6 nests into and is clearly discordant with Member 5 (discordance U5). We thus observe here another alteration phase of the preceding breccia (Member 5), then the filling of the voids newly formed by the breccia of Member 6.

Member 7 – Fine sandstones with bone and gravelly conglomerates

At the western end of the site, where the gallery progressively disappears beneath its dolomite vault, a last member can be discerned (Member 7). This is a fine laminated sandstone, including gravelly zones in places. Calcite veinlets run through these sandstones and highlight the sedimentary or later discontinuities (fractures, compaction, desiccation ...). These laminites lie indifferently on the dolomite, ghost rock or white calcite and clog up the last voids of the gallery right up to the vault. The detrital zones only contain chert fragments and several ferruginous cubic fragments. This thus strongly resembles the coarse fraction in Member 6 and could represent the last stages of this

formation, but with a different deposition mode. In Member 6, we observe no clear stratification whereas hydro-sedimentary sorting is very clear. Lastly, we note the presence of a high concentration of large bones. They could have been floated, but it is more likely that they were brought there by fauna seeking refuge in the back of the cavity.

To the east of the siliceous breccia until the eastern end of the site

In the area to the east of the siliceous breccia until the eastern end of the site, the nature, the composition of the clastic elements and the matrix of the breccia formations, as well as their stratigraphic associations, were correlated for the first time with those described in KB West. Member 1 was identified in this sector, but Members 2, 3 and 4 are absent from the currently visible outcrops. We thus shift directly to Members 5 and 6, which illustrates the extent of discordance in this type of complex karstic infilling.

Member 1

Between the siliciclastic breccia and the southern wall, Member 1 continues towards the east (Figure 3.4). At this level it fills a residual void just 1 m wide (Figure 3.5, Section 5). This stony breccia with a grey matrix and abundant calcite presents a south-facing fabric in places. Here, we are on the small side of the dissymmetric slope. It is interesting that this formation is present all around the siliciclastic breccias. This shows that this member, which is the oldest of the site, largely clogged the entrance zone. Here we are not far from the apex and on account of its geometry, we can imagine that this first infilling could have oriented the ensuing breccia deposition. In this way, the secondary talus, including Members 2, 3

and 4, may not have accumulated in this sector due to a possible 'dam' formed by indurated Member 1 between the dolomitic wall and the siliceous breccia.

Member 5

Member 5, an orangey to pink sandstone, with no apparent stratification, is still preserved against the dolomitic walls (Figure 5, Sections 5 and 6), in marked discordance against Member 1 (vertical contact, moulded voids, unconformity U6). These sandstones are made up of small chert fragments, but also of angular ferruginous elements caught up in a silty indurated matrix. They are comparable in all respects to the preserved sandstones in KB West, on the other site of the dolomitic 'bridge'. We observe in particular cubic ferruginous elements that are not present in the same proportions in all the other sandstone formations (Members 2, 3 or 4).

At the eastern end of the site, the Member 5 sandstones cover a calcite floor sealing a greyish formation that could, on the basis of its facies, be related to Member 1 (Figure 3.1). Here, we also find a remnant of Member 1 against the southern wall and protected by a strip of flowstone. On this floor, the sandstones from Member 5, like those of KB West, cover calcite fragments and even seal the floor truncation. The unconformity U6 is very clear here. This breccia infill ends against the dolomitic wall limiting the site at the east. At this level, it is only preserved against the walls as plaques. It covers blackish sandstone vesicular blocks, with numerous borders and small calcite geodes. We also observe here ghost blocks that were integrated into these sandstones during their deposition. Like in KB West, the presence of these ghost rock clusters and the proximity of the dolomite show that this is the top of the gallery.

The deposition of these sandstones is not easy to understand. We have not identified any clear sedimentary structures as only coatings subsist against the walls or around blocks from Member 1. This fine breccia is thus still part of particular contexts (walls, inter-block voids). Although we cannot discern the deposition mode (run-off, mass movement), it appears to seal an important discordance against Member 1 and it covers the blocks and residual evidences of the latter (U6).

Member 6 – Chocolate breccia with fragments of chert and ferruginous blocks

Member 6 is clearly nested in the Member 5 sandstones. The obvious, but very irregular, contact highlights the existence of discordance between the two breccias (unconformity U5). This member takes up the whole eastern side of the site. It is a breccia of silica blocks (chert and siliceous breccia) associated with a rather high proportion of ferruginous fragments, which are cubic at times (Figures 3.4 and 3.5, Section 7). The matrix is orangey-brown and rather abundant in places. It only covers small siliceous fragments, often blunted, as well as more or less cubic ferruginous fragments. This breccia is stonier than Member 5 and is comparable in all respects to that observed at the west of the site, between the dolomitic bridge and the western limit of the site.

There is no well-marked stratification, even if several coarser levels seem to emerge in places. However, the orientation of the largest chert slabs highlights a general dip towards the east. It is important to point out the presence of small fragments of orangey pink breccia in this member. They may correspond to materials derived from Members 2, 3, 4 or 5, which were further west and higher up, in the proximal part of the talus.

As at the other side of the site, the breccias from Members 5 and 6 are part of the last stages of the infill. In both cases, these two formations are closely associated, even if we observe rather clear unconformities between them. In places, it remains difficult to perceive contact as these levels were disturbed by bioturbation. In this way, at the eastern end of KB east, part of Member 6 is riddled with more indurated tubes. These aspects are the result of the work of termites carving their galleries in this infill and redistributing the matrix (Parkinson *et al.* 2014). This
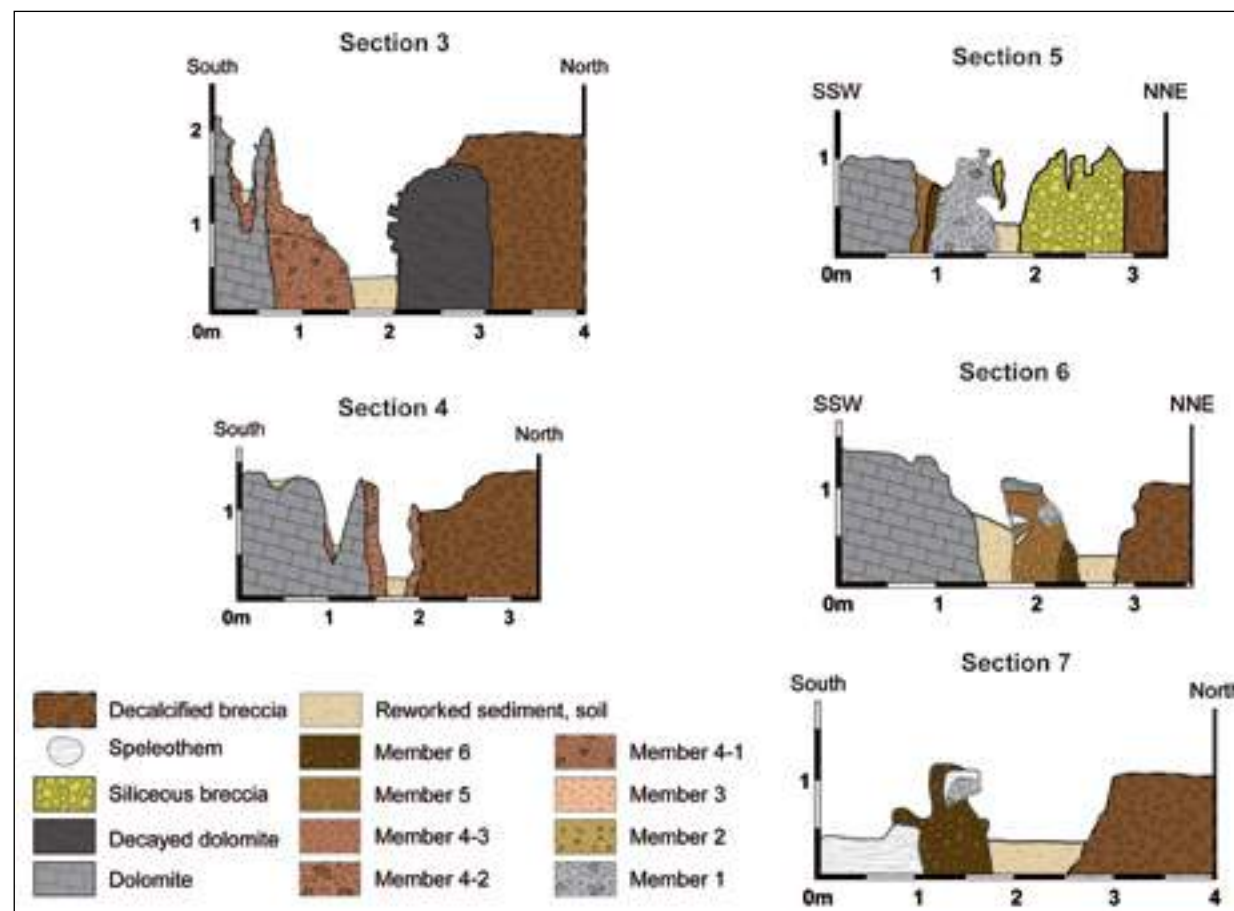

Figure 3.5 *Transversal sections of Kromdraai B East (Sections 3 to 7)*

bioturbation, which also affects Member 1 in places, could have occurred at a very late stage, after these members were cut by the topographic surface and after the partial alteration of these breccias.

The 'holotype block'

In the 'holotype block' sector, a large block of breccia was left by previous excavations (between 34 and 37 m). This appears to be the block where the *P. robustus* holotype, TM 1517, was found (Thackeray *et al.* 2003; Braga *et al.* 2013). It represents a volume of about a cubic metre and is made up of Member 5 and 6, sandstones. However, it covers breccia blocks with a grey matrix derived from Member 1 (Figure 3.5, Sections 6 and 7). Moreover, a remnant of Member 1 is still visible against the southern wall and it is topped by a relatively thin flowstone fragment. All this is incorporated in the thin pinkish breccia. The characterisation of the different breccias enables us to confirm that the whole 'holotype block' is a conglomerate of breccias from Members 1, 5 and 6. Furthermore, we cannot rule out the possibility that other breccia blocks, such as Member 2, for example, may also be incorporated in this conglomerate. These could be identified by systematic thin section observations combined with geochemical analyses. Here, we can also gauge the complexity of the post-depositional phenomena affecting these breccias and thus the difficulty in locating the formerly discovered fossils in the right breccia formation.

INTERPRETATIONS CONCERNING THE EVOLUTION OF THE CAVE

This characterisation of the different breccia combined with complete stratigraphic recording enabled us to infer the evolution of the cavity and therefore the conditions in which the bone remains were trapped. The successive stages of the dismantling of the cave can be identified by the nature of the deposits and they clearly span a long period of time. Four main phases can be distinguished.

Member 1

Member 1 is made up of a dark breccia and presents all the characteristics of internal cavity deposits, with no direct link with the exterior. The matrix is exclusively composed of decayed dolomite (reworked ghost rock) mainly constituted of iron (Fe) and manganese (Mn). These are black-brown silty sands that present no sign of oxidation, such as that which occurs when these materials are exposed on the surface and affected by pedogenesis. The chert fragments do not present the characteristic alteration observed on surface elements: blunted angles and a thick whitish cortex. Here, they are angular and bluish grey, still slightly translucent. We also note the presence of chert slabs, fragments of speleothems, as well as clusters of collapsed ghost blocks. All these deposits are typical of cavities initially formed by fantomisation where the residual weathered and decayed rock is in the process of being emptied (Dubois *et al.* 2014). The ghost rock is evacuated by compaction and erosion along the main circulation axes. Then, as the morphology of the altered rock roof is very irregular, the higher parts are progressively evacuated by the successive internal collapses. Here, this phenomenon was guided by the contact between the siliceous breccia and the dolomite, where the ghost rock preferentially developed. Furthermore, in Member 1, we observe numerous fragments of this siliceous breccia as well as associated cubic twins of oxidised iron.

Most of the detritic infill of the cavity occurred through this contact between the dolomite and the siliceous breccia. The general morphology of the talus and the fabric of the elongated elements highlight this process. During the accumulation of Member 1, there was no direct communication with the surface and we can assume that the entrance was not yet formed at this level. However, there was indirect communication with the surface as rare bones (mainly microfauna and two baboon teeth; Vrba & Panagos 1982) were found there. This type of process is not surprising and can still be observed today in the low parts of Sterkfontein Cave where fauna bring animal remains far from the entrances.

The formation of this member thus corresponds to a relatively early phase in the evolution of the cavity. Communication with the surface is still indirect and the relatively abundant ghost rock is in the process of being evacuated. The orifice straight above the talus apex was not yet open but an indirect connection with the surface existed.

Members 2, 3 and 4

The nature of the breccia at Members 2, 3 and 4 is radically different to that of Member 1. The sandy-silty matrix has a pink to orangey tint deriving from the trapping of superficial formations subject to ferruginous type pedogenesis (oxidised iron). We thus observe here a more direct link with the surface than during the formation of Member 1. Therefore, the morphology of the cave changed and a more direct entrance formed. According to clast layout (fabric) and the morphology of the successive taluses, it must have been located at the contact between the dolomite and the siliceous breccia. The surface formations

(colluvium, soil and bone remains) were thus directly trapped in the cave and accumulated as a talus at the base of the entrance. These different members and the discordances separating them illustrate alternating phases of detrital sediment accumulation, cementation by calcite, then alteration and erosion. Members 2 and 3 are stratified and highlight the progressive formation of the slope. For Member 3, which seals a small stalagmite, the formation process was different. We observe the absence of stratification and an important matrix support covering the calcite blocks. This could represent a partially trapped mud flow in the cavity, formed on the hill slope above the entrance. Member 4 allows us to distinguish the sedimentary mechanism along the slope: the proximal part is mainly made up of fine sandstone materials, whereas the distal part contains more blocks of dolomite, chert and calcite. Note that these blocks, wrapped in the orangey sandy-silty matrix, do not only come from the surface. The presence of calcite shows that this is a progressive dismantling of the gallery vault. The thinning of the vault by surface erosion led to mechanical readjustments causing this instability. This evolution of the gallery can be correlated to a progressive widening of the entrance.

These deposits cover Member 1 in discordance and plug a large part of the residual void in the gallery. In the west, they run into the dolomite bridge formed by a former lowering of the vault. At this level, the cavity is thus totally filled up to the ceiling. To the west of the dolomitic bridge, a residual void remained due to the rise in the vault. However, this void was not yet connected to the surface and was only filled in later during the deposition of Members 5 and 6.

The discordance between Members 1 and 2 (U1) as well as the very different origin of the infills reveals an important morphological evolution of the cavity. The deposits shift from being mostly internal to mostly external inputs, corresponding to the trapping of superficial formations. It is thus likely that these two formations are separated by a long period of time, as erosion had time to decapitate the cave and form a new, more direct entrance. The infill was governed by alternating deposition and erosion phases and is composed of surface inputs as well as internal gallery collapse inputs. They fill most of the east part of the KB site up to the dolomitic bridge that blocks the system and prevents the KB West infill from continuing to be filled by these inputs. The sealing of this part occurs during a third stage.

Recent cosmogenic dates (Dirks *et al*. 2010; Dirks & Berger 2013; Granger *et al*. 2015) give an average rate of erosion between 3 and 5 m/Ma in this area. Given the estimation of the age of these formations (between at least 2.5 and 2 Ma, cf. *infra*) and in keeping with the geometric reconstruction carried out by Partridge (1982), the entrance must have been located about 10 m above the present-day topography.

Members 5 and 6

Members 5 and 6 are absent from the central part of the site (Figures 3.1 and 3.4) and are only present at the eastern and western ends. At KB East, these two breccias are nested in discordance in Member 1. To the west, they are separated from Member 4 by the dolomitic bridge. There must, however, be contact between these two members lower down (unconformity U4), and the ongoing excavations should enable us to confirm this.

It is difficult to perceive the stratigraphic contact between breccias 5 and 6 (U5) in the western part of the site. But they are clearly nested to the west of the 'holotype block', whereas elsewhere, the contact is very disturbed by termite action. Globally, we discern a coherent process with the general distribution of the members and a centrifugal organisation of the different successive members. Thus, to the east, the sandstones making up Member 5 are mainly situated between the siliceous breccias and the 'holotype block'. Member 6 is stonier and is contingent on the eastern edge of the site.

Although these two members are different from a sedimentological point of view, we chose to regroup them as they are still closely associated. In spite of very different granulometry, the composition is a particular feature of these formations. The orangey matrix only covers blunted and altered blocks of chert. There is no dolomite or reworked speleothem fragments, apart from the *in situ* dismantling of older flowstones moulded by these breccias. Lastly, numerous fragments of cubic iron (pseudomorphosis of pyrite cubes) are present.

This composition is comparable in all ways to the elements currently making up the superficial formations around the site. 'Ferruginous soil' type pedogenesis is responsible for the disappearance of all the elements prone to dissolution (dolomite and possible calcite blocks) and the chert fragments are more or less weathered. These are the materials that we find in reworked position in Members 5 and 6. They can be interpreted as resulting almost exclusively from the trapping of superficial colluviums. The important matrix in these two breccias and the

absence of stratifications may derive from mud flows from the surface. The latter rework the superficial formations affected by the pedogenesis on the side, upstream from the entrance of the cavities.

Here, practically no further internal cavity supply (dolomite, calcite) is visible in most of the exposed section thickness. This would tend to show that during the formation of these members, the voids were largely clogged up and even that part of the vault, particularly the central part of KB, no longer exists. The apex of the slope made up by Members 1, 2, 3 and 4 was largely truncated by the topographic surface. Then, only two opposite gallery portions remained. These were mostly filled in and trapped the surrounding colluviums.

Another element enables us to assess the condition of the cavity during the formation of these two members. Indeed, we saw that the upper part of the breccia in Member 5 contains ghost rock fragments. We also found remnants of *in situ* ghost rock in several places, between the dolomitic bridge and the western edge of the site. Although the infilling of the last voids by breccias from Members 5 and 6 resulted in reaching and dismantling these still preserved strips against the vault, this signifies that the cavities were nearly totally clogged.

The abundance of indurated ghost rock fragments, which are scarcely reworked in places, evidences the last stages of the complete sealing of this level. The cavity vault was still present at this level but it was relatively stable given the almost complete filling of the cavity. This information on cavity geometry and the state of sealing enables us to understand why this member hardly contains any blocks of dolomite and

calcite from the roof, but only colluviums plugging the residual void between these two members and the vault.

Member 7

Member 7 is an original formation and is only present at the western end of the site. These fine, stratified sandstones are rich in bones and fill a residual void between the summit of Members 5 and 6 and the dolomitic vault. It is not possible to see at this level if there is discordance with Member 7, but their sedimentary structures are very different.

This type of deposit is frequent in caves currently accessible in this sector (Sterkfontein, Lincoln Cave, etc.). It comes from surface run-off that spreads in these mostly sealed cavities. Often, the exploitation of these cavities by miners led to the accumulation of this type of sediment in culs-de-sac, where detrital discharge alternates with decantation facies. In the case of Member 7, continued vault dismantling or burrow digging may explain the arrival of these materials in a residual void, beyond the parts of the cavity totally sealed by Members 5 and 6. This input could thus have occurred at a relatively late stage in relation to the other members and indicates the advanced dismantling of the cavity vault.

CHRONOLOGICAL LANDMARKS

This detailed stratigraphic record of KB enabled us to identify the different formations making up the infilling of this paleocavity, and also to explain their interrelations. It thus became possible to establish a relative chronology of the deposits and to link them to the history of the cavity.

Correlations with earlier stratigraphies

During 1955–56, Brain excavated little of the indurated breccia and concentrated his efforts on the decalcified parts, down to a depth of 5 m (see Chapter 1). He recorded the provenance of remains according to three horizontal levels. Once the complexity of these breccias is taken into account, with their geometry and significant discordances, it is clear that these levels encompass several members of decalcified breccias. The same applies to a fragment of unquestionably knapped chert found by Brain (1958). Other rare pieces are sometimes observable in the superficial formations. They are part of the residual colluvium material reaching a thickness of 1 m, but they cannot by any means be associated with the underlying decalcified breccias. It is important to note that it is very difficult to differentiate between the different members in the decalcified breccia. It is only possible to follow this complex stratigraphy through the different decalcified facies by using geometric reconstructions of outcrops of indurated breccias by observing the fabric and the abundance of coarse elements.

Brain's excavation only cut into two brecciated formations: a stony breccia and a fine breccia (Table 3.1). The stony breccia is located at the eastern end of KB. He explains that this breccia does not contain dolomite blocks, but only cherts and quartz fragments. The location and his description suggest that this is Member 6. It is also interesting to note that Brain compares this breccia to the breccia he excavated in KA. This is in keeping with our stratigraphic analysis and corroborated by the presence of tools in these two formations. As for the fine breccia, he does not separate it in any way, although he notes the existence

of stratification with alternating more or less coarse formations (Brain 1958).

During the course of the Vrba excavations, five core drillings were carried out and a new stratigraphic interpretation was proposed (Partridge 1982; Vrba & Panagos 1982).

By combining information concerning the type of breccia and paleontological data, we observe a radical change in the type of sedimentation linked to the morphological evolution of the cavity. Members 2, 3 and 4 clearly accumulate in a relatively deep gallery where flowstones can develop and where the walls and vault contribute to sedimentation. The only access

to the cavity is a vertical entrance that operates as a pitfall. On the other hand, Members 5 and 6 result from colluvium inputs into an already largely filled cavity. This evolution illustrates a radical change in the morphology of the cavity. It is still deep during the accumulation of Members 1 to 4, and is largely dismantled during the deposition of Members 5 and 6. A long period of time must thus have separated the infilling of the two parts of the site. During this time lapse, the surface was lowered by several metres owing to erosion, causing the progressive dismantling of the gallery. At a rate of 3 to 5 m per million years (Dirks *et al* 2010; Dirks & Berger 2013; Granger *et al*. 2015), at least several hundred thousand years may have separated the formation of these two breccia complexes.

Ongoing excavations in the tender breccia also seem to point to similar explanations. These excavations focus on the decalcified continuation of Member 2, which is one of the two oldest currently accessible fossiliferous breccisa. The discovery of massive calcite concretions, fossilised where they stood, provides very useful absolute dating possibilities. Member 1 is currently the oldest visible detrital formation. This very thick formation represents one of the first stages of evolution of the cavity. The deposition of this member could have covered a long time period, from the exundation of the karstic conduits after the lowering of the base level, to the overlap of the vault by the topographic surface. During this long period, the packing of the altered dolomite, internal collapse linked to mechanical readjustments and the

Table 3.1 *Breccia matches between the different previous studies (Brain 1958; Partridge 1982)*

Brain (1958)	Partridge (1982)	This paper	Description
Stony breccia	Member 1	Member 1	Grey dark stony breccia
Pink breccia	Member 2	Member 2	Bedded orange breccia, fine grains and blocks
	Member 3	Member 3	Pink sandstone with no sedimentary structure. Several pieces of calcite
		Submember 4.1	Pink bedded breccia and sandstone becoming stonier toward the distal part.
	Member 4	Submember 4.2	Massive pink sandstone becoming stonier toward the distal part.
	Member 5	Submember 4.3	Breccia with more abundant sandy breccia
	Member 1 (KB West formation)	Member 5	Orange sandstone including little pieces of weathered breccia and ferruginous fragments
	Member 2 (KB West formation)	Member 6	Orange to brown breccia with only weathered cherts and ferruginous fragments
	Member 3 (KB West formation)	Member 7	Bedded orange sandstone including gravels layers

development of calcite concretions accounted for most of the sedimentation.

CONCLUSION

The stratigraphic study of the site of Kromdraai highlights, first and foremost, the complexity of the deposits. Their accumulation is linked to the evolution of the cavity and its progressive infill and is reflected by a variable sedimentary record. Thus, the nature of the materials illustrates lateral facies variations, sedimentary dynamics and the progressive dismantling of the cavity with increasingly marked surface influence. In addition, several major discordances, which can cover long periods, separate the different formations.

This stratigraphic study also confirmed that the northern limit of the early excavations did not correspond to the maximum extension of the cavity. Therefore, logically, the fossiliferous deposits continue in this direction.

In the same way, the eastern and western ends of the site do not necessarily mark the gallery terminations. What was interpreted as a rise in the substratum in the centre of KB (Partridge 1982) is in fact only the remains of the gallery vault. It is thus very likely that the cavity extends further along the same axis, beyond the current ends of the site, beneath the dolomitic vault.

Finally, in the central part, between 8 and 11 m below the present-day surface, drill core B1 cut into a void (Partridge 1982). The breccia was decalcified in places and undermined by erosion. The gallery must still be connected to other, still unknown galleries in order to export the material. The permanence of this drainage, combined with decalcification phenomena,

explain the regular evacuations of breccia during the course of the complex history of this infill. Each time, the soft material was extracted and evacuated by the endokarst, which was still in hydraulic connection with the rest of the network. The extension and the deepening of the excavation will soon join this void. It will then be possible to observe the rest of the cavity infill, and perhaps to find other unforeseen extensions.

Now that the detailed stratigraphy has been established, it is possible to envisage absolute dating. The large concretions of fossilised calcite from Member 1 will provide a lower limit for the currently known infill. At the eastern end of KB East, a calcite flowstone developed on the remains of a breccia from Member 1. It is discordantly overlapped by the sandstones from Member 5. The dating of this flowstone would provide a first minimum age for Member 1, even though it is not possible for the time being to gauge how long after the deposition of this first breccia the flowstone formed. In the central part of the site, the small stalagmite that developed on Member 2 is also an excellent marker that could elucidate the age of these first two deposits, including the oldest fossiliferous breccia excavated until now (Member 2). Thus, the large concretions sealed by Member 1, the rest of the flowstone at the eastern end of KB and the small stalagmite on Member 2, provide us with the possibility to obtain a chronological framework for the deposition of the first breccias of the site.

Moreover, when the excavation has reached a sufficient depth, we will be able to carry out cosmogenic dates (Al26/Be10) in order to determine the age of burial of the different colluviums that progressively filled in the rest of the cavity. Recent publications have shown the

pertinence of this dating method (Gibbon *et al*. 2014; Granger *et al*. 2015) and it will then be possible to date the levels with no calcite concretions.

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The Kromdraai hominins revisited with an updated portrayal of differences between *Australopithecus africanus* and *Paranthropus robustus*

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INTRODUCTION

Phylogenetic changes, yet incompletely understood, occurred among hominin taxa during the Late Pliocene (3.0–2.6 Ma), a period of net global environmental changes in Africa (de Menocal 2004) likely associated with faunal turnovers in different regions of this continent (Bobe *et al.* 2002, 2009; Sponheimer & Lee-Thorp 2009). These evolutionary events underlie the origin of the purported monophyletic *Paranthropus robustus* + *P. boisei* clade (hereinafter called *Paranthropus* sensu strict, see below for a definition) and the *Homo* lineage, often considered as sister groups with shared key characters (Dean 1986; Skelton *et al.* 1986; Tobias 1988; Strait *et al.* 1997; Strait & Grine 2004; but see Asfaw *et al.* 1999; Kimbel

et al. 2004). However, there is no consensus on the basal species leading to *Paranthropus* and *Homo*, depending on the phylogenetic role accorded to *A. africanus*, *A. aethiopicus, A garhi* and *Kenyanthropus platyops* (Strait & Grine 2004). The resolution of the transitional evolution from a primitive pre-3.0 Ma *Australopithecus*-like species (sensu strict; see Foley 2013 for a definition) to the more derived *Paranthropus* and *Homo* clades largely depends on the interpretation of the morphological similarities shared by the two latter descendants as reliable guides to phylogeny (i.e., homologies as opposed to homoplasies). This is particularly the case for the masticatory and cranial base features often used to investigate phylogenetic relationships among hominins. Since current methods

fail to unambiguously distinguish homologies from homoplasies, even though further fossil hominin discoveries from the 3.0–2.3 Ma time period will considerably help, they will not suffice to contribute to the understanding of the Late Pliocene cladogenetic events that led to *Paranthropus* and *Homo*.

The chronological gap between the purported origin of a monophyletic *Paranthropus* clade and its diversification into both *P. robustus* and *P. boisei* is often set during the 2.7–2.3 Ma period. The fossil hominin assemblage illustrating this period is dominated mainly by the eastern African and geographically widely distributed *A. aethiopicus* (from Laetoli in Tanzania to the Omo-Turkana basin in Kenya and southern Ethiopia; Harrison

2011) with its highly mosaic and often plesiomorphic face at ca 2.7–2.3 Ma, and the conventionally defined *A. africanus* species with its extensive range of variation sampled at the Sterkfontein, Makapansgat and Taung sites (South Africa), here set at ca 3.0–2.6 Ma, based on the combination of faunal evidence (McKee *et al*. 1995) and absolute dates obtained from sedimentary features securely placed in the stratigraphy of Sterkfontein (Granger *et al*. 2015). The well-dated eastern African post-2.3 Ma *P. boisei* shows a more derived dental and mandibular morphology than the more generalised southern African congenerics (e.g., Suwa 1988) often grouped into *P. robustus* (but see Grine 1984) with no evidence of anagenetic evolution among the various samples of this latter species (Grine 1993).

It has been suggested that at least some KB hominins lie close to the origin of the *Paranthropus* monophyletic clade (see Chapter 1) (Tobias 1988) and may represent a more plesiomorphic representative of *P. robustus*. This is because they were interpreted dentally (Grine 1988; Suwa 1988) and cranially (Braga *et al*. 2013), intermediate between the more plesiomorphic hominins from Makapansgat Members 3 and 4 and Sterkfontein Member 4 and the more derived conditions displayed by South African hominins from the nearby site of Swartkrans. Therefore, further discoveries and analyses of *P. robustus*, as well as closer comparisons with *A. africanus*, will affect how we interpret the source populations for the *Paranthropus* lineage, here considered to exclude the aethiopicus species, as a null hypothesis.

Dating of the KB sample remains problematical, and most scenarios consider that the oldest *P. robustus* did not occur in South Africa prior to 2.0 Ma (e.g., Kimbel

2007; Wood 2011). 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 the immediate common ancestor of *Paranthropus* sensu stricto before 2.3 Ma, here defined as a *P. robustus + boisei* clade. This alternative scenario entails the parallel evolution of certain 'robust' craniodental traits in *A. aethiopicus* and posits 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 as the same species represented in the samples at Swartkrans or Drimolen. In this event, the hypothesis of *A. aethiopicus* as a potential ancestor of *Paranthropus* would be falsified and the elaboration of an alternative phylogenetic model will rest on the discovery of more *Paranthropus*-like hominins securely dated from between 3.0 and 2.3 Ma.

Clarke has questioned the taxonomic unity of the Late Pliocene hominin sample from South Africa. He raised the possibility that dental and cranial specimens recovered in the Sterkfontein Members 2 and 4 and Makapansgat Members 3 and 4 may belong to another species – *A. prometheus* – as the potential ancestor of the *Paranthropus* clade (Clarke 1988, 1990, 1994, 2008). Even though the assessment of the possible presence of a *Paranthropus* precursor at Sterkfontein and Makapansgat is beyond the scope of the present chapter, Clarke's interpretation of morphological variability among the South African Late Pliocene hominins is important to investigate further when seeking for the ancestry of *P. robustus*. Pending further analyses of the Sterkfontein Members 2 and 4/Makapansgat sample conventionally attributed to the *A. africanus* species, here we consider the species *A. africanus* sensu lato, as opposed to the smaller

hypodigm defined by Clarke (1988, 1990, 1994, 2008) as *A. africanus* sensu stricto.

A renewed evaluation of uniquely *Paranthropus*-like features with the use of newly introduced analytical techniques will help to portray the timing and place of the origin of *Paranthropus* in South Africa for at least two reasons. First, several craniodental features have been regarded to play a paramount taxonomic and/or phylogenetic role (e.g., 'thickness', 'prominence' or 'bulbosity' of anatomical structures), but they were often not assessed quantitatively for further statistical analyses. Second, it remains challenging to define accurately true monophyletic groups in the absence of phylogenetically-based statistical methods (as defined in Blomberg *et al*. 2003) that can measure the strength of the phylogenetic signal contained in morphology (e.g., Braga *et al*. 2015).

AIMS OF THIS STUDY

We focus our analysis on several features preserved in the KB hominin sample newly presented here, with particular attention on their stratigraphic provenances (as detailed in Table 4.1).

Specifically, we test the hypothesis that inner dental features confirm the basal status of some KB hominins on the South African *Paranthropus* lineage. We nevertheless acknowledge that only discoveries of further securely dated hominins from the oldest deposits of KB will help to determine whether a *Paranthropus*-like form is represented in the South African fossil record in the pre-2.3 Ma period, as well as more comparisons using the Sterkfontein/ Makapansgat samples.

Table 4.1 *List of the Kromdraai B fossil material unambiguously attributed to a hominin species (updated in November 2014). KRP, Kromdraai Research Project; Unprov., Unprovenianced in stratigraphy; Ind., Individual; L, Left; R, Right; L, Lower; U, Upper*

Catalogue number	Description	Provenience	Citations/Illustrations	Association/ Biological age
TM 1517a	Left part of a calvarium with P3 to M2	*Ex-situ* (possibly Mb 5), 1938	1, 6 (Plates 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 5), 1938	1, 6 (Plate 10)	Ind. 1, late adolescent
TM 1517c	LLP3–LLP4 and URP3 to M3	*Ex-situ* (possibly Mb 5), 1938	6 (Plate 9)	Ind. 1, late adolescent
TM 1517d	Right talus	*Ex-situ* (possibly Mb 5), 1943	5	Ind. 1, late adolescent
TM 1517e	Right proximal ulna	*Ex-situ* (possibly Mb 5), 1938	2, 6 (Plate 12)	Ind. 1, late adolescent
TM 1517g	Right distal humerus	*Ex-situ* (possibly Mb 5), 1938	2, 6 (Plate 12)	Ind. 1, late adolescent
TM 1517k	Distal phalanx, possibly from hallux	*Ex-situ* (possibly Mb 5), 1942	7, 8, 9	Ind. 1, late adolescent
TM 1517n	Intermediate phalanx, possibly cercopithecine	*Ex-situ* (possibly Mb 5), 1942	4, 7, 8	
TM 1517o	Distal manual phalanx, ray II–V, possibly baboon	*Ex-situ* (possibly Mb 5), 1938	2, 6 (Plate 12), 7, 8, 9	
TM 1536	Left mandibular corpus (fragmentary) with I1,I2, di2, dm1–2, M1; L dC	*Ex-situ*, 1941	3, 6 (Plate 11)	Ind. 2, Juvenile
TM 1600	Left mandibular corpus fragments (2) with M2–M3 (fragmt.1) and P3 (fragmt.2)	Decalcified breccia, Unprov., 1955–56	10	Ind. 3, Adult
TM 1601a	Lower right dm1	Decalcified breccia, Unprov., 1955–56	10	Ind. 4, Juvenile
TM 1601b to d	Respectively, Lower right P3, C, P4 germs	Decalcified breccia, Unprov., 1955–56	10	Ind. 4, Juvenile
TM 1601e	Upper left M1 germ	Decalcified breccia, Unprov., 1955–56	10	Ind. 4, Juvenile
TM1601f	Lower right dc	Decalcified breccia, Unprov., 1955–56	10	Ind. 4, Juvenile
TM 1602	Right maxillary fragment with root of P4 to M3	Decalcified breccia, Unprov., 1955–56	10,	Ind. 5, Adult
TM 1603	Upper left M3	Dump, 1944	6 (pp. 98–99)	Ind. 6[1], Adolescent
TM 1604	Lower left dm2 associated with breccia matrix	Decalcified breccia, Unprov., 1955–56	10	Ind. 7, Juvenile
TM 1605	Left innominate	Decalcified breccia, Unprov., 1955–56	10, 11	Ind. 8, Adult
KB 5063	Upper right M1	Unprov. (1977–80)	13	Ind. 9, Adult
KB 5163	Lower right C	*Ex-situ* (Ditsong Museum, Pretoria)	14	Ind. 10, Adult
KB 5222	Upper left M3	Unprov. (1977–80)	13	Ind. 11[2], Juvenile
KB 5223	LL dc, dm1–2; LR dm2; Lower permanent incisors; LR and LL M1s	Member 4 (1977–80)	13, 15, 16	Ind. 12, Juvenile

Table 4.1 *Continued*

Catalogue number	Description	Provenience	Citations/Illustrations	Association/ Biological age
KB 5226	Lower left M3	Member 4 (1977–80)	13	Ind. 13, Adult
KB 5383	Upper right M1	Unprov.[4] (1977–80)	13	Ind. 14, Adult
KB 5389	Upper left I1	*Ex-situ* (Ditsong Museum, Pretoria)	14	Ind. 15, Adult
KB 5503	Lower right dm2	Unprov.	12	Ind. 16, Juvenile
KB 5522	Left humerus shaft fragment	Possibly Member 5 (KRP, 2002)	17	Ind. 1, possibly[3]
KB 5524	Lingual side of a worn molar crown, possibly M1 or M2	Member 6 (KRP, 2002)	18	Ind. 1, possibly[3]
KB 6067	Petrous part of a left temporal bone	Member 4 (Ditsong Museum, Pretoria)	18	Ind. 17, Juvenile
KW 6087a,b	Fragment of the right mandibular corpus exposing the dm2 germ with half roots completed	Member 2 (18/04/2014)	This paper	Ind. 18, AGE

Comparative data sources: (1) Broom 1938a; (2) Broom 1938b; (3) Broom 1941; (4) Broom 1942; (5) Broom 1943; (6) Broom and Schepers 1946; (7) Day and Thornton 1986; (8) Day 1978; (9) Skinner *et al*. 2013; (10) Brain 1981; (11) Robinson 1972; (12) Thackeray *et al*. 2001; (13) Vrba 1981; (14) de Ruiter 2004; (15) Grine 1982; (16) Braga & Thackeray 2003; (17) Thackeray *et al*. 2005; (18) Braga *et al*. 2013.

Notes:

*Only the root(s) completely or partially preserved; ** Crown or root(s) partly damaged

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

[2] KB 5222 has been considered as representing the same individual as TM 1600. However, there is no evidence that these two specimens come from the same stratigraphic unit (member) because TM 1600 cannot be tied precisely to any of the successive breccia members of KB.

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

[3] See Thackeray *et al*. (2001) & Braga *et al*. (2013) for details.

[4] Same provenience as KB 5063.

We critically assess dental features preserved in the southern African Late Pliocene and Early Pleistocene assemblages that have been previously considered as taxonomically diagnostic (Robinson 1956; Grine 1982, 1985; Tobias 1991; Skinner *et al*. 2008, 2009). In order to contribute to unravelling the phylogenetic relationships among this sample, and more specifically to help resolving the relationships of *A. africanus* and *P. robustus*, we use recent analytical advances in morphometric analyses well suited to capture the complexity in terms of morphologies and variability

(e.g., Durrleman *et al*. 2012). We newly describe the yet unexposed inner 3D anatomy of 23 fossil hominin specimens housed at the Ditsong National Museum of Natural History (Pretoria, South Africa) (Table 4.2), and we mainly aim to determine whether the morphological differences between the KB and Swartkrans samples either represent relatively minor distinctions, as expected as normal variation within a single species, or are more consistent with a greater antiquity of the KB sample still retaining a number of more primitive traits found in some *A. africanus*

specimens from Sterkfontein. As detailed in Table 4.2, our comparative sample from Sterkfontein is too small to supply conclusive evidence of distinctions between *A. africanus* and *P. robustus*, even if we hope to obtain more comparative data from this site in the near future.

MATERIALS

We used micro-ct (μCT) data to expose and measure the 3D inner anatomy of a total of 41 lower teeth

derived from mandibles or isolated, with no or very limited signs of wear (five lower permanent canines, 'LC'; five lower second deciduous molars, 'dm$_2$'; eight lower first premolars, 'P$_3$'; nine lower first permanent molars, 'M$_1$'; eight lower second permanent molars, 'M$_2$' and six lower third permanent molars, 'M$_3$') from infant (no permanent teeth in functional occlusion), juvenile (permanent teeth but not third molars in functional eruption), subadult (with third molars emerging but not in functional occlusion) and adult fossil hominin specimens sampling *Australopithecus* and *Paranthropus* in the Late Pliocene and Early Pleistocene of South Africa (Table 4.2). Since sex is unknown for the most of fossil specimens, it was not incorporated in our analysis as a variable.

We preliminarily investigated nine teeth belonging to five specimens from Kromdraai B: TM 1517 (P$_3$, M$_1$ and M$_3$), TM 1600 (M$_2$ and M$_3$), TM 1601b, c (P$_3$ and LC, respectively), KB 5503 (dm$_2$) and KW 6087 (dm$_2$) newly reported here (the only KB specimen investigated here that is unambiguously provenianced in stratigraphy). In addition to the KB specimens, our *P. robustus* sample consists of 25 teeth belonging to 14 specimens. From Member 1: (SK 96 LC; SK 92 LC; SK 841 dm$_2$; SK 64 dm$_2$ and M$_1$; SK 3978 dm$_2$; SK 857 P$_3$; SK 34 P$_3$; SK 6 P$_3$, M$_1$, M$_2$ and M$_3$; SKW 5 P$_3$, M$_1$, M$_2$ and M$_3$; SK 63 M$_1$ and M$_2$; SK 25 M$_1$; SK 843 M$_1$ and M$_2$; and SK 23 M$_2$ and M$_3$), and from Member 2: (SKX 4446 M$_1$ and M$_2$) of the nearby site of Swartkrans.

In order to test whether some KB specimens appear dentally more similar to *Australopithecus*, we also investigated seven teeth belonging to four specimens from the apparently homogeneous stratigraphic Member 4 layer of the Sterkfontein site (STS 50 LC; STS 51 LC and P$_3$; STS 52 P$_3$, M$_2$ and M$_3$; and STS 24

M$_1$). All these latter specimens have been attributed to the conventionally defined *A. africanus* species even though the taxonomic position of some of them (e.g., Sts 52) is still debated. The μCT data were obtained using the X-Tek (Metris) XT H225L system at the South African Nuclear Energy Corporation, Pelindaba (NECSA, www.necsa.co.za), the Scanco Medical X-Treme micro-CT scanner at the Institute for Space Medicine and Physiology (MEDES) in Toulouse, and the Nanotom GE Sensing at the French Research Federation Fluides Energie Réacteur Matériaux et Transferts (FERMaT) in Toulouse, with isometric voxel dimensions ranging from 7.2 to 90.5 μm (Table 4.2).

Methods: Morphometrics

We first imported the μCT data into the Avizo v7.0 software package (www.vsg3d.com/avizo) for the segmentation and the reconstruction of surface models (via triangulated 'meshes' simplified to 100 000 faces) of either the enamel dentine junction (EDJ) or the outer enamel surfaces (OES) (Table 4.2). Then, instead of classical landmarks and semi-landmarks-based morphometric approaches (also called 'geometric methometric methods', GMMs); we use a more detailed 3D morphometric approach (called 'diffeomorphisms'). In the following sections, we briefly explain the main reasons for this methodological choice and the differences between diffeomorphisms and GMMs. We also briefly present the usefulness and specifics of diffeomorphisms.

Beyond geometric morphometric methods: Diffeomorphisms, from a global to a local analysis of dental shapes

Geometric morphometric methods are the most popular procedures currently used to investigate shape differences between samples of fossil hominin teeth. GMMs encode shapes of whole landmark configurations as either Procrustes residuals or thin-plate spline coefficients (called partial warp scores). However, GMMs have some shortcomings that have been overlooked. One of these limitations is that GMMs require an adequate coverage of the form to be investigated and, as stated in several publications, "we cannot find changes within particular regions unless we have landmarks within them" (Zelditch *et al.* 2004:28). Therefore, outside the landmark and semi-landmark areas, results based on GMMs contain no information about what may have happened, and are therefore limited in the characterisation of the numerous grooves, pits and reliefs giving the teeth their shapes and that, importantly, may not be homologous between the surfaces to be compared. GMMs have another important limitation in that they cannot capture highly local shape changes, namely, a large change limited to a few set of landmarks (called the Pinocchio effect). As explained in Zelditch *et al.*: "if we do not have evidence that some landmarks are largely independent of the others, then we can apply an interpolation function to understand changes between landmarks" (2004: 132). This well-known problem has been emphasised in several studies (e.g., Márquez *et al.* 2012). Geometric morphometric methods spread local differences over the whole shape, and the measures of shape variation at any given local region depends on the pattern of variation at its neighbouring areas. Therefore, interpolation functions such as thin-plate splines (TPS) employed in GMMs do not measure the deformations present beyond the regions spanning subsets of landmarks but instead produce the smoothest possible interpolation and tend to spread local information globally for visualisation only (Marquez *et al* 2012). In this case, highly localised deformations will influence deformations at other

regions. The medical image computing community has taken an alternative approach to the GMM (semi)landmark-based approach in order to establish correspondences between surfaces by aligning several features automatically using both local and global features, such as conformal factors on surfaces. In this approach, the deformations (i.e., differences between surfaces) are mathematically modelled as so-called diffeomorphisms. They rely on all data points represented on the continuous 3D surface without utilising explicit point correspondences, and are not contingent on the numbers and positions of landmarks sparsely selected by an observer. Diffeomorphisms have first been used in evolutionary anthropology by Durrleman *et al.* (2012) where the most important differences between this method and GMMs have been detailed. Diffeomorphisms are computed though the use of a similarity metric between the surfaces, the so-called currents, an approach already applied on various applications in the field of computational anatomy (Glaunès 2005; Vaillant & Glaunès 2005; Qiu *et al.* 2007; Vaillant *et al.* 2007; Li *et al.* 2010; Durrleman *et al.* 2012). The currents metric measures how well two surfaces are superimposed. The optimal deformation maximises the superimposition of the source surface onto the target surface, while minimising the kinetic energy. The consequence of this minimal energy principle, but also the topology-preserving constraint, is that points do not follow straight lines during deformation, but curved trajectories instead. The deformations are subsequently used in the statistical approaches. Importantly, the current metric is insensitive to small-scale surface variations, as well as on how the surfaces are sampled (Vaillant & Glaunès 2005; Vaillant *et al.* 2007). In the case of teeth, the advantage of using diffeomorphisms is that one can directly compute the

Table 4.2 *List of fossil hominin teeth investigated in this study with newly described features subsequently used for statistical multivariate analyses. Both sides are represented and teeth are fully formed, unless specified. R, Right; L, Left; d, Erupting but developing roots; Un., Unerupted crown; Mb, Member; Unprov., Unprovenienced; **A.**, **Australopithecus**; **P.**, **Paranthropus**; KW, Kromdraai B; SW, Swartkrans; ST, Sterkfontein; LB, Lower bank; HR, Hanging remnant*

Specimen	Description	Taxon	Provenience	Pixel	EDJ	OES	Growth
Lower permanent canines							
TM 1601c		*P. robustus*	KB, Unprov.			L	
SK 96		*P. robustus*	SK, HR 1	10.500	L d	L d	
SK 92		*P. robustus*	SK, HR 1	14.167	R d	R d	
STS 51		*Au. africanus*	ST, Mb 4	10.330	R	R	Un.
STS 50		*Au. africanus*	ST, Mb 4	10.567	L	L	Un.
Lower second deciduous molars							
KW 6087		*Paranthropus sp.*	KB, Mb 2	7.20	R d	R d	
KB 5503		*P. robustus*	KB, Unprov.	13.98	R	R	
SK 841	with dm2,M1	*P. robustus*	SK, HR 1	14.9	L	L	
SK 64	with dm1,dm2	*P. robustus*	SK, HR 1	32.5	L	L	
SK 3978	with dm1,dm2 (R & L)	*P. robustus*	SK, HR 1	42.85	L	L	
Lower first premolars							
TM 1517		*P. robustus*	KB, possibly Mb E	13.98	L **		
TM 1601b		*P. robustus*	KB, Unprov.	13.98		L d	Un.
SK 857		*P. robustus*	SK, HR 1	15.25	R d	R d	
SK 34		*P. robustus*	SK, HR 1	90.49	R		
SK 6	with P3,P4,M1–M3	*P. robustus*	SK, HR 1	56.00–32.40	L		
SKW 5	with P3,P4,M1–M3	*P. robustus*	SK, HR 1	67.50	R		
STS 51		*Au. africanus*	ST, Mb 4	10.33	R d	R d	
STS 52		*Au. africanus*	ST, Mb 4	41.00	R		

Table 4.2   *Continued*

Specimen	Description	Taxon	Provenience	Pixel	EDJ	OES	Growth
Lower first permanent molars							
SK 64	with dm1,dm2	*P. robustus*	SK, HR 1	32.5	L d		
SK 63		*P. robustus*	SK, HR 1	41.0	R	R	
SK 25		*P. robustus*	SK, HR 1	54.3	L		
SK 843	with M1–M3	*P. robustus*	SK, HR 1	33.8	R		
SK 6	with P3,P4,M1–M3	*P. robustus*	SK, HR 1	56.0– 2.4	L		
SKW 5	with P3,P4,M1–M3	*P. robustus*	SK, HR 1	67.5	R		
TM 1517b	with C*,P3,P4,M1–M3	*P. robustus*	KB, possibly Mb E	61.0	R		
SKX 4446	with P4–M2	*P. robustus*	SK, Mb 2	40.7	R		
STS 24		*Au. africanus*	ST, Mb 4	27.2	L	L	
Lower second permanent molars							
SK 63		*P. robustus*	SK, HR 1	41.0	R d		
SK 843	with M1–M3	*P. robustus*	SK, HR 1	33.8	R		
SK 6	with P3,P4,M1–M3	*P. robustus*	SK, HR 1	56.0–32.4	L	L	
SKW 5	with P3,P4,M1–M3	*P. robustus*	SK, HR 1	67.5	R	R	
TM 1600	with P3,M2,M3	*P. robustus*	KB, Unprov.	25.6	R		
SKX 4446	with P4–M2	*P. robustus*	SK, Mb 2	40.7	R	R	
SK 23		*P. robustus*	SK, HR 1	70.1	L	–	
STS 52		*Au. africanus*	ST, Mb 4	41.0	R		
Lower third permanent molars							
SK 6	with P3,P4,M1–M3	*P. robustus*	SK, HR 1	56.0–32.4	L	L	
SKW 5	with P3,P4,M1–M3	*P. robustus*	SK, HR 1	67.5	R	R	
SK 843	with M1–M3	*P. robustus*	SK, HR 1	33.8	R	R	Un.
TM 1517b	with C*,P3,P4,M1–M3	*P. robustus*	KB, possibly Mb E	61.0	R	R	
TM 1600	with P3,M2,M3	*P. robustus*	KB, Unprov.	25.60	R		
SK 23		*P. robustus*	SK, HR 1	70.10	L		
STS 52		*Au. africanus*	ST, Mb 4	41.0	R	R	

continuous 3D surface deformation between crowns with distinct cusps' morphologies.

For tooth each class here considered separately (dm$_2$, LC, P$_3$, M$_1$, M$_2$ and M$_3$), we describe and we compare the patterns of differences within pairs of surfaces (from a 'source' to a 'target' surface) as follows: (i) inter-individual OES-to-OES differences; (ii) inter-individual EDJ-to-EDJ differences; and (iii) intra-individual EDJ-to-OES differences. Importantly, when surfaces show post-mortem fissures (e.g., KW 5503, Figure 4.2) that may produce some biases in the comparisons, they were used only as target surfaces and not as sources for the assessments of the aforementioned differences.

Multidimensional scaling

After calculating the patterns of differences within pairs of surfaces finding one-to-one correspondences of point pairs, we obtained distances matrices for each tooth class (e.g., dm$_2$). We then used a metric multidimensional scaling (MMDS) analysis (with Matlab) to compare each specimen in two-dimensional scatterplots. More specifically, we used the MMDS that creates a configuration of points for which the pairwise interpoint distances approximate the original pairwise morphological dissimilarities.

Surface distance maps of 3D enamel distribution across the crown

Some labour-intensive procedures allow the measure-ment of enamel volumes and proportions (e.g., Kono 2004; Olejniczak *et al*. 2008), but they clearly do not measure enamel thickness. As yet, all studies aiming to map enamel thickness in 3D use the 'closest point' (CP) algorithm (generally with the help of commercial

software such as Avizo) to minimise the difference between the EDJ and OES. Although 3D mapping derived from the CP algorithm may suffice to detect gross changes, this method has clear limitations in locations where both surface boundaries present different folding patterns. Unrealistic discontinuities in the thickness measurements may then occur. It has been shown also that the CP method results show significant underestimates of the measured thickness in areas of high curvature (e.g., Fischl & Dale 2000). Therefore, alternative methods are needed to measure and compare the 3D patterns of enamel thickness among fossil hominins. Ideally, these measurements should approximate the cellular processes responsible for the developmental changes in enamel thickness by considering any given point on the EDJ as structurally (at the prism level) and developmentally 'homologous' with only one point on the OES. Since the prisms do not find the shortest path from the EDJ to the OES, but instead curve in their passage from these two surfaces (the topography of the latter surface not reflecting that of the former one), a thickness metric of the crown should avoid a CP approach and rather try to take into account this structural complexity.

We use here a deformation of one surface boundary to the other one as a proxy to measure the thickness between two surfaces. Among all topology-preserving 3D deformations mapping one surface to another, we will seek for the one that minimises the kinetic energy of the deformation. The consequence of the topology-preserving constraint and the minimal energy principle is that points do not follow straight lines during deformation, but curved trajectories instead. We propose to use the length of these trajectories as a measure of thickness. Points on the source surface

do not reach the closest point on the target surface, but target points that are smoothly varying from one location to another, thus avoiding discontinuities in the thickness measurements. We expect these point trajectories to mimic more closely the prism structure, although this would need to be confirmed with histological data. A similar approach has been taken to measure cortical thickness in the medical imaging community (Das *et al.* 2009) with a slightly different deformation model and using image instead of surface data. Alternative methods to measure cortical thickness in the computer vision and medical image computing communities include the method of Fishl & Dale (2000), which average the closest point distance from one surface to another and vice versa.

The deformation is computed between the two surfaces without the need to find a priori corresponding points on both surfaces. These correspondences are established by the deformation instead. This is possible because of the use of similarity metric between surfaces, the currents metric, which measures how well two surfaces are superimposed without the need to specify such point correspondence across the surfaces. The 'C' is defined then as the one that maximises the superimposition between the deformed source surface and the target surface, while minimising a kinetic energy term. This approach has been applied on various applications in the field of computational anatomy (Qiu *et al.* 2007; Vaillant *et al.* 2007; Li *et al.* 2010; Durrleman *et al.* 2012). This relaxed optimisation problem does not produce a surface-to-surface matching, but a deformed source surface which lies as closely as possible to the target surface. This matching inaccuracy is often negligible in practice for the thickness measurements. We also emphasise that an exact surface-to-surface matching

is often not desirable, as the surfaces are known only at the resolution of the image and at the precision of the method used to segment them. We then obtain surface distance maps of 3D enamel thickness across the crown, visualised using a colour scale ranging from dark blue ('thinner') to red ('thicker').

THE LOWER PERMANENT CANINES

Since the seminal study by Robinson (1956), and despite the great potential of the lower permanent canine to distinguish *A. africanus* from *P. robustus*, the detailed morphology of this tooth has surprisingly received very limited attention and most analyses have focused on size.

Previous shape data

When compared to the *P. robustus* teeth from Swartkrans (e.g., SK 92 and SK 96, Figure 4.1) and Drimolen (e.g., DNH-79; Moggi-Cecchi *et al.* 2010), the most salient taxonomic morphological features of the markedly asymmetrical *A. africanus* sensu lato LC crown (e.g., STS 50 and STS 51, Figure 4.1) are reported as seen in buccal view with three important features: (i) a strong lingual incisal ridge forming sometimes a sharpened crest; (ii) a relatively pointed crown tip located well distal to the mesio-distal mid-plane; and (iii) a very high mesial shoulder (placed at a position of approximately one-fourth to two-thirds of its total unworn height) where the mesial arm of the incisal margin is shorter than the much longer distal arm, which slopes steeply downwards where it forms an accessory distal cuspulid (or 'talonid') (Robinson 1956; Tobias 1991). However, these potentially taxonomically useful traits have not been quantified yet, in particular in terms of the three-dimensional distribution of enamel thickness.
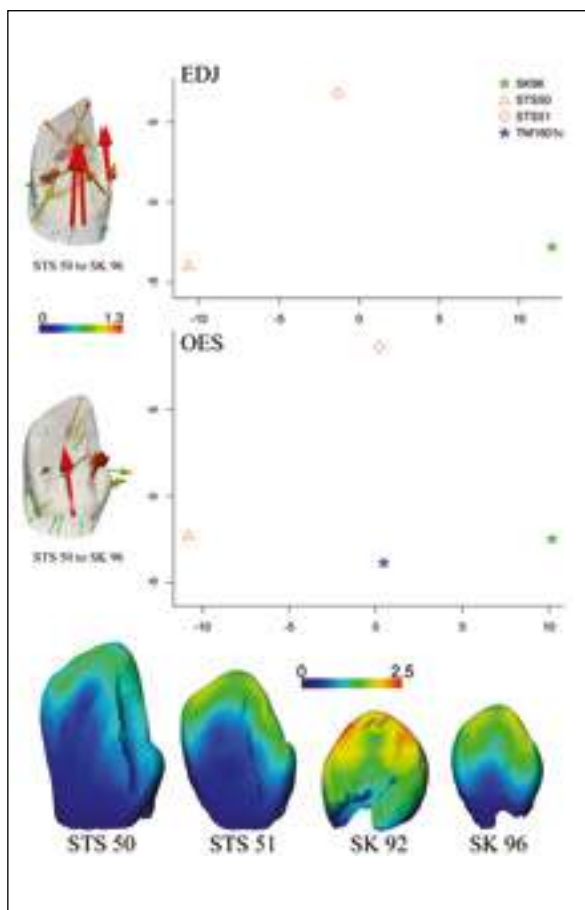
Figure 4.1 *Results obtained for four lower permanent canines (LC) with distances between specimens obtained after multidimensional scaling of diffeomorphic mappings of both EDJ and OES surfaces (top) and surface distance maps of 3D enamel distribution across the crown (bottom). The pairwise morphological dissimilarities between the two specimens at the extremes of variation are represented by vectors with different sizes and colours (top left), depending on the intensity of the differences. Scales for both vectors of deformations and enamel thickness are indicated in mm.*

Previous size data

Comparatives studies in South African fossil hominins have mainly focused on the overall size of the crown, as represented by the mesiodistal (MD) and buccolingual (BL) diameters, with less attention given to its height. The mean and extreme values obtained for *A. africanus* sensu lato and *P. robustus* from Swartkrans and Drimolen are 9.5 and 8.4–10.7 mm (n = 22; SD = 0.6), 7.6 and 6.9–8.7 mm (n = 11; SD = 0.6) and 7.6 and 7.3–8.1 mm (n = 3; SD = 0.4) for MD diameter; 10.1 and 8.7–12.2 mm (n = 25; SD = 0.8), 8.0 and 7.2–9.2 mm (n = 15; SD = 0.6), and 8.3 and 7.6–8.8 mm (n = 3; SD = 0.6) for BL diameter (Moggi-Cecchi *et al.* 2006, 2010). There is only a very limited overlap in lower canine overall crown size between *A. africanus* and *P. robustus*. When we compare TM 1601 values (MD: 7.5 mm, BL: 8.2 mm) of the only LC from KB as yet recovered, we observe that they fall well within *P. robustus* variability. Interestingly, the *A. sediba* values for the MH1 specimen are 8.0 mm and 8.5 mm, respectively for MD and BL diameters, and fit better in the *P. robustus* ranges than in the *A. africanus* sensu lato ones. Kaszycka (2002:81) reported significant differences in LC crown height between *A. africanus* (n = 11; mean = 14.3 mm; range = 12.8–16.1; SD = 1.2) and *P. robustus* from Swartkrans (n = 4; mean = 11.1 mm; range = 10.7–12.1; SD = 0.6). The only measurable LC crown height from KB (TM 1601c) shows a value of 12.5 mm, intermediate between the non-overlapping *P. robustus* and *A. africanus* ranges.

There are only very limited data on the LC root size. Ward *et al.* (2001) reported that in extant African ape and human canine, the LC root dimensions are tightly correlated with crown dimensions. Therefore, one would reasonably expect that crown size also

accurately reflects crown size in fossil hominins. Despite the absence of direct evidence about LC root size, some information is available on the LC alveolus size. When they investigated LC alveolus size on a limited sample of specimens, de Ruiter *et al.* (2013) reported taxonomically discriminant dimensions between *A. africanus* (n = 4; MLD 40, STS 7, STS 36 and STS 52) and *P. robustus* (n = 3; SK 12, SK 23 and SK 34) in the MD and labiolingual (LL) axes (as defined in Wood 1991:296) with non-overlapping MD and LL ranges of respectively 7.1–9.0 mm and 9.7–11 mm in *A. africanus*, and 6.0–6.8 mm and 7.0–8.0 mm in *P. robustus*.

The taxonomic discriminatory power of the LC overall size is much increased when considered relative to the size of the lower postcanine dentition within each individual (using ratios of crown surfaces expressed as MDxBL for each pair of LC combined with either one of the two premolars or the one of the three molars). It is then apparent that *A. africanus* has relatively larger lower permanent canines than does *P. robustus*.

Dimorphism

It has been considered that male-biased sexual dimorphism (i.e., with body size in males being the larger) explains at least part of intra-species variations in LC size (mainly crown height) in fossil hominins. However, patterns of LC sexual dimorphism may well be contrasted among living and fossil hominoid species. Moreover, the analysis of LCs values in a large sample of 84 extant anthropoid species revealed that LC crown height shows a greater range of intra-species dimorphism than any other LC measurement and may subsequently represent a better discriminator between taxa with high degrees of male-male competition and those that do not (Plavcan & van

Schaik 1997). Therefore, when compared to MD and BL diameters, dimorphism in LC crown height should be "strongly preferred" when inferring patterns of sexual dimorphism among fossil hominin species, even though canine and body size dimorphisms are imperfectly correlated in extant anthropoid species, because the total range of intra-species body weight dimorphism represents only 70%, 74% and 71% that of LC crown height, MD and BL diameters, respectively (Plavcan & van Schaik 1997:354).

The basal or MD diameter, as well as the labial crown height of the LC is known to be highly sexually dimorphic, not only in the two most dimorphic genera of living great apes (with no overlapping ranges between females and males), but also in the less dimorphic common and pygmy chimpanzees (see Suwa *et al.* 2009, Figures S7 and S8). However, LC crown size dimorphism appears to be reduced relative to body size at least in *A. afarensis* (Leutenegger & Shell 1987; Richmond & Jungers 1995; Plavcan 2003), and reduction of canine crown dimorphism in this latter species appears to precede that of canine root dimorphism (Ward *et al.* 2001. When they used the binomial dimorphism (BDI) approach first established by Reno *et al.* (2003), Suwa *et al.* (2009) obtained a male/female ratio of 1.114 for LC crown dimorphism (with a 95% confidence interval of +/-1.130, indicating that higher or null values may occur).

Results

EDJ and OES morphology

The MMDS analysis excluded the SK 92 LC because both its EDJ and OES morphology appeared too distinct from the other LCs to allow a satisfactory alignment

before the diffeomorphic mapping. At the EDJ level, the two *A. africanus* LCs (STS 50 and STS 51) appeared very distant to the single *P. robustus* specimen (SK 96) represented in our sample (Figure 4.1). Since STS 50 and SK 96 appeared at the extremes of variation of both the EDJ and OES MMDS analyses, we represented the deformation between these two specimens with the former *A. africanus* LC aligned onto the latter *P. robustus* one ('STS 50 to SK 96'). Not surprisingly, most of the changes observed from STS 50 to SK 96 consisted mainly in the reduction of crown height. Due to the bad preservation of its EDJ, the TM 1601c LC from KB was added in the MMDS analysis of the OES only. It appeared morpholocially intermediate between STS 50 from Sterkfontein (*A. africanus*) and SK 96 representing *P. robustus*.

Surface distance maps of enamel distribution across the crown

Comparisons of surface distance maps of enamel distribution across the LC crown between *A. africanus* and *P. robustus* are reported here for the first time. Even though our sample comprises only two specimens representing each species, we observe a clear difference between *A. africanus* and *P. robustus* in both lingual and buccal views (Figure 4.1). In *P. robustus*, enamel thickness increases distinctly at mid-crown height to the apex where it appears much thicker (with absolute values reaching 2 to 2.5 mm) than in *A. africanus*. In this latter species, enamel thickness appears very thin (less than 1 mm) in most of the lingual and buccal faces, and increases moderately on both sides of the crown tip, at the levels of the mesial and distal incisal ridges.

THE LOWER SECOND DECIDUOUS MOLARS

Despite its considerable amount of variability, the outer morphology of the crown of the lower second deciduous molar (dm$_2$) (Figure 4.2) has received much attention for a taxonomic use among the South African australopiths (Grine 1982). The dm$_2$ OES have been described in great detail but two other potentially useful dm$_2$ features have yet to be quantified, namely, the EDJ and the 3D distribution of enamel thickness.

Previous shape data

Three diagnostic taxonomic features observed at the dm$_2$ OES have been proposed to distinguish *A. africanus* when compared to *P. robustus* (Grine 1982): (i) the accessory trigonid ridge (or crest) in *A. africanus*, which forms a double anterior fovea (or trigonid basin) between the protoconid and the metaconid, is considered as less developed than the more pronounced distal trigonid crest (or distal marginal ridge). On the contrary, this accessory ridge tends to be more strongly developed in *P. robustus*, which also show a more transverse distal fossid; (ii) the protoconid in *A. africanus* is set mesial to the level of the metaconid, while these cusps are more aligned transversally on the *P. robustus*; and (iii) a faint and oblique ridge usually represents a protoconidal cingulum in *A. africanus*, while no feature is shown by the *P. robustus* molars.

Among the *P. robustus* dm$_2$s, the tuberculum sextum or C6 was reported as absent or minimally developed on KB teeth, while it was almost invariably present but moderately developed on the Swartkrans teeth (Grine 1982, 1984). Moreover, Grine (1982) observed that the mesial marginal ridge of only the Kromdraai dm$_2$s
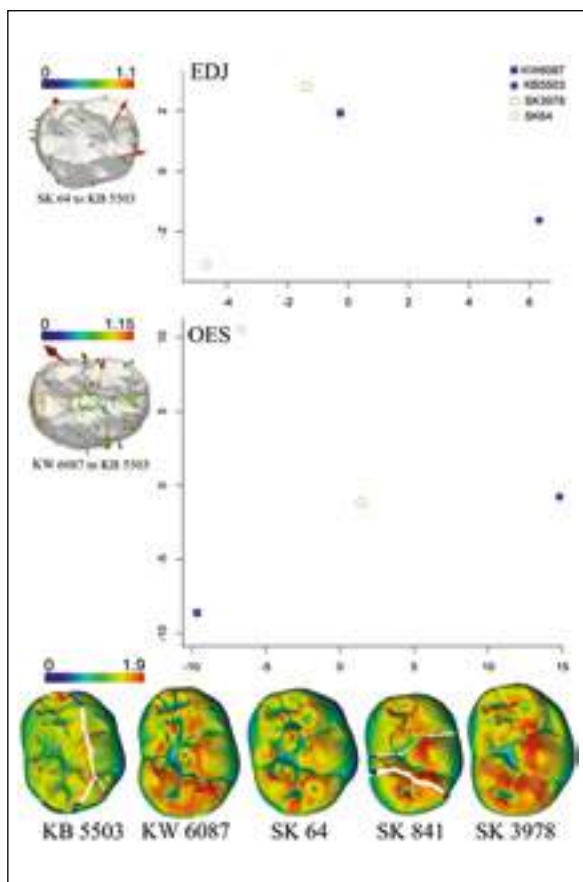
Figure 4.2 *Results for five lower second deciduous molars (dm2) with distances between specimens obtained after multidimensional scaling of diffeomorphic mappings of both EDJ and OES surfaces (top) and surface distance maps of 3D enamel distribution across the crown (bottom). The pairwise morphological dissimilarities between the two specimens at the extremes of variation are represented by vectors with different sizes and colours (top left), depending on the intensity of the differences. Scales for both vectors of deformations and enamel thickness are indicated in mm.*

was incised in its middle by one or more deep fissures delimitating one or two incipient mesial cuspulid(s) – a morphology not reported in any other *P. robustus* specimens know at this time. Since then, two dm$_2$ have been recovered at Kromdraai (KB 5503 and KW 6087) (Table 4.1) and are newly described here.

Previous size data

The mean and extreme values obtained in the four samples representing *A. africanus*, *P. robustus* from the Swartkrans, Drimolen and Kromdraai sites are 12.0 and 10.6–12.8 mm (n = 9 ; SD = 0.8), 12.9 and 12.2–13.6 mm (n = 10; SD = 0.4), 11.8 and 11.5–12.2 mm (n = 3; SD = 0.4), and 12.4 and 11.9–12.8 mm (n = 3; SD = 0.5) for MD diameter; and 10.2 and 9.0–11.0 mm (n = 8; SD = 0.6), 10.6 and 9.7–12.1 mm (n = 10; SD = 0.7), 10.1 and 9.9–10.3 mm (n = 4; SD = 0.2), and 10.2 and 9.8–10.5 mm (n = 4; SD = 0.4) for BL diameter (Moggi-Cecchi *et al.* 2006, 2010). Therefore, there is some overlap in dm$_2$ overall crown size between *A. africanus* and *P. robustus*. Moreover, as shown in Figure 4.2a, the overall crown size of KB 5503 and KW 6087 fit well within the *P. robustus* variability sampled at Swartkrans, as exampled by three specimens (SK 64, SK 841and SK 3978).

Results

EDJ and OES morphology

The MMDS analyses of diffeomorphic data for both the dm$_2$ EDJ and OES do not separate the Swartkrans and Kromdraai samples (Figure 4.2). The KW 6087 EDJ appears morphologically closer to the three Swartkrans specimens than to KB 5503. The SK 64 dm$_2$ from Swartkrans and the KB 5503 specimen appeared at the extremes of variation of

the EDJ MMDS analysis. When we represented the deformation between these two specimens with the former aligned onto the latter one ('SK 64 to KB 5503'), we observed that they differed mainly in the more mesial placement of both the protoconid and metaconid in KB 5503 (Figure 4.2). A different diffeomorphic mapping is observed in the OES MMDS analysis in which the two KB dm$_2$s (KB 5503 and KW 6087) appeared at the extremes of variation (Figure 4.2). When we represented the deformation between these two specimens with KW 6087 aligned onto KB 5503 ('KW 6087 to KB 5503'), we observed that they differed in the distal and lingual expansion of the hypoconid in KB 5503. In the absence of data from Sterkfontein specimens, we still need to test further morphological differences between *A. africanus* and *P. robustus* with the help of this method.

Surface distance maps of enamel distribution across the crown

As for the LC, comparisons of surface distance maps of enamel distribution across the dm$_2$ crown among fossil hominins are reported here for the first time. Our sample size is very limited and we do not observe clear differences between the Swartkrans and Kromdraai samples, as shown in occlusal views (Figure 4.2a). The differences observed between the two Kromdraai specimens (KB 5503 and KW 6087) notably exceed the variability measured within the Swartkrans sample.

THE LOWER PREMOLARS

Regarding the LC and dm$_2$, only the premolar OES have been described in great detail with the aim to distinguish 'robust' versus 'non-robust' australopiths.
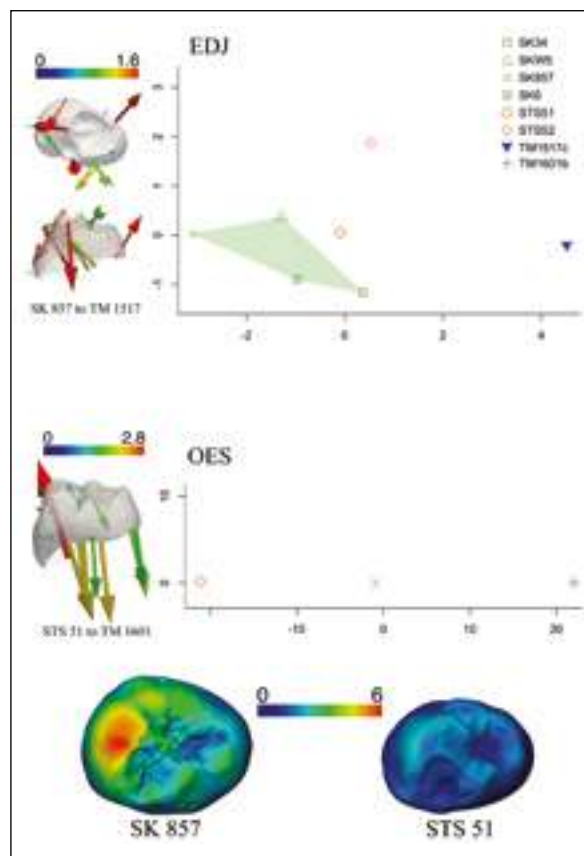
Figure 4.3 *Results for eight lower first premolars (P$_3$) with distances between specimens obtained after multidimensional scaling of diffeomorphic mappings of both EDJ and OES surfaces (top; with TM 1517c EDJ included in the analysis and represented in the large graph and without TM 1517c EDJ in the small graph) and surface distance maps of 3D enamel distribution across the crown (bottom). The pairwise morphological dissimilarities between the two specimens at the extremes of variation are represented by vectors with different sizes and colours (top left), depending on the intensity of the differences. Scales for both vectors of deformations and enamel thickness are indicated in mm.*

No clear differences have been observed between *A. africanus* and *P. robustus* in the P$_3$ OES overall size. Even though some attempts have been made to describe the premolar EDJ in one *A. africanus* specimen (Braga *et al*. 2010), this feature and the three-dimensional distribution of enamel thickness still require much attention.

Previous shape data: crown morphology

The OES of the lower first premolar (P$_3$) crown probably shows some of the clearest morphological differences among hominin taxa, with minimal overlap between, on the one hand, *P. boisei* and *P. robustus*, and on the other hand, the 'non-robust' australopiths (i.e., *A. afarensis* and *A. africanus*) and early *Homo* investigated at this time (Robinson 1956; Suwa 1988; Suwa *et al*. 1996). Interestingly, this separation was not as clear in the P$_4$s as in the P$_3$s because the P$_4$ morphology seen in *P. robustus* appeared more conservative and showed only incipiently the buccolingual and distal talonid expansion so conspicuous in *P. boisei* P$_4$s (Suwa 1988).

Suwa (1988) observed that when compared to the condition of the P$_3$ OES seen in *A. afarensis* and *A. africanus*, *P. robustus* and *P. boisei* shared a derived morphology, likely present in their last common ancestor. He added that the specimens from KB showed minimal expressions of this derived morphology, "toward the lower end of the range of the Swartkrans sample" (Suwa 1988:204). This derived morphology corresponds to a buccolingual expansion of the crown with an increased talonid size and the reduction of occlusal surface relief. The most conspicuous derived features reported in both *P. robustus* and *P. boisei* P3s are: (i) the mesially positioned metaconid relative to the axis of the mesial

and distal protoconid crest (situated transverse to the protoconid in *Australopithecus*); (ii) the high placement (relative to the total crown height) of the lingual end of the buccal segment of the mesial marginal ridge (low in *Australopithecus*); (iii) the low transverse crest hardly forming a separation between the anterior and posterior fovae (a high prominent crest connects the protoconid and metaconid tips and forms a clear demarcation between the fovae in *Australopithecus*); (iv) a large distolingual cusplet; and (v) a reduced mesiobuccal asymmetry, as seen from the buccal basal contour relative to the axis of the mesial and distal protoconid crests.

Previous shape data: root morphology

The variation in the mandibular premolar root form is also interesting to investigate evolutionary trend between *A. africanus* and *P. robustus*. After a detailed radiographical investigation of root morphology of both P$_3$s and P$_4$s among the eastern African hominins available at this time, Wood (1988) inferred a primitive condition for *P. robustus* and concluded that it was typically represented in some *A. africanus* specimens (e.g., MLD 29 and TM 1518). The P$_3$ primitive condition was described as a two-rooted tooth composed of an oblique mesiobuccal and a transversely orientated distal component containing one and two pulp canals, respectively. The P$_4$ primitive condition consisted of a two-rooted tooth with the symmetric and transversely orientated mesial and distal components not noticeably displaced buccolingually with respect to each other, each containing two pulp canals. In both P$_3$ and P$_4$ primitive conditions, the roots bifurcation occurred within the cervical third of the root height.

Wood (1988) concluded that an evolutionary trend towards a derived root reduction (i.e., single-rooted

premolars) occurred only in the southern African 'robust' lineage, independently of *P. boisei* in which the opposite trend occurred (i.e., two-rooted premolars). The first stage for the P_3 evolutionary changes among the southern African hominin was the alteration from the primitive condition just described to a two-rooted mesiobuccal and distolingual system, as represented at Kromdraai (TM 1600). The next transition to Tomes' root form required the suppression of the distobuccal inter-radicular process to produce continuity between the mesiobuccal and distolingual root components (each containing a separate pulp canal). Cervical to the level of bifurcation, the root cross section shows mesiobuccal and distolingual clefts, of which the mesiolingual is typically the more developed. This root morphology was found in P_3s from Swartkrans and Sterkfontein (Robinson 1956). The reduction of the mesiolingual cleft and the progressive apical migration of the bifurcation site (so that the root tip only appeared bifid) were the final stages in the pathway towards single-rooted P_3s. The trend towards root reduction in P_4s was described a less complex, apparently just involving the progressive apical displacement of the bifurcation, with a concomitant reduction in the size of the roots and a shift from a mesiodistally flattened to a more rounded root form and finally to a single root.

Since Wood's study (1988), advances in imaging and measuring root morphology in 3D allow us to quantify premolar root morphology. However, we first need to increase our sample of lower premolars from KB to test further the hypothesis of an evolutionary trend in premolar root morphology from a primitive southern African form, possibly represented at Sterkfontein Members 2/4, toward the more derived *P. robustus* as represented at Kromdraai and Swartkrans.

Results

EDJ and OES morphology

Since the TM 1517 left P_3 is partly damaged at its mesio-buccal quadrant (protoconid) (the right P_3 of TM 1517 being more damaged), but represents the only P_3 EDJ from KB that is yet measurable, the MMDS analysis of diffeomorphic EDJ data have been made separately with and without this specimen. Importantly, the inclusion of TM 1517 in the EDJ MMDS analysis did not change the pairwise distances among the six specimens from Sterkfontein (STS 51, STS 52) and Swartkrans (SK 6, SK 34, SK 857 and SKW 5) (Figure 4.3). It is noteworthy that the P_3s' EDJ variability among the Swartkrans sample is relatively limited. Moreover, the differences observed between TM 1517c and the two Sterkfontein P_3s was much larger than that observed within the Swartkrans P_3s. Moreover, the TM 1517c P_3 and three *P. robustus* specimens from Swartkrans (SK 857, SKW 7 and SK 6) were situated at the extreme limits of variation (Figure 4.3). The specimen that appeared morphologically closer to the TM 1517 P_3 was STS 51 from Sterkfontein; the pairwise difference between TM 1517 and STS 51 appearing much larger that any difference observed between two *P. robustus* teeth from Swartkrans (Figure 4.3b). TM 1517c from KB and SK 857 from Swartkrans appeared at the extremes of variation of the EDJ MMDS analysis (Figure 4.3). When we represented the deformation between these two specimens, with the latter aligned onto the former one ('SK 857 to TM 1517c'), we observed that they differed mainly in the downward and lingual displacement of the metaconid. The OES MMDS analysis included only three specimens that appeared equally distant from each other, and will therefore not be discussed further here.

Surface distance maps of enamel distribution across the crown

Comparisons of surface distance maps of enamel distribution across fossil hominins' P_3 crowns are reported here for the first time. Since we used only specimens with no or very limited wear, only two P_3s have been investigated so far, with STS 51 and SK 857 representing *A. africanus* and *P. robustus* respectively. Even if a definite interpretation is obviously premature due to our very small sample size, it is noteworthy that the patterns shown by STS 51 and SK 857 were very different (Figure 4.3). The *A. africanus* STS 51 P_3 shows a relatively thin enamel layer (less than 3 mm) distributed homogeneously all over its crown (enamel thickness increases slightly at the level of the two main cuspids). This pattern contrasts very much with that observed in the *P. robustus* SK 857 P_3, which appears much thicker (more than 3 mm) across most of the crown. When compared with STS 51, enamel thickness is distributed less homogeneously, with the metaconid tip being notably the thickest area (reaching 6 mm).

THE LOWER PERMANENT MOLARS

No clear differences between the overall size of *A. africanus* and *P. robustus* in the permanent molars' OES have been observed (e.g., Moggi-Cecchi *et al.* 2006). The lower permanent molars currently represent the fossil hominin teeth that have been the most studied with the use of μCT. However, as yet, no method has been proposed to test statistically possible taxonomic differences in local enamel distribution across the enamel cap of lower permanent molars.
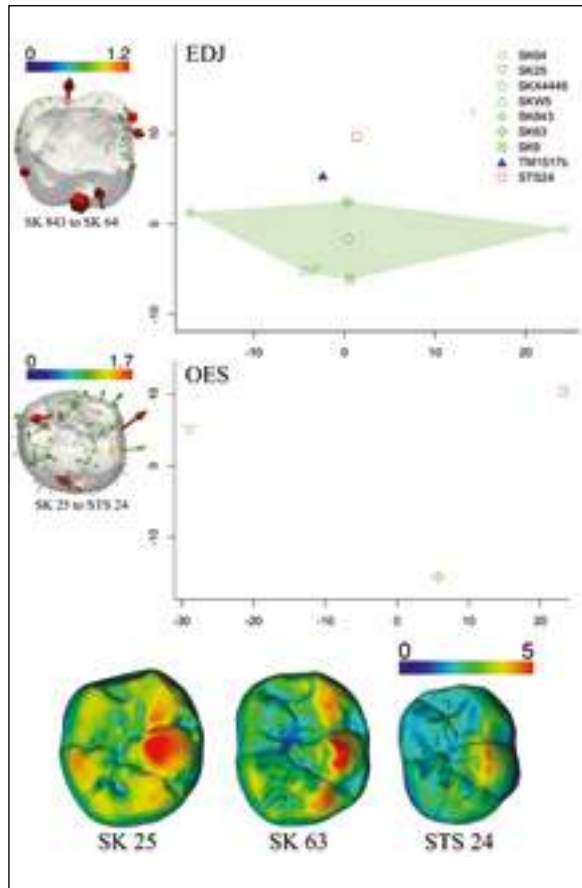
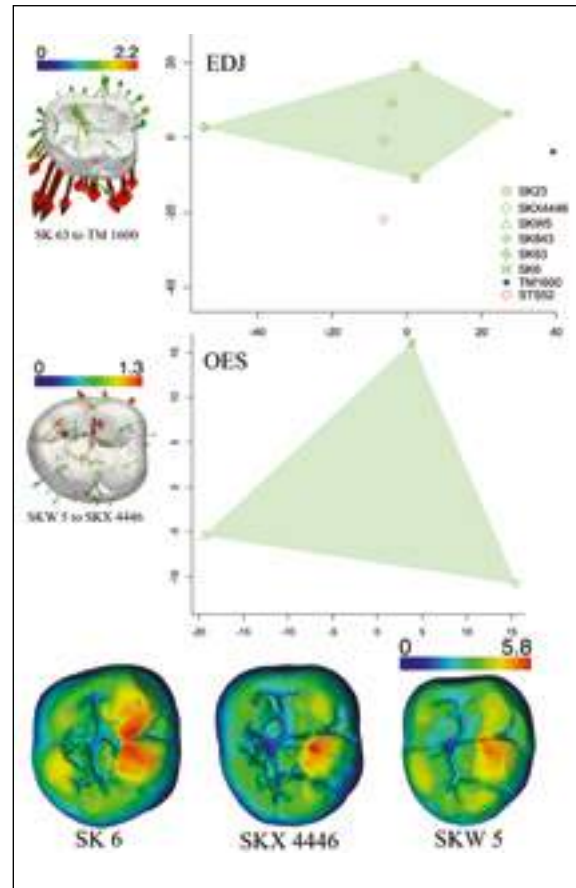**Figure 4.4** *Results for nine lower first permanent molars (M₁)*

Figure 4.5 *Results for eight lower second permanent molars (M₂)*
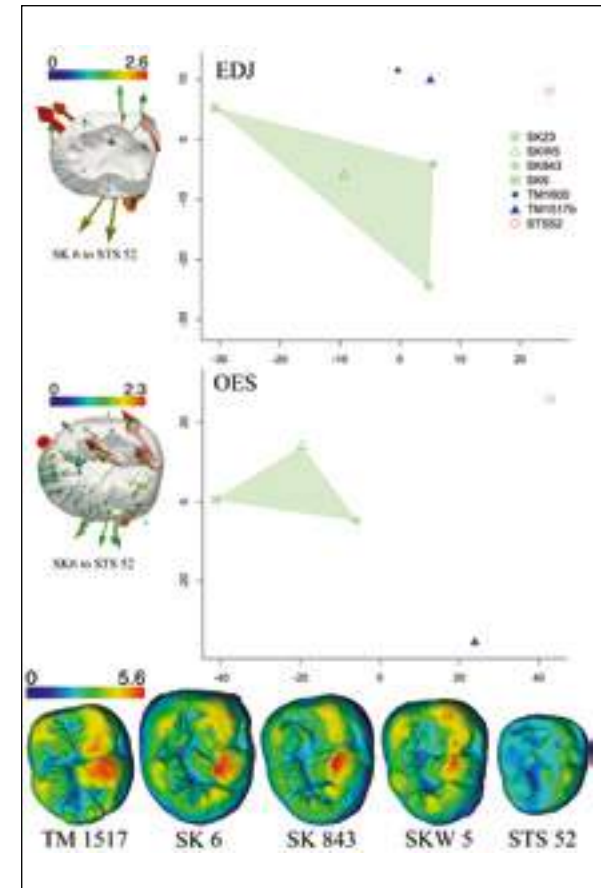
Figure 4.6 *Results for seven lower third permanent molars (M₃)*

With distances between specimens obtained after multidimensional scaling of diffeomorphic mappings of both EDJ and OES surfaces (top) and surface distance maps of 3D enamel distribution across the crown (bottom). The pairwise morphological dissimilarities between the two specimens at the extremes of variation are represented by vectors with different sizes and colours (top left), depending on the intensity of the differences. Scales for both vectors of deformations and enamel thickness are indicated in mm.

Previous shape data: crown morphology

As for the lower deciduous molars, a large number of studies have investigated differences in OES permanent molar morphology among the Pliocene and early Pleistocene australopiths. However, contrary to the lower deciduous molars, the morphology of the lower permanent molars has been investigated at both the OES and EDJ levels with the help of geometric morphometrics in order to determine whether *A. africanus* and *P. robustus* could effectively distinguished on these grounds (Skinner *et al.* 2008, 2009). In these studies, the *P. robustus* sample was composed of a few isolated teeth (two M_1s, six M_2s and five M_3s) from the Drimolen, Swartkrans and Sterkfontein sites. It was suggested that at each molar position, the dentine horns were 'slightly higher' in *A. africanus* when compared to *P. robustus* (Skinner et al. 2008). Moreover, the distal half of the *P. robustus* M_3s was described as buccolingually narrower and distally extended at the cervix level compared to *A. africanus*. Importantly, Skinner *et al.*'s (2008) geometric morphometric analysis could not demonstrate the general consensus opinion that the cusp apices would more closely spaced in *P. robustus*, as compared to *A. africanus*. Another important taxo-specific feature was the protostylid expression observed across the buccal face of the EDJ, but not at the OES (Skinner *et al.* 2009). In *A. africanus* the protostylid crest was described to extend mesially around the base of the protoconid dentine horn, whereas in *P. robustus* the same crest was observed to be limited only between the dentine horns of the protoconid and hypoconid. Further tests of the taxonomic usefulness of these interesting observations on more specimens, especially teeth associated with crania, that have been the focus of taxonomic discussions, might shed light on more distinct lower permanent molar features that could reliably help distinguishing *P. robustus* from *A. africanus*.

Enamel thickness distribution has also received much attention to determine whether *A. africanus* and *P. robustus* could be reliably distinguished. Attempts have been made to describe enamel thickness and to compare statistically *A. africanus* and *P. robustus* using overall indices and simple bivariate statistics (Olejniczak *et al.* 2008). Olejniczak *et al.* (2008) argued that *P. robustus* enamel was not hyper-thick, and that *A. africanus* enamel was relatively thinner than that of modern humans. The 3D enamel distribution maps showed that australopith molar enamel was thickest over cusp tips, while recent humans had thicker enamel surrounding cusp base. The observed differences in 3D patterns were not considered as useful for australopith taxonomy. The previously purported 'hyper-thick' patterns reported on sections of *P. robustus* teeth (Grine & Martin 1988) was not warranted when 3D data were considered. However, as yet no method has been proposed to test statistically possible taxonomic differences in local enamel distribution across the enamel cap.

Results

EDJ and OES morphology

Only the MMDS analyses of diffeomorphic data for both the M_3 EDJ and OES show the clearest morphological differences between the KB, *A. africanus* and *P. robustus* specimens, with no overlap between these categories (Figure 4.6). As regards the M_3s' EDJ, the two KB specimens (TM 1517 and 1600) appeared morphologically similar and distinct from any other fossil hominin (Figure 4.6). The next specimen appearing closer to TM 1517 is STS 52 from Sterkfontein. However, the variability observed among the four specimens from Swartkrans (SK 6, SK 23, SK 843 and SKW 5) largely exceeded the differences between *A. africanus* and the two KB specimens. SK 6 from Swartkrans and STS 52 from Sterkfontein appeared at the extremes of variation of the EDJ MMDS analysis. When we represented the deformation between these two specimens with the former aligned onto the latter one ('SK 6 to STS 52'), we observed that they differed mainly in the reduction in crown height at the protoconid level and the disto-buccal expansion of the hypoconulid (Figure 4.6). The MMDS analysis for the M_3s OES is made with fewer specimens. The SK 6 and SKW 5 M_3s from Swartkrans appeared much closer to each other than to either STS 52 or TM 1517. Moreover, these two latter specimens were also very distinct.

Surface distance maps of enamel distribution across the crown

Comparisons of surface distance maps of enamel distribution across the M_1 crown did not show clear-cut differences between the single *A. africanus* specimen STS 24 and *P. robustus* as represented by SK 25 and SK 63 (Figure 4.4). In all instances, enamel was thicker at the cusp tips than at their bases. In the two *P. robustus* M_1s (SK 25 and SK 63) enamel thickness increased significantly at the level of all the three buccal cuspids (from the protocopid, mesially, to the hypoconulid, distally), while in the single *A. africanus* M_1 (STS 24), enamel thickness increased significantly only at the level of the hypoconid (Figure 4.4).The M_2s surface distance maps of three *P. robustus* specimens showed remarkably similar patterns of enamel distribution across the crown with the hypoconid showing distinctively the thickest values (the protoconid being

also thick enamelled in SK 6 only) (Figure 4.5). As is the case with the MMDS analyses of diffeomorphic data, only the surface distance maps of the M_3 morphological differences between *A. africanus* (STS 52) and *P. robustus* were represented by specimens from both Swartkrans (SK 6, SK 843 and SKW 5) and Kromdraai (TM 1517). In this latter species, both the protoconid and hypoconid showed the thickest values across most of their surfaces (until 5–6 mm), with the other main cusp apices also appearing thicker than 3 mm (Figure 4.6). The single *A. africanus* M_3 (STS 52) showed a markedly distinct pattern of enamel distribution than in *P. robustus*. The STS 52 M_3 was much thinner enamelled in all the areas of its crown, with its metaconid appearing as thin as the protoconid, while the *P. robustus'* protoconid thickening appeared more extensive than at the metaconid level.

DISCUSSION AND CONCLUSIONS

The main aim of this study was to obtain newly described inner dental features that could confirm the basal status of some KB hominins on the *Paranthropus* lineage in the South African fossil record. The first issue to address is therefore the identity of the immediate ancestor of *Paranthropus*. *A. africanus* is often considered as morphologically well suited to represent the precursor of *Paranthropus* (Skelton *et al.* 1986). Even if the age of *A. africanus* is irrelevant to its phylogenetic status, it is important to compare with the age of another purported ancestor of *Paranthropus*, namely *Au. aethiopicus* at ca 2.7–2.3 Ma in East Africa. Cosmogenic nuclide datings of hominins from the Jacovec cavern (Partridge *et al.* 2003) and Silberberg grotto (Granger *et al.* 2015) within the Sterkfontein cave system indicate that an *Australopithecus* species of close *Paranthropus* affinities (e.g., Clarke 1988; Partridge *et al.* 2003) was established in South Africa

at least 1 Ma earlier than *Au. aethiopicus*, roughly at the same time as *Au. afarensis*, a species that occupied much of eastern Africa until at least 3.0 Ma. Moreover, *Au. afarensis* is usually considered as morphologically too distinct from *Paranthropus* to have been its immediate ancestor (see Kimbel & Delezene 2009; but see Rak *et al.* 2007). We therefore consider that *A. africanus* represents the most reasonable Late Pliocene candidate ancestor of *P. robustus*, and we hypothesise that some Sterkfontein hominins retain a number of as yet undescribed inner-dental phylogenetically-informative features that may indicate either a cladogenetic or an anagenetic model of evolution from the former to the latter species. Importantly, even though some evolutionary biologists consider that a single lineage cannot be subdivided into genera or species without cladogenesis, we do not exclude the possibility of an anagenetic change from *A. africanus* to the KB hominins.

The *A. africanus* and *P. robustus* samples show strong inner-dental differences newly reported here, but *P. robustus* is often represented by twice or three times as many teeth. As already emphasised, our comparative sample from Sterkfontein is very small. Therefore, our conclusions are only preliminary and await further validation from additional μCT data to provide definitive evidence.

The clearest morphological differences observed between *A. africanus* and *P. robustus* specimens correspond to the 3D enamel thickness distribution across the LC (Figure 4.1), P_3 (Figure 4.3), M_1 (Figure 4.4) and M_3 (Figure 4.6) crowns. Enamel thickness could be measured accurately in only five *A. africanus* unworn teeth (LC in both STS 50 and STS 51, P_3 in STS 51, M_1 in STS 24, and M_3 in STS 52)

that we compared to a larger sample of *P. robustus* specimens from Swartkrans and one single tooth from KB (M_3 in TM 1517). In all types of teeth and in most areas of their crowns, *A. africanus* is markedly thinner enamelled than *P. robustus* from either Swartkrans or KB. Even if we acknowledge that it is relatively simple for a particular morphological feature to be contrasted between two specimens without consideration of others that may display intermediate configurations, we observe that the apparent trend for a thinner enamel distribution in *A. africanus* is observed in premolars, molars and canines, the two latter categories being represented by at least two specimens in *P. robustus*. Moreover, we observe remarkably similar patterns of 3D enamel thickness distribution among our *P. robustus* sample from Swartkrans for the lower second deciduous molars (Figure 4.2) and for the lower first, second and third permanent molars (respectively, Figures 4.3, 4.4 and 4.5). It is also noteworthy that the type specimen of *P. robustus* from KB (TM 1517) is very close to the Swartkrans specimens in its patterns of 3D enamel thickness for the lower third permanent molars (Figure 4.5).

To the best of our knowledge, only Olejniczak *et al.* (2008:408) yet depicted differences between *A. africanus* and *P. robustus* in the three-dimensional distribution of enamel in lower molars. Their results did not show clear taxonomic differences and instead argued for similar pattern of enamel thickness distribution between these two species. Therefore, the results presented in this study with the use of a new method contradict only Olejniczak *et al*'s (2008) results obtained from the ICP algorithm. We therefore update our portrait of dental differences between *A. africanus* and *P. robustus*. Our future use of more comparative material representing *A. africanus* will help us to test further our observed trend for markedly

thinner enamel in this latter species as compared *to P. robustus*.

The KB *P. robustus* hominins have long been considered as distinct from their congenerics from the nearby site of Swartkrans. Do our results support the hypothesis that the morphological differences between the KB and Swartkrans samples represent distinctions as expected as normal variation within a single *P. robustus* species?

Only the P_3 EDJ morphology shows an important morphological difference between four *P. robustus* specimens from Swartkrans and one KB hominin (TM 1517), the variability among the former Swartkrans specimens being relatively limited. Two specimens from Sterkfontein Member 4 and attributed to *A. africanus* (STS 51 and STS 52) appear morphologically closer to the four *P. robustus* P_3s from Swartkrans than to TM 1517 from KB (Figure 4.3). Unfortunately, as yet, the lower first premolar sample from KB is very limited and only TM 1517 could be studied at the EDJ level due to the relatively bad preservation status of the two other KB specimens, TM 1600 and TM 1601.

In conclusion, we newly describe important inner 3D dental features that may contribute to unravelling the phylogenetic relationships among the South African hominins in the near future. Indeed, we found evidence of new distinctions between *A. africanus* and *P. robustus* across most of the permanent dentition, at both anterior and postcanine levels. One hominin specimen from KB Member 2 (KW 6087) is newly reported in this study. The lower second deciduous molar (Figure 4.2) represents the first reported occurrence of a hominin from the oldest

fossiliferous deposits of KB. However, in the absence of comparative data for *Au. africanus'* unworn lower second deciduous molars, the taxonomic attribution of KW 6087 is uncertain but compatible with *P. robustus*. A larger sample of specimens from the oldest fossiliferous deposits of KB that could be dated and compared with specimens from both Swartkrans and Sterkfontein, will greatly help us to test whether the patterns of differences newly reported here are consistent with a plesiomorphic status of the KB hominins, indicative of their ancestral status for the *P. robustus + boisei* clade, giving rise before 2.3 Ma to the split of *P. boisei* in East Africa and *P. robustus* survivors in South Africa. Moreover, new hominin discoveries at Kromdraai will be needed to clarify the co-occurrence of both *P. robustus* and early *Homo* across the various temporal periods represented at this site.

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Some preliminary interpretations of the oldest faunal assemblage from Kromdraai

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INTRODUCTION

The fossil assemblage presented here has been discovered since April 2014 and comes mainly from KB Member 2, one of the two oldest fossil-bearing stratigraphic units known thus far at Kromdraai. This assemblage represents the first evidence of a faunal assemblage at KB that is homogeneous and stratigraphically older than any found in previous published records at KB. The descriptions given here are only preliminary. We focus on only part of the 2 200 newly discovered fossils (numbered from KW 6068 to KW 8280) attributed to birds, carnivores, cercopithecoids and bovids. These new fossils will be considered further elsewhere.

THE BIRDS

Methods

The species nomenclature follows Dickinson and Remsen (2013) and Dickinson and Christides (2014). The osteological terminology follows Baumel & Witmer (1993). The fossil birds were compared with recent bird skeletons of the following species, stored in the Bird section of the Ditsong National Museum of Natural History (TM) and in the Dipartimento di Scienze della Terra of the Torino University (Marco Pavia Ornithological Collection, MGPT-MPOC): *Coturnix coturnix, Alectoris graeca, Pternistis afer, P. capensis, P. natalensis, P. swainsoni, Dendropteryx sephaena,*

Peliperdix coqui, Scleroptila afra, S. gutturalis, S. levaillantii, S. shelleyi, Columba guinea, C. palumbus, Streptopelia capensis, S. decipiens, Turtur afer, Treron calvus, Pterocles namaqua, Grus grus, G. antigone, G. carunculatus, Anthropoides paradisaea, Balearica regulorum, Ciconia abdimii, C. ciconia, C. episcopus, C. nigra, Ardea cinerea, Threskiornis aethiopicus, Platalea alba, Geronticus calvus, Bostrychia hagedash, Plegadis falcinellus, Accipiter nisus, Buteo buteo, Circus cyaneus, Tyto alba, T. capensis, Strix aluco, Asio capensis, A. otus, A. flammeus, Falco amurensis, F. columbarius, F. concolor, F. naumanni, F. rupicoloides, F. subbuteo, F. tinnunculus, F. vespertinus, Sturnus vulgaris and *Lamprotornis purpureus.*

Order Galliformes
Family Phasianidae
***Scleroptila* sp.** (Figure 5.1, A-C)

Material examined
One complete left ulna (KW 6226); one distal right tibiotarsus (KW 6270); one proximal right tarso-metatarsus (KW 6238)

Description
Ulna: KW 6226 is a complete bone with no damage, but as for other bones from Kromdraai B, is slightly abraded.

Tibiotarsus: KW 6270 is a distal part with the shaft broken proximally to the pons supratendineus and where the sulcus extensorius is still present, even if weak. The distal end is very well preserved, with even the tiny edges of the trochlea cartilaginis tibialis in caudal view.

Tarsometatarsus: KW 6238 is a well preserved bone with only the distal end missing as the shaft is broken proximally to the foramen vasculare distale and the spur is broken off. All the rest of the bone is complete, including the whole hypotarsus, and not abraded with the shaft locally encrusted by cemented sediment. KW 6270 and KW 6238 are very similar in conservation, characteristics and measurements and could belong to the same individual, even if they were not found in anatomical connection.

Remarks
The Galliform bones found at Kroomdraai B belong to a middle-sized taxon of the Phasianidae, as they are overall smaller than *Afropavo* or the various Numididae species and bigger than *Coturnix*. The great number of the middle-sized African Phasianidae, except for *Ptilopachus*, were once listed under the genus *Francolinus*, but we are following Dickinson and Remsen. (2013) considering the presence of four different genera, often treated as subgenera (Louchart 2011). It was possible to compare the fossil bones with the genera *Dendropteryx*, *Peliperdix*, *Pternistis* and *Scleroptila*. The bones are bigger than *Peliperdix coqui* and smaller than *Pternistis afer*, *P. capensis* and *P. swainsoni*.

The complete ulna KW 6226 is bigger than *Dendropteryx sephaena* and *Pternistis natalensis* and closer resembles *Scleroptila* as the olecranon is more lateral than all the other taxa. Among the various examined *Scleroptila* taxa it is more similar to *S. levaillantii*. The tibiotarsus KW 6238 and the tarsometatarsus KW 6270 are smaller and stouter than *Pternistis natalensis* and similar in size with *Dendropteryx sephaena*, which is slender. More in general they are closely similar to *Scleroptila*, particularly *S. shelleyi*.

The ulna KB 6226 and the partial feet, assuming that KW 6238 and KW 6270 belong to the same individual, seem to pertain to different species, as the first is more similar to *Scleroptila levaillantii* and the latter to *S. shelleyi*, but given the high number of species often sympatric and the lack of detailed study of fossil Phasianidae from southern Africa, it is preferred to refer those bones to *Scleroptila* sp. This prudent approach also follows the opinion of Louchart (2011) and Göhlich & Mourer-Chauviré (2005) who stated that the osteological differences within the small-sized Phasianidae can be detected with almost complete skeletons or at least complete bones, but it becomes almost impossible with fragmented material.

As far as we know, this represents the oldest record of the genus ever, as the other fossil record of the taxon is represented by a single tibiotarsus from the Middle Pleistocene of Florisbaad, South Africa (Manegold & Brink 2011), with also possible records from the Holocene of Sibudu Cave, South Africa (Plug & Clark 2008).

This taxon, as all the other francolins, suggests the presence of open habitat, somewhat covered by dense vegetation with open areas used for feeding.

Order Cioniiformes
Family Treskiornithidae
Geronticus* cf. *calvus (Figure 5.1, E-G)

Material examined
One proximal left coracoid (KW 6156); one proximal right coracoid (KW 6151); two proximal right radii (KW 6155, KW 6157); one distal left carpometacarpus (KW 6254A); two right distal carpometacarpi (KW 6149, KW 6254B); one complete right phalax I digit majoris (KW 6139)

Description
Coracoid: KW 6151 belongs to a young bird, already fledged, and shows the processus acrocoracoideus damaged as the whole facies articularis clavicularis. The cotyla scapularis is well defined and separated from the facies articularis humeralis. The processus procoracoideus is damaged and the foramen nervi supracoracoidei. The extreme proximal part is

characterised by a pneumatized shallow sulcus musculi supracoracoidei. KW 6156 is very similar to KW 6151 but belongs to an adult bird, even if the bone surface is not perfectly preserved. It shows the proximal end greatly damaged with the processus acrocoracoideus and facies articularis clavicularis broken off, as also the processus procoracoideus.

Radius: KW 6157 is a perfectly preserved proximal end with only small damage close to the tuberculum bicipitalis radialis. KW 6155 has more shaft preserved, but the proximal end is worse preserved than KW 6157 with small damages in all the edges.

Carpometacarpus: KW 6149 is overall well preserved, with a slightly eroded bone surface, as with most of the Kromdraai B fossils. The distal end is entirely preserved, except for the medial part of the facies articularis digitalis majoris, which is broken off. The os metacarpale minus is broken at its distal end but the junction with os metacarpale major is still preserved. In KW 6254A, almost half of the os metacarpale major is preserved, while the os metacarpale minus is broken at its distal end in correspondence with the symphysis metacarpalis distalis. KW 6254B is generally more damaged than the other two carpimetacarpi with the symphysis metacarpalis distalis and the extreme distal part of the os metacarpale minus showing small damages, including the lateral edge of the facies articularis digit majoris.

Phalanx I digit majoris: KW 6139 is a complete, well preserved specimen with only a little damage on the distal end.

Remarks

The different bones belong to at least three individual; one of them a nearly fledged bird. In fact, KW 6156 shows the typical features of a young bird, with the porous bone surface and some weakly developed parts. The comparison with the skeletons of very young *Threskiornis aethipicus* (TM 74074) and *Geronticus calvus* (TM 43318) reveals that the facies articularis clavicularis is fully developed and the sulcus musculi supracoracoidei became deeper in adult birds (e.g. TM 71399 and TM 33434 respectively). The individual variability among the various examined recent Threskiornitidae skeletons is similar to that shown by the fossil bones.

The coracoids are attributable to Ciconiiformes and the presence of the foramen nervi supracoracoidei clearly indicates their attribution to Treskiornithidae, the only Family within this group with this character, and exclude the Ciconiidae, the other birds with similar overall morphology to the fossils. Ciconiidae can also be excluded by its wide, rounded and deep
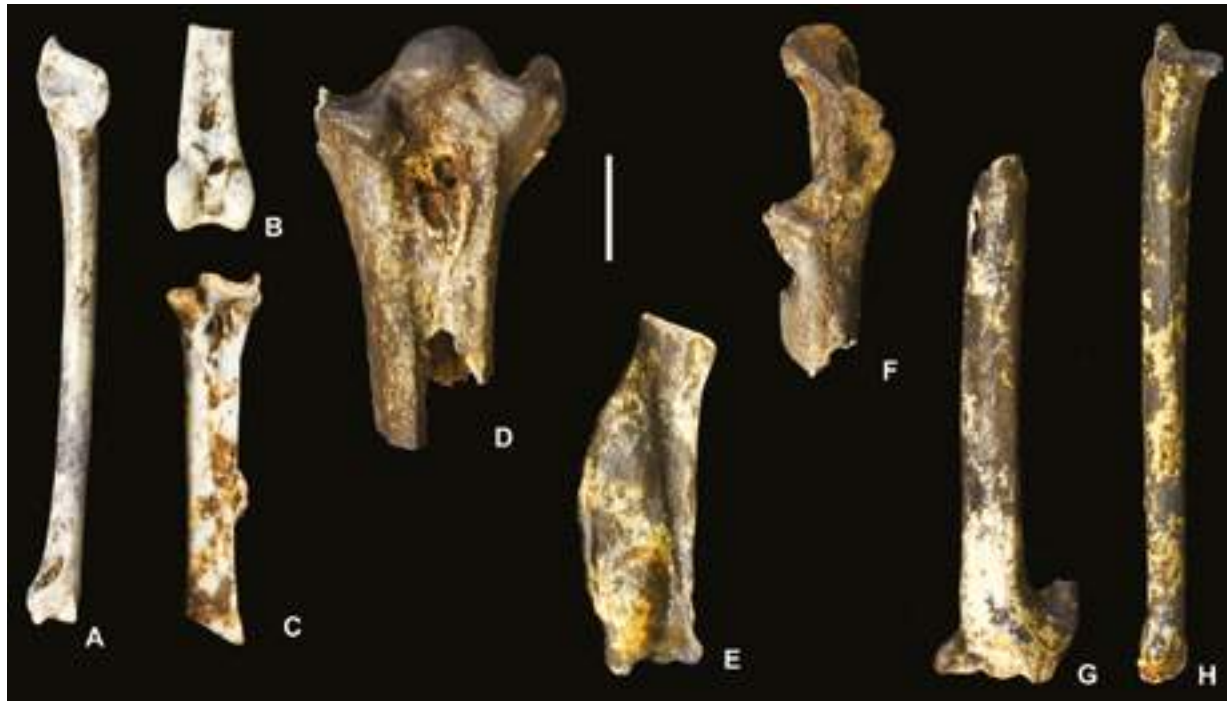

Figure 5.1 *Fossil birds from Member 2 at Kromdraai B (South Africa). (A–C)* Scleroptila *sp.: (A) left ulna KW 6226 cranial view, (B) right tibiotarsus KW 6270, cranial view, (C) right tarsometatarsus KW 6238, dorsal view; (D)* Anthropoides *cf.* paradiseus *right tarsometatarsus KW 6187, dorsal view; (E–G)* Geronticus *cf.* calvus*: (E) right phalanx I digit majoris KW 6139, dorsal view, (F) right coracoid KW 6151, dorsal view, (G) right carpometacarpus KW 6149, ventral view;.(H)* Falco *cf.* tinnunculus*, left ulna KW 6148, cranial view. The scale bar represents 1 cm.*

cotyla scapularis and not squared with a sharp lateral side as in the fossils and in Treskiornithidae. In addition, KW 6151 shows, despite damage, a hint of the facies articularis clavicularis already bigger than in a complete coracoid of Ciconiidae (e.g. *Ciconia abdimii*).

Among the Treskiornithidae, the size of the fossil bones clearly excludes their attribution to *Plegadis*, the smallest of the African Treskiornithidae. The two coracoids from Kroomdraai B more closely resemble *Geronticus* than *Threskiornis* for the following characters:

1. Wide shaft, even distally to the foramen nervi supracoracoidei.

2. Sharp medial side of the shaft caudally to the foramen nervi supracoracoidei.

3. Less pointed lateral side of the cotyla scapularis.

The fossil bones also more recall *Geronticus* than *Bosthrychia* because of:

1. Processus acrocoracoideus more protruding cranially.

2. Wider area between the facies articularis humeralis and processus acrocoracoideus in lateral view.

3. Wider foramen nervi supracoracoidei.

4. Cotyla scapularis bigger and more protruding laterally.

The two proximal radii found at Kromdraai B belong to Threskiornitidae and not to Ciconiidae for the facies articularis humeralis protrudes much more ventrally. Among the Threskiornithidae the fossil are referable to *Geronticus* rather than to the other genera for the following characters:

1. Rounded proximal end, ellipsoidal in *Threskiornis.*

2. Angled aspect of the tuberculum bicipitale radiale.

3. Size clearly bigger than that of *Plegadis*.

The wing phalanges of Ciconiidae are proportionately much slender with the rectilinear lateral edge and not convex as in the fossil and in Threskiornithidae. In dorsal view, the fossil shows a vascular channel on the lateral side of the bone as deep as in *Geronticus*, while it is less visible in *Threskiornis*. The same phalanx of *Bostrychia* is stout, thus clearly different than the fossil bone.

The three distal fossil carpimetacarpi can be referred to Threskiornithidae because they show a rounded and regular medial edge of the facies articularis digitalis majoris and not irregular as in Ciconiidae. More in detail, they are more similar to *Geronticus* than to the other Threskiornithidae in having the following characters:

1. Ventral end of the edge of the facies articularis digitalis majoris not protruding laterally (as it does in *Threskiornis*).

2. Proximo-distally less wide symphysis metacarpalis distalis in ventral view (wide in *Bostrychia*).

3. Larger size than in *Plegadis*.

The various Threskiornithidae bones found at KB can thus be referred to *Geronticus* on the basis of their size and morphology. They are overall very similar to the extant *G. calvus* to which they are tentatively referred. In fact, the fossil species *G. apelex*, described from the Pliocene of Langebaanweg, South Africa (Olson 1985), is smaller in all the long bones, but the fragmentary status of the Kroomdraai B fossil does not allow to perfectly evaluate the size of the various elements and thus the specific attribution is still dubitative. The other species of the genus *Geronticus* are the living *G. eremita* and the fossil *G. olsoni* and *G. balcanicus*, described from the Pliocene of Morocco (Mourer-Chauviré & Geraads 2010) and Bulgaria (Boev 1998) respectively, which are different in size and morphology.

The data presented here and the preliminary analysis of the newly excavated remains seems to indicate that *Geronticus* cf. *calvus* is the most abundant bird species of KB. They represent the second fossil record of this species, as the only other fossil record of the species is the very recently discovered skull from Bolt's Farm Cave, which is older in age (Pavia *et al.* in prep). This species is an endemic South African bird currently living in mid- to high-altitude grasslands areas and breeds usually in small colonies on cliffs in mountains and often near water – in river gorges or by waterfalls. The bones of young individuals indicating the presence of a breeding colony, thus testify the presence of cliff and water very close to the site.

Order Gruiformes
Family Gruidae
Anthropoides cf. *A. paradiseus* (Figure 5.1, D)

Material examined

One proximal right tarsometatarsus (KW 6187)

Description

The preserved proximal end is dark brown in colour and is quite well preserved, except for some broken parts. In dorsal view, the lateral side of the cotyla lateralis is damaged. The tuberositas musculi tibialis cranialis is well evident. In plantar view, the crista mediali flexoris digitorum longus (Mayr 2015) is damaged in its proximal part.

Remarks

The size of the specimen is comparable with the various species of the genus *Grus*, *Balearica*, and *Anthropoides paradiseus*, while it's definitively bigger than *A. virgo*. The fossil is different from *Balearica* for the following characters:

1. Eminentia intercotylaris wider and not slightly tilted laterally.

2. Eminentia intercotylaris not protruding dorsally.

3. Lateral side of the cotyla lateralis markedly concave.

4. Foramen vascuare proximale mediale opens inside a vascular groove rather than in a flat area.

5. The same foramen is not at the end of a prominent crest, as in *Balearica*.

6. The wide channel well evident medially to the foramen vasculare proximale mediale is absent in *Balearica*.

7. The whole hypotarsus ends distally to the tuberositas musculi tibialis cranialis, while is proximally in *Balearica*.

The morphology of the proximal part of the tarsometatarsus of *Grus* and *Anthropoides* is quite similar and KW 6187 is overall more similar to *Anthropoides paradiseus* (even if it shows the eminentia intercotlaris slightly narrower and more pointed) than to *Grus carunculatus*, in particular for the hypotarsus morphology. The measurements of the fossil specimens are perfectly comparable with *Anthropoides paradiseus*, thus smaller than *Grus carunculatus*, the only African species of the genus. The fragmentary status of KW 6187 and its smaller

Table 5.1 *Measurements in mm of the more complete fossil bird remains from Member 2 at KW. The asterisk (*) indicate damaged bones.*

Taxon	Number	Bone	Total length	Proximal width	Proximal depth	Distal width	Distal depth	Shaft width	Shaft depth
Scleroptila sp.	KW 6226	Ulna	54.3	6.9	8.7	6.0	6.0	2.9	4.5
Scleroptila sp.	KW 6238	Tarsometatarsus	-	8.5	8.6			4.2	3.3
Scleroptila sp.	KW 6270	Tibiotarsus	-	-	-	7.9	7.4	4.2	3.5
Geronticus cf. *calvus*	KW 6139	Wing phalanx	34.1	8.0	7.2	9.7	5.4	4.5	10.6
Geronticus cf. *calvus*	KW 6149	Carpometacarpus	-	-	-	11.2	7.4	4.9	5.9
Geronticus cf. *calvus*	KW 6155	Radius	-	6.5	8.0	-	-	-	-
Geronticus cf. *calvus*	KW 6157	Radius	-	6.6	8.7	-	-	-	-
Geronticus cf. *calvus*	KW 6254 a	Carpometacarpus	-	-	-	10.8	7.2	-	-
Geronticus cf. *calvus*	KW 6254 b	Carpometacarpus	-	-	-	11.2	7.2	4.9	5.6
Anthropoides cf. *paradiseus*	KW 6187	Tarsometatarsus	-	22.7	21.5	-	-	-	-
Falco cf. *tinnunculus*	KW 6148	Ulna	62.2	6.8	6.4	4.9	5.8	4.0	4.5
Sturnidae gen. et sp. indet.	KW 6246	Humerus	32.5*	9.3*	-	8.0	3.7	3.1	2.6
Sturnidae gen. et sp. indet.	KW 6269	Humerus	-	-	-	7.8	3.7	3.2	2.4

morphological differences does not allow to attribute it to *Anthropoides paradiseus* with certainty.

The tarsometatarsus from KB represents the oldest record of *Anthropoides* so far and the first fossil record of *A. paradiseus*. New findings in the next excavations campaigns could reveal the exact affinities of the Kromdraai specimens within *Anthropoides*. *Anthropoides paradiseus* currently live in open grasslands or thick bushes.

Order Columbiformes
Family Columbidae
cf. *Streptopelia* sp.

Material examined
Cranial part of sternum (KW 6143)

Description
The material examined consists of a cranial part of a sternum with apex carinae also preserved. The bone is poorly preserved and the bone surface suggests a young individual. The left sulcus articularis coracoideus is quite complete, while the right one is broken. The spina interna is well developed and rounded, while the spina externa is absent. The pila carinae is well developed with the foramen pneumaticum wide and deep.

Remarks
The size, proportion and morphology, particularly of the rostrum sterni, suggest to refer KW 6143 to *Streptopelia*, even dubitatively. The extreme African diversity of the genus and the poor preservation of the bone due to the age of the individual, do not allow to refine this attribution. Fossil Columbidae of small size, referred to *Streptopelia*, are quite common in the African fossil record, from the Pliocene (Louchart 2011, Manegold *et al.* 2013) to the Late Pleistocene (Plug & Clark 2008). The various *Streptopelia* species now live in mixed environments, even if they favour the open habitats, from savannahs to steppes.

Order Accipitriformes
Family Accipitridae
Gyps sp.

Material examined
Phalanx 3 digit II (KW 6583)

Description and remarks
The ungueal phalanx belongs to a big-sized bird of the Accipitridae. The less distinctive furrowed trochleae articulares with the dorsally converging rims and the less prominent processus extensorius and processus flexorius are characters typical of Aegypiinae vultures, a subfamily that includes the genera *Aegypius* and *Gyps*. The KB ungueal phalanx can be referred to *Gyps* rather than to *Aegypius* for the less developed processus flexorius (Manegold *et al.* 2014). The present-day great diversity of *Gyps* in Africa, with three species currently living in South Africa, and the great similarities in the ungueal phalanges within the vultures do not allow to better the systematic attribution.

The African fossil record of vulture is relatively scarce, with isolated remains of uncertain affinities from the Miocene of Toros Menalla (Accipitridae gen. et sp. indet in Louchart *et al*. 2008) and from the Pliocene of Laetoli (Louchart 2011). On the contrary, the recently described *Aegypius varswaterensis* from the Pliocene of Langebaanweg, South Africa (Manegold *et al.* 2014) represents the earliest, unequivocal, and most substantial evidence of the crown-group Aegypiinae in the world. The record of *Gyps* in the Early Pleistocene of KB is the oldest record of the genus in Africa.

The vultures of the genus *Gyps* are always related to the presence of big mammals in great abundance as they are scavengers, and to cliffs or big trees where they build the nests.

Order Strigiformes
Family Tytonidae
Tyto sp.

Material examined
Shaft of a left humerus (KW 6152)

Description
The whole surface of the bone is not well preserved and its structure seems to indicate a young age of the individual. On the proximal part of the shaft, the distal end of the crista deltopectoralis is preserved. On the distal side, the proximal part of the fossa musculi brachialis is visible and not very deep. The whole shaft is cranio-caudally S-shaped and the proximal and distal parts of the shaft are ventrally shifted from the major axis of the bone.

Remarks
The fossil belong to a middle-sized Strigiformes, and following its shape and the morphology of the preserved part it can referred to *Tyto* similar in size to both *T. alba* and *T. capensis*, thus smaller than the extinct *T. richae*, recently described from the Pliocene of Langebaanweg

(Pavia *et al.* in press). The fragmentary status of the bones does not allow to refine its attribution, as *T. alba* and *T. capensis* are extremely similar in size, particularly in the forelimb bones. Both the African Tytonidae currently live in open habitats, with *T. capensis* more strictly related to the grassy areas.

Order Falconiformes

Family Falconidae

Falco cf. **tinnunculus** (Figure 5.1, H)

Material examined

One complete left ulna (KW 6148)

Description

Complete and very well preserved left ulna with only the dorsal side of the processus cotylaris dorsalis slightly damaged.

Remarks

The fossil from KB belongs to a small-sized Falconiidae, rather than to a similar-in-size Accipitridae that are overall similar, for the following characters:

1. More pointed olecranon.
2. Cotyla dorsalis more squared.
3. Tuberculum ligament collateralis ventralis less evident.
4. Condylus ventralis ulnaris less expanded ventrally.

Among the various small-sized *Falco* species, KW 6148 is comparable in size with *F. amurensis, F. naumanni, F. tinnunculus*, and *F. vespertinus*. It is also comparable in size with *F. columbarius*, which has never been recorded

in sub-Saharan Africa and of which the presence in the Early Pleistocene of KB seems unrealistic. In addition to the size, the fossil species can be referred to *F. tinnunculs* for the following characters:

1. Olecranon more protruding proximally.
2. Convex cranial side of the olecranon.
3. Big and wide cotyla dorsalis with pointed cranial edge.
4. Big and ventrally wide condylus dorsalis ulnaris.
5. Tuberculum carpale more pointed and more protruding ventrally, even if this character is not very well marked in the fossil bone.
6. Angular proximal edge of the tuberculum carpale.

Falco tinnunculus is widespread in Eurasia and most of Africa and lives in open and partially forested habitats from sea level up to 4 500 m ASL.

Order Passeriformes

Family Sturnidae

Sturnidae gen. et sp. indet.

Material examined

Complete, damaged, right humerus (KW 6246); distal end of a right humerus (KW 6269)

Remarks

The complete humerus belongs to a middle-sized species of Passeriformes. The presence of the two deep and clearly separate fossae in the proximal end allow to refer this specimen to the Sturnidae, better than to the other bird families of the same size. The

distal fragment KW 6269 is very similar in size and shape and thus is here referred to Sturnidae. The Family Sturnidae is very diversified in Africa at present and the fossil remains have never been studied in detail. New material from Kromdraai B could allow to better their taxonomic attribution. The extreme diversity within the Sturnidae does not allow any ecological inference, as they live in very different habitats, even if they generally avoid dense forests.

Ecological indications

Some of the various taxa recognised at KB have specific ecological needs, thus they could help in the paleoenvironment reconstruction of the area during the Early Pleistocene. In particular, the taxa suggest the presence of a grassy environment with scattered trees. The presence of breeding *Geronticus* cf. *calvus* also indicates rocky cliffs and water, probably a canyon or a narrow valley, very close to the fossil site where they made the nests. The presence of cliffs are also suggested by *Gyps* sp. and *Falco* cf. *tinnunculus*.

THE CERCOPITHECOIDS

Previous finds

The successive excavations conducted at Kromdraai delivered a wealth of dental and skeletal remains representing *Cercopithecoides williamsi Gorgopithecus major, P. angusticeps and Papio robinsoni* (Broom & Robinson 1950:242-245; Freedman 1957:121-262, 1970:109-110; Brain 1981; Vrba 1981:17-60). In their study of the bone remains from KB (KW), Freedman and Brain (1972:1-16) described as much as 12 maxillary and mandibular pieces and 118 isolated teeth sampling a minimum of 37 monkey individuals. In terms of represented species,

the cercopithecoid assemblage from Kromdraai A (KA) is similar to the one from KW, but it differs in terms of relative frequencies, *P. robinsoni* being predominant and *Gorgopithecus* rare at KW, whereas the opposite is true at KA (Freedman & Brain 1972:1-16; Delson 1988:317-324). Moreover, the colobine *C. williamsi,* widely represented in KW, is absent at KA. Scarce remains attributed to *Parapapio jonesi* or to *Cercocebus* sp. were also tentatively identified at KA (Freedman 1957:121-262, 1970:109-110; Brain 1981; Delson 1984:199-281, 1988:317-324).

Here we provide first qualitative and quantitative information on new cercopithecoid craniodental (*i.e.,* one partial cranium labelled KW 6582 and one isolated tooth) and postcranial remains (*i.e.,* one calcaneus and one distal humerus) still embedded in a breccia block. By using advanced imaging techniques, we virtually extracted the osteodental remains and tentatively assessed their taxonomic status by comparing their morphostructural features with other South African fossil cercopithecoids and extant representatives.

Methods

In May 2015, the breccia block (approximately 144 x 120 x 86 mm) bearing the fossil monkey remains was detailed by micro-focus X-ray tomography at the Necsa imaging facility (Pelindaba) with an isotropic voxel size of 79.7 μm. The isolated tooth, a lower third molar (M3), was imaged separately at a spatial resolution of 13.6 μm. The virtual reconstruction of the specimens embedded in the block and of the isolated tooth was performed through a semi-automatic segmentation process using Avizo v8.0 (Visualization Sciences Group Inc.) (Figures 5.2, A and 5.3, A–C).

By using similar comparative data available in our files for ten fossil and 78 extant specimens representing a whole of 14 monkey genera (*Cercocebus, Cercopithecoides, Cercopithecus, Chlorocebus, Colobus, Dinopithecus, Erythrocebus, Lophocebus, Macaca, Mandrillus, Papio, Parapapio, Piliocolobus, and Theropithecus*), a comparative geometric morphometric (GM) analysis of the right inner ear of the KW 6582 cranial specimen was performed on the reconstructed virtual surface by placing three sets of semi-landmarks along the lateral and posterior semicircular canals (20 equally spaced semi-landmarks per canal) and along the outer circumference of the cochlea (40 equally spaced semi-landmarks) (Gunz *et al.* 2012:529-543; Braga *et al.* 2013:447-456; Beaudet *et al.*, 2016). Following Procrustes superimposition, a canonical variate analysis (CVA) was performed to examine overall morphological variation of both the extant and fossil specimens considered in this study, and the taxonomically undetermined specimen KW 6582 was thus projected onto the shape space to identify its closest neighbours (Gittins 1985).

The body mass of KW 6582 was estimated by using non-phylogenetic equations established for the catarrhine primates (Braga *et al.* 2015:447-456) based on the external length of the cochlea (RECL) and the surface of the oval window (OWA).

The outer mesiodistal (MD) and buccolingual (BLm, BLd and BLh) crown diameters, as well as the hypoconulid breadth (BLh), were assessed for the isolated lower M3 and compared to a number of Plio-Pleistocene South African and extant cercopithecoid specimens representing a whole of six genera (*Cercopithecoides, Colobus, Dinopithecus, Gorgopithecus, Papio* and

Parapapio) available in the literature (Freedman 1957:121-262; Swindler 2002; Heaton 2006). Comparative fossil specimens are from Bolt's Farm, Cooper's, Kromdraai A and B, Makapansgat, Skurweberg, Swartkrans, Sterkfontein and Taung (Freedman, 1957:121-262).

The dimensions of the calcaneus and the distal humerus were assessed on the virtual reconstruction and compared to fossil cercopithecoid specimens from Cooper's D (DeSilva *et al* 2013:381-394) and to extant baboons (Jolly 1972:1-122; http://eskeletons.org/).

Material

KW 6582 is a partial cranium that preserves the right side from the mastoid process to the lateral orbital margin. Its maximum length is 104 mm (Figure 5.2, A). The petrous bone is nearly complete, including a mostly intact bony labyrinth, and the opening of the carotid canal is visible inferiorly, as well as the subarcuate fossa on the inner surface. The external temporal surface exhibits well-developed suprameatal crest and post-glenoid process and the initial slope of the zygomatic process. While most of the sphenoid is missing or crushed, the supraorbital margin is only slightly damaged and it is still in connection with the frontal process where marked zygomatico-temporal and zygomatico-facial foramina are found. Even if incomplete, the supra-orbital torus is only moderately developed. Compared to the South African fossil record considered in this study, the weak supraorbital torus is consistent with the description of *Parapapio* (Freedman 1957:121-262; Heaton 2006), but the overall robustness of KW 6582 better fits the condition characterising the large-bodied papionin *Gorgopithecus,* notably as represented by the male cranium KA 192 (Figure 5.2, B). Interestingly,

the morphology of the virtually extracted cochlea and of the posterior and lateral semicircular canals (Figure 5.2, C) fall among the extant papionin variation in the negative values of the first component of the CVA, close to the living *Papio* condition (Figure 5.2, D). The KW 6582 body mass estimated by the external length of the cochlea (RECL: 12.0 mm) and by the surface of the oval window (OWA: 2.4 mm²) is 29.7 and 34.1 kg, respectively, which is compatible with the body weight ranges of male *Papio robinsoni* and male and female *Gorgopithecus major*, but which exceeds
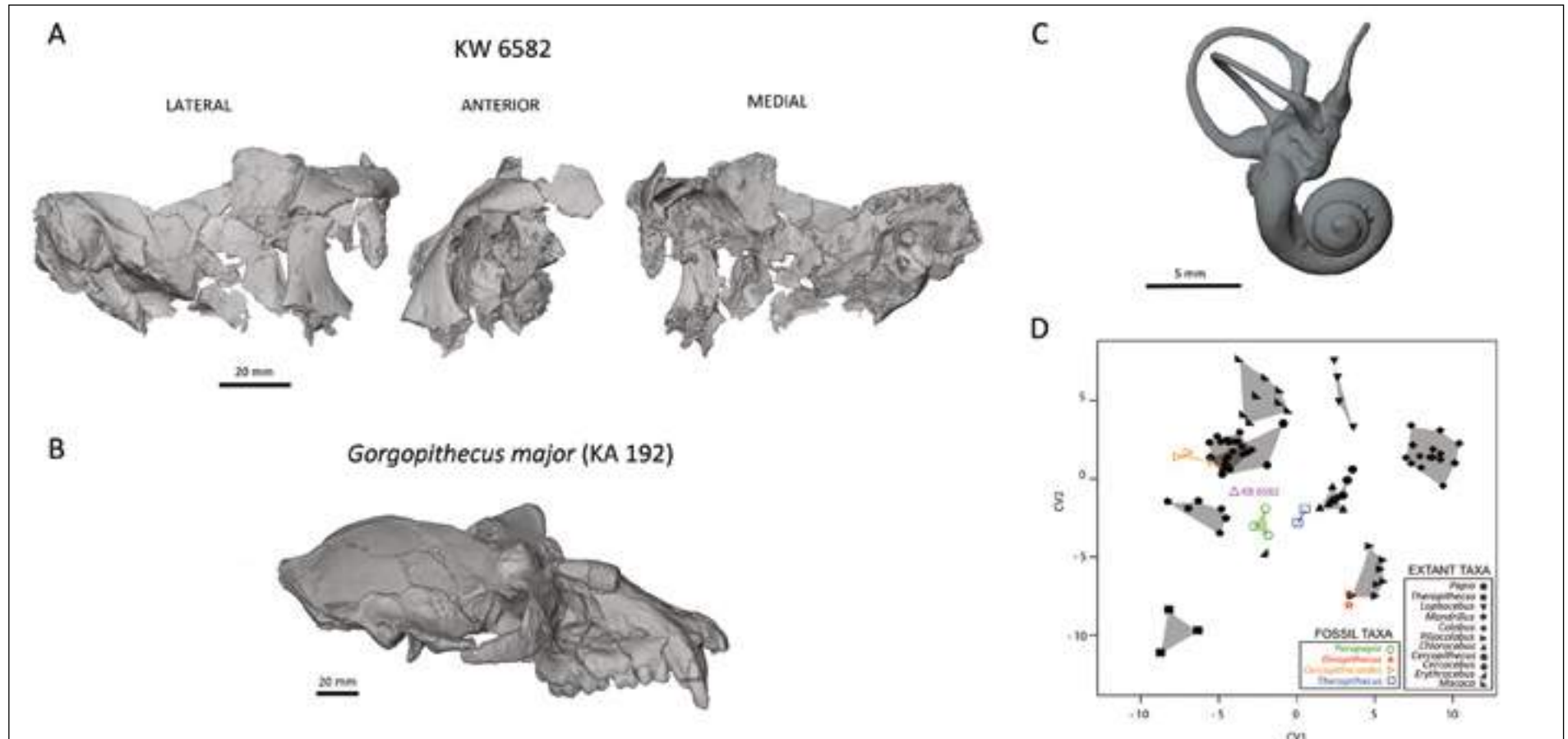

Figure 5.2   *3D virtual rendering of KW 6582 in lateral, anterior and medial views (A). The profile and overall size is compared to Gorgopithecus major (KA 192) (B). Virtual reconstruction of the bony labyrinth extracted from the KW 6582 cranium (C). Canonical variate analysis (CVA) of the Procrustes-registered shape coordinates of the labyrinth morphology calculated for the KW 6582 specimen and compared with the evidence from some Plio-Pleistocene and extant cercopithecoid specimens (D).*

the variability recorded for *Papio angusticeps* and *Cercopithecoides williamsi* (Delson *et al.* 2000:1-159).

The crown of the isolated lower molar is bilophodont, with four high cusps connected by two transverse ridges, and flares outward laterally on the buccal aspect (Figure 5.3, A). A well-formed hypoconulid is present on the distal shelf, together with a distinct tuberculum sextum. The mesial buccal cleft, as well as the medial buccal one set between protoconid and hypoconid, is shallow. The pulp cavity bears five horns in correspondence of the cusps and is separated apically into two canals filling each root branch. Its overall morphology, consistent with a papionin lower left third molar (LLM3) (Delson 1975:167-217; Swindler 2002), differs from the high-crowned and columnar-cusped specialised cheek teeth of *Theropithecus* (Jolly 1972:1-122). Because of some only moderate occlusal wear having affected the cusps (stage 4B; Delson 1973) and the presence of open root apices, it certainly represents a young adult individual. We compared its mesiodistal (MD) and buccolingual (BL) crown diameters to the evidence from a number of Plio-Pleistocene specimens and two extant taxa (Table 5.2). In this comparative context, the combined measures closely fit the condition of

Table 5.2 *Crown length (mesiodistal, MD), mesial (BLm), distal (BLd) and hypoconulid (BLh) breadths (in mm) of the isolated LLM3 from Kromdraai B compared to the estimates from some Plio-Pleistocene and extant cercopithecoid specimens/samples. M, male; F, female. [a]Kromdraai B; [b]Kromdraai A; [c]Cooper's; [d]Swartkrans; [e]Bolt's Farm; [f]Sterkfontein; [g]Makapansgat; [h]Taung; [i]Skurweberg.*

Specimen/Taxon	Origin	N	MD	sd	n	BLm	sd	n	BLd	sd	n	BLh	sd
Undetermined KW specimen	KW[a]	-	16.5	-	-	11.5	-	-	9.6	-	-	5.5	-
Papio angusticeps[1]	KA[b], CO[c]	7	14.7	0.5	7	10.3	0.3	7	9.1	0.5	6	6.0	0.9
Papio robinsoni[1]	SK[d], CO[c], BF[e]	19	17.2	1.1	17	11.0	0.9	17	9.8	0.8	17	6.8	0.6
Papio izodi[2]	STS[f]	12	13.4	1.0	9	9.6	0.7	9	8.8	0.9	9	5.7	1.1
Parapapio whitei[1]	STS[f]	6	16.4	0.5	5	11.1	0.2	5	10.3	0.4	2	6.5	0.4
Parapapio jonesi[1]	KA[b], SK[d],STS[f], MP[g]	13	12.7	0.7	10	9.3	0.3	12	8.4	0.4	10	5.0	0.4
Parapapio broomi[1]	STS[f], MP[g]	16	14.7	0.6	12	10.2	0.5	14	9.3	0.5	9	6.2	0.6
Parapapio antiquus[1]	TG[h]	4	14.7	0.9	2	9.7	-	1	9.4	-	-	-	-
Gorgopithecus major[1]	KA[b]	4	20.0	0.8	4	12.4	-	4	11.5	0.6	3	8.2	0.4
Dinopithecus ingens[1]	SK[d], SB[i]	9	21.4	0.9	9	13.5	0.6	9	11.4	1.0	5	9.2	1.8
Cercopithecoides williamsi[1]	CO[c], STS[f], MP[g]	8	11.7	0.4	5	8.1	0.2	7	8.0	0.5	6	5.0	0.7
Papio cynocephalus M[3]	extant	26	16.1	0.8	26	11.3	0.8	25	10.3	0.7	25	6.3	1.1
Papio cynocephalus F[3]	extant	26	14.3	0.8	25	10.2	0.5	24	9.5	0.7	23	5.5	0.7
Colobus polykomos M[3]	extant	43	9.6	0.7	44	6.3	0.5	43	6.2	0.5	40	4.2	0.5
Colobus polykomos F[3]	extant	26	9.4	0.7	24	6.0	0.4	25	5.9	0.3	25	4.1	0.7

Comparative data sources: [1]Freedman 1957:121-262; [2]Heaton 2006; [3]Swindler 2002.

Papio robinsoni and extant male *Papio*, and exceed the proportions displayed by *P. angusticeps* and *Cercopithecoides williamsi*.

The breccia block also contains the nearly distal third of a left humerus, including the articular end (Figure 5.3, B). The preserved diaphyseal portion (length: 69.2 mm) is triangular in cross-section, with a flattened posterior side. The distal part is separated from the shaft by an oblique fracture with some bone loss medially, and the lateral and medial epicondyles are eroded. The trochlea has a distally-extending medial flange, beyond the level of the capitulum,

and the articular surface is relatively smooth. The olecranon fossa is rounded in shape and relatively deep. Overall, the morphology and proportions of the distal humerus from Kromdraai B are compatible with those of a cercopithecoid taxon (Swindler & Wood 1973; DeSilva *et al*. 2013:381-394). Its dimensions are detailed in Table 5.3, which also provides comparative information about two cercopithecoid fossil specimens from Cooper's D (DeSilva *et al* 2013:381-394) and extant baboons (Jolly 1972:1-122). In this framework, the fossil from Kromdraai nears the proportions of the Cooper's D specimen CD 7275, likely representing a large papionin (DeSilva *et al*. 2013:381-394).

Finally, we virtually extracted from the breccia a well-preserved right calcaneus (Figure 5.3, C), whose dimensions are detailed in Table 5.4 and compared to one extant *Papio cynocephalus* male specimen available on http://eskeletons.org/. Its articular facet for the cuboid is deep and concave. The middle articular facet is well developed and projected laterally, and the posterior facet is large and dorso-posteriorly oriented. On the plantar surface, the calcaneal tuber at the posterior end creates a marked step/drop and the peroneal tubercle is prominent. As a whole, the morphology is close to the condition described for extinct and extant cercopithecoids, especially to the terrestrial papionins (Swindler & Wood 1973;

Table 5.3 *Distal humerus dimensions (in mm) of the undetermined specimen from Kromdraai B compared to the estimates from two Plio-Pleistocene and four extant cercopithecoid specimens. CD, Cooper's D; ML, mediolateral; AP, anteroposterior; PD, proximodistal; M, male; F, female.*

Measurements	Undetermined KW specimen	CD 7275[1]	CD 9486[1]	*Papio anubis* M (spec. AMNH 82097[2])	*Papio anubis* F (spec. AMNH 82096[2])	*Theropithecus gelada* M (spec. U Primatol[2])	*Theropithecus gelada* M (spec. AMNH 60568[2])
Biepicondylar breadth	35.3	35.7	30.7	45	34.5	36.5	36
ML breadth of distal articulation	26.6	26.6	22.9	30	26.0	22.5	25
AP width of distal articulation	14.9	21.5	17.7	-	-	-	-
AP breadth of trochlea	18.9	13.1	12.3	15	14.0	14.0	13
PD height of capitulum	16.5	11.0	10.1	-	-	-	-
ML breadth from medial trochlear keel to lateral epicondyle	27.9	34.3	27.1	-	-	-	-
ML breadth of olecranon fossa	16.9	16.7	-	-	-	-	-
PD height of olecranon fossa	13.6	13.6	-	-	-	-	-

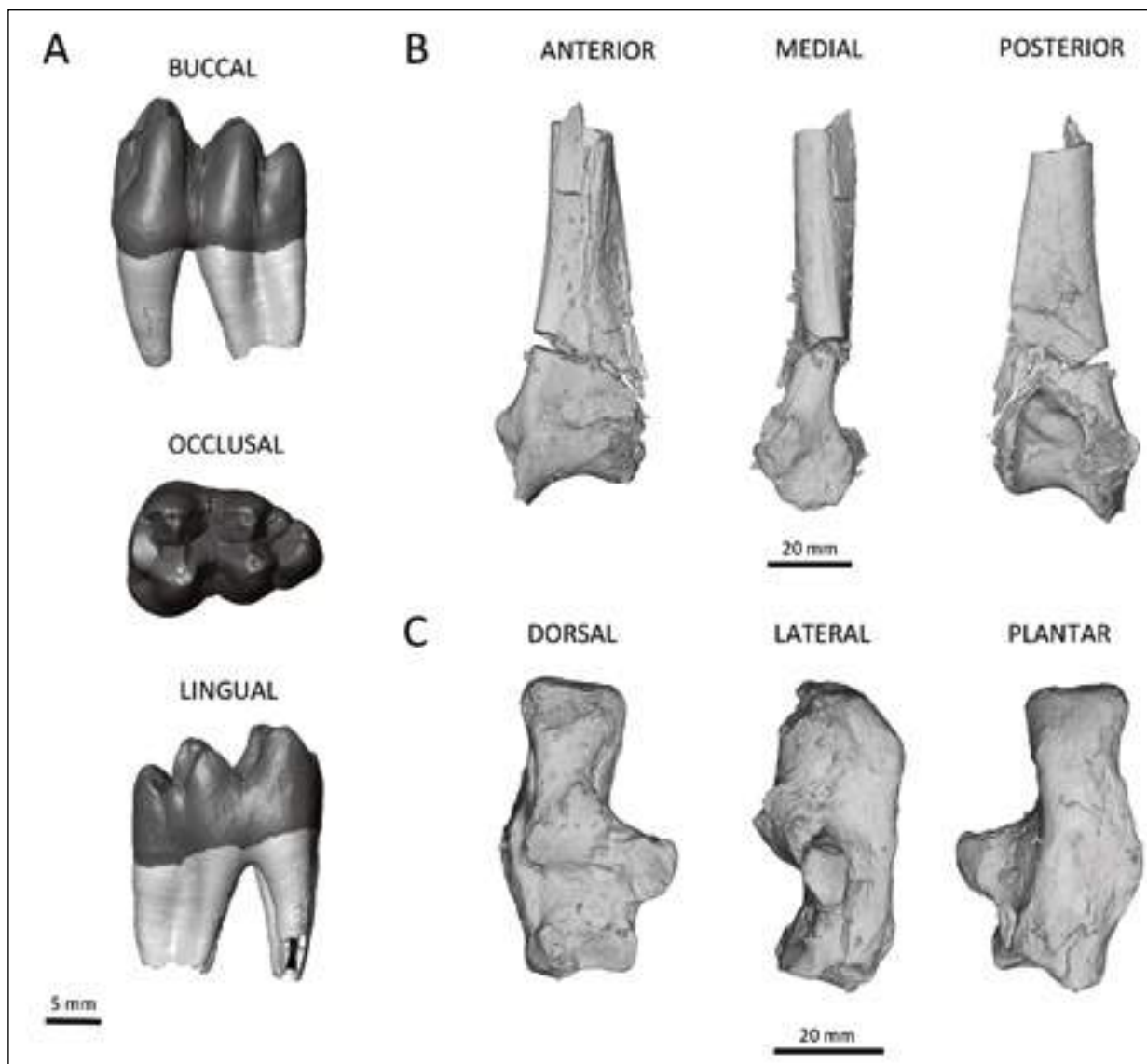**Comparative data sources:** [1]DeSilva et al. 2013:381-394; [2]Jolly 1972:1-122.

Figure 5.3 *Virtual reconstruction of the lower isolated M3 (A) in buccal, occlusal and lingual views. The distal humerus (B) and the calcaneus (C) extracted from the block of breccia are shown in anterior, medial, posterior and dorsal, lateral and plantar views respectively.*

Pina *et al.* 2011:385-394) whereas the overall size exceeds the extant *Papio* condition (Table 5.4).

Taxonomic attribution and paleoenvironmental indications

Given that in extant *Papio* a lower third molar completes its crown formation and emerges between approximately four and seven years (Dirks *et al.* 2002:239-252) and that the epiphyses of the distal humerus and the calcaneus fuse at the age of (approximately) four and six years old respectively (Bramblett 1969:161-171), the possibility that the cranial, dental and postcranial elements physically associated within the block of breccia represent a single young adult individual is not excluded.

Based on the limited set of morphological, dimensional and structural features specifically considered in this study, we note that KW 6582 and the associated lower third molar show affinities with the extinct taxa *Papio robinsoni* and *Gorgopithecus major*. Conversely, the assignment of the postcranial remains, while likely representing the same taxon, is more problematic. Nonetheless, pending the availability of a larger Plio-Pleistocene comparative record, the most parsimonious solution is to generically attribute the distal humerus and the calcaneus to a large terrestrial fossil papionin taxon.

The presence of a large form of papionin at KW is somehow informative for the reconstruction of the paleoenvironmental context. In fact, while *Papio robinsoni* is considered as an open habitat monkey (Elton 2001:115-126), the large body size of *Gorgopithecus major* implied a terrestrial behaviour of typical 'savannah' baboon and probably required

a relatively narrow ecological tolerance (Szalay & Delson 1979; Bettridge & Dunbar 2012:1278-1308). An attribution of the new fossil material reported here to either of these taxa will therefore indicate an open environment at the time of formation of the Kromdraai B Member 2 deposits.

THE BOVIDS

Introduction

The aim of this section of the report is to provide a preliminary account of the newly discovered bovids from Member 2 at KW. The bovid materials of the Kromdraai B Extension locality are fragmentary and there is a lack of well-preserved skull and horn core specimens, which hampers the diagnosis to lower levels of taxonomy. However, in spite of the fragmentary state of the materials certain taxa could be diagnosed to species level and are of substantial interest, given their biochronological and biogeographical meaning.

Results

The present sample is dominated by Alcelaphini, with some Caprini, Antilopini, an oribi, *Ourebia ourebi,* and an eland, *Taurotragus oryx*. The Alcelaphini are diverse and include at least five morphological categories. The largest is a species of *Megalotragus*, but it is not possible at the moment to diagnose it to the East African form, *M. kattwinkeli*, or to the southern African forms, *M. eucornutus* or *M. priscus*. The most commonly represented taxon is an ancestral version of the blue wildebeest, *Connochaetes taurinus prognu*, followed by a slightly smaller wildebeest-like alcelaphine species, which is suggested here to be *Connochaetes gentryi*, which is known from Turkana basin and the older levels of the Olduvai sequence (Harris 1991; Gentry 2010). Moreover, there is postcranial evidence for *Numidocapra crassicornis*, which has an Early Pleistocene record in North and East Africa (Gentry 2010). A fragmentary horn core (KW 6296) is tentatively assigned to *Damaliscus lunatus*, which is the extant tsessebe that occurs as several geographic subspecies in southern and eastern Africa. The species is known in the fossil record since

the Middle Pleistocene (Vrba 1997). Medium-sized alcelaphines listed in Table 5.5 may belong to either the tsessebe or to an as yet unidentified *Damaliscus*-like alcelaphine.

Table 5.5 *Preliminary list of bovid materials from the Kromdraai B Extension Site, according to the number of identified specimens (NISP).*

Bovidae	NISP
Tragelaphini	
Taurotragus oryx	1
Alcelaphini	
Megalotragus sp.	1
Connochaetes taurinus prognu	11
Connochaetes sp. cf. *C. gentry*	8
cf. *Numidocapra crassicornis*	3
Damaliscus sp. cf. *D. lunatus*	1
Indet. medium-sized alcelaphines	17
Caprini	
Indet.	6
Antilopini	
Indet.	8
Neotragini	
Ourebia ourebi	1
Indet.	1
Bovidae indet.	
Large	2
Large-medium	61
Small-medium	6

Table 5.4 *Calcaneus dimensions (in mm) of the undetermined specimen from Kromdraai B compared to the estimates from one extant* Papio cynocephalus *male specimen. ML, mediolateral; PD, proximodistal.*

Measurements	Undetermined KW specimen	*Papio cynocephalus*[1]
PD length	56.9	46.4
PD length anterior segment	21.4	15.7
PD length anterior segment and posterior articulation	37.4	28.6
posterior facet length	15.6	12.9
anterior articular facet length	12.4	7.9
ML breadth	30.1	21.4

Comparative data source: [1]http://eskeletons.org/

A small number of caprine specimens appear to be of the same size as *Makapnia broomi* (Gentry 2010), but the available materials are not sufficient to allow a more accurate diagnosis. The oribi is represented by a complete anterior proximal phalanx (KW 6348) and is similar in size and morphology to the extant species, showing the flare typical of the anterior phalanges in this species, but also seen in antilopines. A neotragine horn core fragment could not be identified to genus or species.

Discussion

Given the marked diversity of Alcelaphini and the absence of Reduncini and Hippotragini, the character of the palaeoenvironment reflected by the Kromdraai B bovid sample is that of a semi-arid grassland. The co-occurrence of *Connochaetes taurinus prognu* and what is likely to be *C. gentryi* is also noteworthy, since this is reminiscent of the Late Pliocene and Early Pleistocene localities in Kenya and of the older levels at Olduvai (Harris *et al*. 1988, 1991; Gentry 2010). The fossil record of *Numidocapra crassicornis*, as known at present (Vrba 1997), starts in the Early Pleistocene, but the presence of this species at Kromdraai B would not be in disagreement with the co-occurrence of the two forms of *Connochaetes*. The tsessebe is of interest, since it would be an early occurrence of the species, if confirmed. The presence of Makapania-like caprines would also be in accordance with an End-Pliocene/Early Pleistocene age for the bovid assemblage from Kromdraai B, since it is abundant at Makapan Limeworks Members 3 & 4 (Gentry 2010). A similar caprine also occurs in the basal levels of Olduvai (Gentry & Gentry 1978; personal observation).

From a biogeographic perspective the Alcelaphini and to a lesser extent the Caprini are of interest, since they clearly show biogeographic connection between eastern and southern Africa, suggesting the presence of dispersal corridors in this time between the two subregions of Africa. This would be in contrast to the endemism seen later in Middle and Late Pleistocene mammalian faunas of southern Africa (Brink 2016).

THE CARNIVORES

Background

The Kromdraai carnivores (including both KA and KB) have been largely studied. Generic and specific identifications have been discussed and modified several times (e.g., Ewer 1954, 1955, 1956a, 1956b, 1956c; Hendey 1973; Brain 1981; Vrba 1981; Turner 1984a, 1984b, 1986). A review of data on Kromdraai carnivores highlights the high richness and specific diversity of these bone accumulations. Five different families (Felidae, Canidae, Hyaenidae, Herpestidae and Viverridae), 18 genera and a minimum of 22 species have been identified. Five Hyenids have been identified, each one from a different genus: *Pachycrocuta, Crocuta, Hyaena, Parahyaena* and *Proteles*. Even if debated by Reynolds (2012), the most important point about Canids is the identification of the first African raccoon dog at KA, *Nyctereutes terblanchei* (Ficarelli *et al.* 1984). Viverrids and Herpestids are relatively rare; four genera have been identified (*Crossarchus, Atilax* at KA, *Herpestes* and *Viverra* at KB) including two species (*Crossarchus transvaalensis* and *Atilax mesotes*). Felids dominate the carnivore spectrum, including Felinae (*Caracal* and *Panthera*) and Machairodontinae (*Homotherium, Megantereon* and *Dinofelis*).

The Kromdraai carnivores have been regarded less represented and diversified at KB (eight taxa) than at KA (14 taxa). As a consequence, the biochronological interpretations for KB were more limited. However, the taphonomical analysis led by several authors such as Brain (1981) highlights the importance of carnivore influence in the bone accumulation formation and modification. Consequently, the carnivore species identification is more than ever necessary in order to characterise paleoecological and paleoenvironmental context in which both carnivore and human has evolved. Here we first review previous work on the KB carnivores from the excavations of Brain and Vrba. Then, we provide preliminary descriptions of the material from the new excavations.

Previous carnivore identifications at Kromdraai B

The story of the KB carnivores is slightly less complex than that of KA, but there are still specimens under discussion. For example, the excavations undertaken by Vrba recovered what may be the only partial skeleton of *Megantereon whitei* (discussed further below) known thus far and that still need to be compared with other machairodont taxa.

In the first record of carnivores from KB, Hendey (1973) describes Brain's findings from decalcified deposits (Brain 1958) (see Chapter 1). This list is subsequently used in Brain (1975) and Brain (1981) with some minor amendments. The second stage of publications comes with Vrba's excavation (see Chapter 1). The carnivore assemblage recovered during this period is briefly described and discussed in Vrba (1981). Subsequently, individual specimens have been discussed in a number of papers, but there

has been no updated review since Vrba (1981). As a result, the very interesting material uncovered during these excavations have not received much attention. Indeed the KB material is not considered in the most recent review of the African carnivores (Werdelin & Peigné 2010). As the taxonomy has undergone considerable alterations in the last 30 years, and a number of specimens have been re-assigned to different species, it is appropriate to review our current understanding of the KB assemblage before discussing the most recent findings from the new excavations. This summary is largely based on the literature, but is also supplemented by personal observation made on the specimens housed in the Palaeontology Department of the Ditsong National Museum of Natural History, Pretoria.

Hyaenidae

Hendey (1973) identified three specimens (KB 295, KB 2936 and KB 3250) as *Hyaena* cf. *brunnea* (= *Parahyaena brunnea*, the brown hyaena) and this identification was repeated in Brain (1975, 1981). KB 295 is a lower M1 and Hendey (1973) did not refer it at full species level because it was a heavily worn isolated tooth. He also noted that it could possibly be related to *Hyaena hyaena makapani* (Hendey, 1973:104). Following further preparation of the specimen, which revealed new diagnostic features, and a metric analysis, Turner (1986, Figure 3) identified it as *Hyaena hyaena*, the striped hyaena. This is the first record of the striped hyaena from the Cradle sites, although there are many individuals known from the Makapansgat limeworks deposits. KB 2936 and KB 3250 are a distal metapodial fragment and a 1st phalanx respectively.

Hendey (1973) also described in detail a highly polished mandible from an aardwolf, *Proteles* sp., which is larger than the modern aardwolf *Proteles cristatus*, with a shorter diastema (Table 5 in Hendey 1973). Following the discovery of similar sized specimens at Swartkrans, Hendey (1974a) named the fossil taxon *Proteles transvaalensis* based on the Swartkrans material and tentatively referred KB 2945 to this new species.

Mustelidae

Hendey (1973) identified a distal humerus (KB 3258) as *Viverra* sp., and this was reported by Brain (1981). The presence of a large civet would be significant as they are very rare in African fossil deposits. However, reanalysis by Gommery *et al.* (2008) showed it to be the humerus of a honey badger, which they determined to be *Mellivora* sp. It is very similar to another distal humerus from Cooper's D (CD 7327) identified as *Mellivora capensis* (O'Regan *et al.* 2013) and there appears to be little reason to not assign it to the extant species.

Herpestidae

Two cranio-dental mongoose specimens (KB 290 and KB 2944) were identified as *Herpestes* sp. They were suggested to be intermediate in size between *H. sanguineus* (= *Galerella sanguinea*) and *H. ichneumon* (Hendey 1973). The same two specimens are reported in Brain (1981). Hendey (1974a) described new material from Swartkrans as *Herpestes* cf. *sanguineus*, and suggested that the KB specimens might also represent this species. There is no mention of any fossils of the smaller Carnivora in Vrba (1981), although small mammals were reported as being under study. Hendey noted that "much more will

have to be learnt of the smaller fossil viverrids [incl. herpestids] of Africa before material such as that from KB can be viewed in a meaningful light" (1973:103). Perhaps surprisingly, this is still largely the case some 40 years later, although more specimens have been recovered from decalcified deposits that have been sieved such as those at Cooper's D (de Ruiter *et al.* 2009) and Drimolen (O'Regan & Menter 2009), and the recent excavations at KB have recovered a variety of herpestid specimens (see below).

Canidae

Hendey (1973) listed nine canid specimens as Canidae, but did not identify them further. He subdivided the material into two groups and suggested that the size difference between them may indicate that two separate species were present – one slightly larger than the modern black-backed jackal (*Canis mesomelas*) and one of similar size to both *Canis mesomelas* and the side-striped jackal *Canis adustus*. Hendey suggested that several of the larger-sized specimens may be associated: i) KB 3320, an upper Canine and KB 2947, a lower M fragment; ii) KB2930, a proximal metapodial and KB$_1$2931, a 2nd phalanx; and iii) KB 3255, a maxillary fragment and KB 3246, an upper canine. The final specimen from the 'larger' material is KB 292, a premaxillary fragment. In addition to these were the two slightly smaller specimens: KB 3257 an I^2, and KB 3253, an upper canine. Brain (1975, 1981) lists them all together under *Canis* sp., and refers to them as 'jackal' in the 1975 publication. No further canid material was excavated in Vrba's excavation. Hendey's (1973) discussion of the possible identification of the KB canid material discusses many different species and sub-species that all fall under the general 'jackal-sized canid' category. Many of these were named by Ewer or Broom based

on individual specimens that may be anomalous (e.g. *Canis brevirostris* from Sterkfontein). It therefore seems sensible to retain Brain's (1975) identification of this material as *Canis* sp. (jackal) pending a revision of the fossil Canidae within the southern African sites.

Felidae

Felinae

Five postcranial specimens were described by Hendey (1973:107) as being from "a medium-sized felid". While he felt they were most likely to represent leopard, the possibility of their belonging to another medium-sized felid such as possibly *Felis crassidens* was also considered. *Felis crassidens* was named by Broom (1948) on the basis of material from KA, and was the mistaken result of amalgamating both cheetah and leopard cranio-dental remains into the same individual (Turner 1984b). Therefore, the KB material could not belong to this species. Hendey (1973) suggested that the felid material may have come from two separate individuals: Group 1: KB 2885 (distal radius), KB 2901 (proximal ulna); and Group 2: KB 3259 (astragalus), KB 3249 (1st phalanx), KB 3252 (2nd phalanx). Brain (1975) repeated this list, but gave the identification of this material as *Panthera pardus*, while Brain (1981) added one additional specimen: KB 2903, a navicular.

Hendey (1973) listed also 11 specimens found in Layer 2 that he identified as possibly *Megantereon*. Nine of these specimens were suggested to be from one individual: KB 2948, right MC5 fragment; KB 2937 + KB 2939, left MC4; KB 2932 + KB 2935, left MC3; KB 2933, metapodial fragment, and three 2nd phalanges KB 2934, KB 2938 and KB 2940. A second grouping of two specimens (KB 2942, right

astragalus and KB 2946, right calcaneum) were also thought to be from one individual, possibly the same animal as the previous grouping. These specimens were all subsequently assigned to cf. *Panthera pardus* by Vrba (1981). Vrba (1981) also identified three associated fragmentary metatarsals (KB 5335A) as cf. *Panthera pardus*, noting that they were unlikely to be *Megantereon* and that small differences in robusticity may be seen between the fossil and modern leopards. Three additional metapodia from KB in the Ditsong Museum collections also belong to a very small pantherine (KB 2886, KB 2887 and KB 3332, unpublished specimens). While not specifically mentioned in earlier publications, the specimen numbers indicate they must be from the 1956 Brain excavation. As discussed by O'Regan & Menter (2009), the postcrania of the leopards from Drimolen and KB are at the lower end of the size range for modern leopards, suggesting that there may have been some palaeoecological difference between the modern cats and their fossil counterparts.

Machairodontinae

Megantereon

The specimens identified by Hendey (1973) as possibly *Megantereon* were reassigned by Vrba (1981) to cf. *Panthera pardus* (see above). However, Vrba (1981:33-39) also figured and described a partial skeleton of a machairodont cat (KB5333), as *Megantereon* cf. *gracile*. Subsequent revisions of the genus *Megantereon* have identified all African specimens as *Megantereon whitei*. This specimen is potentially the only known partial skeleton of *M. whitei*, but has not yet been studied and published in full. Parts of the specimen are much eroded, the skull is missing and only fragments of the scapula and radii remain, but the axial skeleton, hind limbs and foot bones are all well represented.

The skeleton was associated with an upper canine (KB 5380), which has a flattened cross-section and no crenellations, indicating it is unlikely to be *Dinofelis* or *Homotherium*.

Dinofelis sp. (?piveteaui)

Two associated specimens from the same individual (KB 5224a and b) represent a second machairodont genus at KB and were excavated during the 1970s. They were identified by Vrba (1981) (largely through association with KB5333 above) as *Megantereon* cf. *gracile*, by Turner (1986) as *Megantereon cultridens* and were later assigned to *Dinofelis barlowi*? by Werdelin and Lewis (2001). Additional comparative *Dinofelis* material that has been more recently excavated and published from sites including Cooper's D and Motsetse (La Cruz *et al.* 2006) and Drimolen (O'Regan & Menter 2009) has helped to make the identification of these specimens more secure. KB 5224a is an isolated and fragmentary M_1. Although the roots are present for both cusps, the crown of the paraconid is missing. The protoconid has a tiny talonid and is worn through to the dentine on the buccal surface. It also has a distinctive pinching on the interior of the protoconid that forms the tip of the cusp. KB 5224b is a moderately well-developed ascending ramus fragment, broken just below the condyle, and with just the posteriormost edge of the M_1 alveolus present. The masseteric fossa is very well-defined and the approximate height from the superiormost tip of the ramus to the top of the condyle is estimated to have been ~32 mm. In comparison with KA 64, an undoubted *Megantereon* specimen, the posterior border of the ascending ramus in KB5224b is not anteriorly shifted and the height is certainly not as reduced as that of *Megantereon*. These differences are also apparent when KB 5224b is compared with the

Megantereon mandibles illustrated in Palmquist *et al.* (2007) and Christiansen & Adolfssen (2007). The M[1] is also much larger in KB 5224a and the *Megantereon* specimen (KA 64) does not have the enamel pinching on the protoconid. It seems that KB 5224a,b does not represent *Megantereon* (*contra* Vrba (1981) and Turner (1986).

The ascending ramus is a very good visual and size match for the *Dinofelis* mandible KNM-ER 30397 from Kanapoi, illustrated in Werdelin & Lewis (2001, Figure 6), although Kanapoi is a much older deposit. In comparison with South African *Dinofelis* specimens, the M[1] (KB 5224a) is relatively small, but the broken M[1] of *D. piveteaui* from KA (KA 63) also shows the beginnings of the enamel pinching on the protoconid. It is also a good size match for this specimen (although KB 5224b is from a slightly smaller cat). The pinching on the protoconid is also seen in the Cooper's D and Motsetse *Dinofelis* specimens and is not present in the *Megantereon* specimen KA 64. The *D. barlowi* mandibles available are larger and heavier than the KB specimen, but the M[1] protoconids are too damaged to see if the pinching is present in *D. barlowi*. However, given the difference in robusticity between the two species, it seems that the KB specimen is *Dinofelis* as first suggested by Werdelin & Lewis (2001), but that it is closer in size and morphology to *D. piveteaui* than *D. barlowi*.

Machairodontinae indet.

Hendey referred to an additional specimen (KB 3248, a distal metapodial) as an unknown species, "[P]ossibly either a machairodont or the 'false sabre-tooth' *Dinofelis*" (1973:107). Brain (1975, 1981) reported this as possibly *Dinofelis* sp. indet, Vrba (1981) suggested it was *Megantereon* and Werdelin

& Lewis (2001) included it within their attribution of KB 5224a and b as *Dinofelis barlowi*. It is obviously difficult to make attributions of genus or species to a fragmentary metapodial as it clearly represents a larger felid and is likely to be machairodont.

In summary, the work previously undertaken at KB has revealed a sparse, but taxonomically diverse carnivore fauna, although few specimens were disagnostic at the species level. The identification of

Table 5.6 *Composite faunal list for Kromdraai B. See text for discussion of individual specimens and taxa (including taxonomic updates for the earlier material).*

Family	Taxon	Successive Excavations			
		Brain	Vrba	Braga and Thackeray	Composite list
Hyaenidae	*Hyaena hyaena*	X			X
	Parahyaena brunnea			X	X
	Proteles cf. *transvaalensis*	X			X
Canidae	cf. *Lycaon*			X	X
	Canis cf. *mesomelas*			X	X
	Canis sp. (jackal-sized)	X		X	X
	Vulpes sp.			X	X
Herpestidae	*Galerella* cf. *sanguinea*	X			X
	Herpestes sp.			X	X
Mustelidae	*Mellivora capensis*	X		X (sp.)	X
	Aonyx capensis			X	X
	Prepoecilogale bolti			X	X
Viverridae	*Civettictis* cf. *civetta*			X	X
Felidae	*Dinofelis* sp. (? *piveteaui*)		X		X
	Dinofelis cf. *barlowi*			X	X
	Megantereon whitei		X		X
	Machairodontinar indet.	X			X
	Panthera pardus	X	cf.		X
	Medium-sized felid (caracal/serval)			X	X

the new material from the site has added considerably to this list (Table 5.6).

The new carnivore assemblage from Kromdraai B

The ongoing fieldwork at Kromdraai (see Chapter 1) has revealed an important bone assemblage with many new carnivore remains. Analysis of these specimens has implications for both the biochronology and palaeoecology of the KB deposits. In particular, the species identification and relative abundance within the locality can contribute to the characterisation of the trophic chain and inform our understanding of hominin palaeoecology within these complex environments.

Our study includes only a small sample of the specimens recovered during the ongoing excavation. We have observed (in this preliminary analysis) a total of 89 bone carnivore remains. These specimens have been referred to six Families (Canidae, Felidae, Hyaenidae, Mustelidae, Herpestidae and Viverridae), twelve or thirteen genera (*Lycaon*, *Canis*, *Vulpes*, *Panthera*, *Dinofelis, Caracal* or *Leptailurus, Parahyaena, Aonyx, Mellivora, Prepoecilogale, Civettictis* and *Herpestes*). Four species have been clearly identified: *Panthera pardus, Parahyaena brunnea, Aonyx capensis* and *Prepoecilogale bolti*.

Two main quantification units are used in this study: the number of identified specimens (NISP) and the minimum number of individuals (MNI). Our measurement protocol follows Von den Driesch (1976). We selected several measurements that we considered as relevant for this study and the results are expressed in milimeters. Two main measurements

are used for teeth: length (L) and width (W). Long bones are described using five main variables: greatest length (GL); proximal end transverse length (Bp); proximal end antero-posterior length (Lp); shaft transverse length (Bs); shaft antero-posterior length (Ls); distal end transverse length (Bd); and distal end antero-posterior length (Ld).

Family Canidae Fischer de Waldheim, 1817
Genus Lycaon Brookes, 1827
cf. *Lycaon* (Figure 5.4, A-D)

Material examined

NISP = 8; MNI = 2

Fragmented olecraneon of a left ulna (KW 6411); radius shaft (KW 6889 + KW 6895); horizontal ramus of a right mandible including p3 and p4 (KW 6970); left navicular (KW 7415); right humerus shaft (KW 7433); radius shaft (KW 7520); distal metapodial and shaft fragment (KW 7609)

Description and remarks

KW 6970 is a fragment of a right mandible, consisting of a small portion of horizontal ramus including p3 and p4 and alveolus of p2. Tooth wear indicates that it was an old individual. Teeth are typical of canid. Both p3 and p4 are composed of a prominent protoconid covering about half of the crown length, with a posterior cusp that is most developed on the p4. These teeth are quite long and narrow (p3 L = 12.4, p3 W = 4.9; p4 L = 13.2, p4 W = 5.9). Wild dog premolars are characterised by their high crown and sharpness; in the case of KW 6970, even if the crowns are slightly worn, it seems that protoconid

would not have been high and sharp as the extant wild dog. Morphologically, KW 6970 p4 looks like *Xenocyon* spp (low crown, absence of anterior cusp flanking protoconid) like the identified *Xenocyon* p4 (AMNH 102520) as figured in Harstone-Rose *et al.* (2010, Figure 3.3, III:302). However, considering metrical data, KW 6970 p4 appears smaller than both *Lycaon sekowei* from Gladysvale (p4 L = 16.1, p4 W = 8.3) and *Xenocyon* spp. (p4 L = 16.5±1.2, p4 W = 7.6±0.7). On the contrary KW 6970 p4 fits with extant *Lycaon pictus* p4 (p4 L = 13.2±0.6, p4 W = 6.7±0.4).

The humerus is represented by a right shaft (KW 7433), comprising the proximal part including the deltoid tuberosity and part of the humeral crest which is well marked. The upper part reveals a transversal compression, which excludes felids. On the other hand this compression is not so marked as to be typical of hyenids. According to these morphological features, this humerus is referred to a wild dog-sized canid and related to cf. *Lycaon*.

Two radius shafts also represent a large canid which could be an extinct wild dog (KW 6889, KW 6895 and KW 7520). These remains reveal the typical features of canid radius. The shaft is heavily compressed from anterior to posterior view which consequently gives an oval shape to the shaft cross-section. The shaft axis is slightly curved, whereas is heavily curved in hyenids and straight in felids. Considering the specimens size, small canids are excluded. Consequently, we tentatively assign these remains to the large wild dog cf. *Lycaon*.

KW 6411 is a fragmented left ulna and is closely related to medium-sized canid. The upper part of

the olecraneon is missing, and the edges have been gnawed by a carnivore. The remaining diaphysis has a particular feature, nearly similar to the morphology observed in felids: the caudal edge of the ulna is nearly straight and transversally flattened. However, the trochlear notch is a typical for felids. Based on general morphology of the trochlear notch, hyenids are also excluded. KW 6411 is too large to be related to a small-sized canid such as foxes (genus *Vulpes*) or jackal-like (genus *Canis*). Based on its morphology and size, this specimen is referred to the wild dog cf. *Lycaon*. However, further comparative data will be required to confirm this identification.

The navicular KW 7415 is referred to a large-sized canid based on its general morphology which excludes both felids and hyenids. It measures L = 22.6, W = 17.5 and height (H) = 15.1.

KW 7609 is a distal metapodial with shaft. According to the morphology of the distal end, we tentatively relate this specimen to a large-sized canid which could be the wild dog.

The evolutionary story of wild dog is poorly known. At KA, two specimens (KA 1288 and KA 1556) are known to be related to an ancient form of wild dog, *Xenocyon atrox* or *Xenocyon africanus*. Another Pleistocene species of African hunting dog *Lycaon sekowei* has been recognised from two South African Pleistocene sites, Cooper's cave D (ca 1.5–1.4 Ma) and Gladysvale (ca 0.9 Ma) (Hartstone-Rose *et al*. 2010). This species is particularly characterised by dental morphology (closely related to *Lycaon*) and an intermediate size between *Lycaon pictus* and *Canis lupus*. A detailed comparison between *L. sekowei* (including the postcranial remains from Gladysvale)

and the Kromdraai material is needed to refine our identifications.

Genus **Canis** *Linnaeus, 1758*

Canis cf. *mesomelas*

Material examined

NISP = 11; MNI = 2

Partially-complete left scapula (KW 7077); left third upper incisor (KW 7089); partially-complete right ulna (KW 7246); anterior part of a left fourth lower premolar (KW 7361); right third upper incisor (KW 7367); crown of a canine (KW 7372); right second lower incisor (KW 7378); proximal end with shaft of a left second metacarpal (KW 7439); anterior part of axis (KW 7542); left femoral head (KW 7581); left calcaneum (KW 7607)

Description and remarks

There are five small canid teeth. KW 7089 and KW 7367 are third upper incisors. The third upper incisor is characterised by its caniniform shape and its prominent cingulum located at the base of the crown under the wear surface. KW 7372 is a fragmented canine, which could not be precisely identified as an upper or a lower canine. Morphologically, this specimen is typical of small canid (high crown and transverse compression). KW 7378 is a second lower incisor characterised by a main cusp flanked laterally by a small denticle. KW 7361 is a fragment of a fourth lower premolar. Based on their morphology and metrics, all these teeth are consistent with a jackal-sized canid.

KW 7542 is a fragment of axis. This anterior portion fits with small canids and similar in size to a jackal.

A partially complete left scapula has been referred to a jackal-sized canid (KW 7077). In spite of the large portion of preserved bone, no measurements can be taken. Both the glenoid cavity and dorsal edge are broken. However, the overall shape and morphological features are characteristic of canids, and the general size excludes small foxes. Consequently, this specimen is tentative referred to *Canis* cf. *mesomelas*.

An almost complete right ulna has been identified and referred to *Canis* cf. *mesomelas* (KW 7246). This specimen is still partially within a small breccia block which limits the measurements and description of morphological features. The only measurement we could record is the breadth of ulnar notch (12.1mm). The same measurement in black-backed jackal *Canis mesomelas* is comprised between 11.4 and 11.8 mm in four specimens, between 9.6 and 9.9mm in bat-eared fox *Otocyon megalotis* (n = 4) and between 7.2 and 7.8 mm in cape fox *Vulpes chama* (n = 4). Thus KW 7246 is clearly larger than the extant foxes, and slightly bigger than modern black-backed jackal, but much smaller than the larger *Lycaon* species.

KW 7439 is a damaged proximal articulation and shaft of a left second metacarpal. Considering the morphology, size and metrics (Bp = 6.4) it best fits a jackal-sized canid (extant *C. mesomelas* Bp = 5.2-5.5, n = 4). Further analysis, including an extended dataset of modern species, will greatly improve the identification.

KW 7581 is the proximal end (femoral head) of a left femur. The general morphology fits with a small

carnivore and especially with a small-sized canid. It is much closer in size to jackals than foxes, and is therefore referred to a jackal-sized canid.

The complete left calcaneum KW 7607 is typical of small-sized canid. According to the general morphology and some particular features (such as the morphology of *tuber calcanei* and *sustentaculum tali*), small felids (e.g. *Felis* spp.), viverrids (e.g. *Civettictis* spp.) and small hyenids (e.g. *Proteles* spp.) are excluded. The greatest length of KW 7607 (GL = 37.6) is comparable with the small canid from Cooper's D identified as *Canis* cf. *mesomelas* (GL = 31.6–34.9, n = 3; Fourvel, work in progress) even if Kromdraai specimen is somewhat larger (this difference could reflect sexual dimorphism and correspond to a large adult male).

All these above dental and post-cranial elements can be referred to a small canid. Foxes can be excluded because of their overall size; both cape fox and *Vulpes skinneri* are considerably smaller than jackals. According to the morphology and metrical data collected on the Kromdraai assemblage it seems reasonable to assign these specimens to a jackal *Canis* cf. *mesomelas*. However, further analysis, including an extended dataset of extant jackal, is needed to refine this identification.

cf. *Canis* sp.

<u>Material examined</u>
NISP = 3; MNI = 1

First phalange (KW 7024a); proximal end with shaft of a first phalange (KW 7024b); first phalange (KW 7245)

<u>Description and remarks</u>

Three first phalanges, two complete (KW 7024a, KW 7245) and an almost complete (KW 7024b) are similar to the small canids. However, no particular features observed on these specimens allow us to refine their taxonomic identification.

Various species of small canids could be found at Kromdraai such as the two jackals, *Canis mesomelas* and *Canis brevirostris* (identified at Sterkfontein member 4), the South African viverrin dog *Nyctereutes terblanchei* or the foxes *Vulpes chama* or *Vulpes pulcher* (even the new species from Malapa *Vulpes skinneri*). Morphologically, these phalanges seem to be too large to be referred to the foxes and are more similar in size to the jackals.

We could not exclude the viverrin dog but no particular features have been already described for *Nyctereutes* phalanges. Considering the occurrence of jackal remains, compared to the scarcity of *Nyctereutes* specimens, it seems reasonable to assign these three phalanges to cf. *Canis* sp.

Genus **Vulpes** *Linnaeus, 1758*

Vulpes **sp.** (Figure 5.4, E-F)

<u>Material examined</u>
NISP = 3; MNI = 1

Horizontal ramus of a left mandible including the second lower molar (KW 6500); left third lower incisor (KW 7294a); talonid fragment of a left lower carnassial (KW 7294b)

<u>Description and remarks</u>

The left mandible KW 6500 is closely related to a small-sized canid. This specimen consists in a portion of horizontal ramus including the second lower molar (m2). The relatively small size of the specimen excludes a jackal-like species. Metrical data reveal that the m2 fits within the range of foxes (genus *Vulpes*) (L = 6.9, W = 5.3), but we have not yet been able to refine the identification to species, although this may be possible in future.

Two isolated teeth have been related to a small canid, smaller than jackals, and consequently potentially a small fox. KW 7294a is a right third lower incisor and KW 7294b is a posterior part (protoconid and talonid) of a left lower carnassial.

The fragmentary m1 KW 7294b provides the most interesting information (protoconid L = 4.4; talonid L = 5.3, W = 5.5). The protoconid is high and sharp, and flanked by a well-developed metaconid (about half height of the protoconid). The talonid is relatively long and comprised of well-developed entoconid and hypoconid (this higher than the entoconid). There is a marked hypoconulid which is closely associated to the hypoconid. All these morphological features have been recorded in the recently defined Malapa's fox *Vulpes skinneri* (Hartstone-Rose *et al.*, 2013), however the fragmentary state of KW 7294b means we could not assign it to *V. skinneri*. We have personally observed the same talonid feature in Broom's *Vulpes pulcher* from KA (KA 1289). According to Ewer's description (1956a) of *V. pulcher* (mainly metrics), KW 7294b could be possibly referred to this species. However, considering the scarcity of *V. pulcher* remains and our poor knowledge of this extinct species, we currently assign KW 7294b to *Vulpes* sp.

Several fox species have been recognised in the South African fossil assemblages. The extinct fox *Vulpes pulcher* was named by Broom (1939), based on the description of an almost complete mandible from Kromdraai. Ewer (1956a) confirmed Broom's attribution and made a clear distinction between *V. pulcher* and the extant Cape fox *Vulpes chama* based on larger dental proportions in the extinct species. Recently a new fox species has been described from the Early Pleistocene site of Malapa, *Vulpes skinneri* (Hartstone-Rose *et al.* 2013). This species, even if it is closely related to *V. chama*, is different from the extant species based on some dental features. KW 6500 is metrically similar to *V. skinneri*, but morphology of the m2 seems to exclude this identification. The same observation can be made about m1 KW 7294b, which has similarities to both *V. skinneri* and *V. pulcher*, but according to the fragmentary state of the specimen it seems most reasonable to assign it to *Vulpes* sp.

Canidae gen. et sp. indet

Material examined

NISP = 2

Canine fragment (KW 7275); acetabulum fragment of a left innominate (KW 7327).

Description and remarks

KW 7275 is a crown fragment of an undetermined canine. KW 7327 is an acetabulum fragment of a left innominate. These two specimens reveal typical canid features, but are too poorly preserved for any more precise identification. We could only suggest that these specimens could be potentially referred to a large-size (KW 7275) and a small-size (KW 7327) canid.

Family Mustelidae Fischer, 1817
Genus Prepoecilogale *Petter, 1987*
Prepoecilogale bolti (Figure 5.4, G-H)

Material examined

NISP = 1; MNI = 1

Right mandible including p2, p3, p4, m1 and alveolus of m2 (KW 7359)

Description and remarks

KW 7359 is a complete right mandible of a small mustelid. Such small specimens are rarely found because of field and sieving methods. The mandible includes all the premolars (from p2 to p4) and the carnassial (m1). The alveolus confirms the presence of a second molar which is now missing. Measurements are given in Table 5.7

The morphology of the carnassial, composed of a long trigonid and a well-developed talonid, is diagnostic of a mustelid. According to our measurements, KW 7359 is nearly similar to *Poecilogale albinucha* and smaller than *Ictonyx striatus* (Condyle-Infradental length: KW 7359 = ~29.9 mm; *P. albinucha* = 28.7–29.3, n = 2; *I. striatus* = 33.6–39.2, n = 6).

However there are morphological differences between KW 7359 and *P. albinucha*. KW 7359 has three premolars (p2 to p4) and two molars (m1 and

Table 5.7   *Lower raw teeth measurements. Data in millimetres. Min-Max (N Individuals)*

	Kromdraai	Cooper's D	Laetoli	Ahl Al Oughlam	Extant	
	KW 7359	**CD 3896**	**LAET 1358**	**1331**	*P. albinucha*	*I. striatus*
p2 L	1.7	-	-	-	NA	2.1–2.6 (6)
p2 W	1.2	-	-	-	NA	1.3–1.5 (6)
p3 L	3.0	-	-	-	2.9–3.2 (2)	3.4–3.6 (6)
p3 W	1.5	-	-	-	1.6–1.7 (2)	1.6–1.8 (6)
p4 L	3.5	-	-	-	3.8–4.0 (2)	4.0–4.6 (6)
p4 W	1.8	-	-	-	1.9–1.9 (2)	2.2–2.4 (6)
m1 L	6.1	6.1	5.6	5.8	6.1–6.1 (2)	6.8–7.2 (4)
m1 W	2.6	2.5	2.5	-	2.6–2.9 (2)	3.1–3.3 (4)
m1 Paraconid L	2.1	-	-	-	2.2–2.4 (2)	2.2–2.4 (3)
m1 Protoconid L	2.3	-	-	-	2.0–2.1 (2)	2.0–2.6 (3)
m1 Trigonid L	4.4	-	-	-	4.1–4.2 (2)	4.5–4.8 (4)

m2) while *P. albinucha* has no p2 and m2. Those teeth are present in *I. striatus,* but the tooth row length is smaller in KW 7359 (15.8 mm; *I. striatus* = 18.6–20.4, n = 6). The size of the carnassial m1 (L = 6.1, W = 2.6) fits with *P. albinucha* (L = 6.1, n = 2; W = 3.8–4.0, n = 2;) and the extinct species *Prepoecilogale bolti* from Cooper's D (L = 6.1, W = 2.5 *in* O'Regan *et al*. 2013) and Laetoli Upper Unit (L = 5.6, W = 2.5 *in* Werdelin & Dehghani 2011). KW 7349 carnassial is morphologically similar to the Laetoli specimen, including a well-developed metaconid, which is the only difference with Cooper's D specimen in which the metaconid is not so well marked.

In African Plio-pleitocene context, the small mustelid *Prepoecilogale bolti* is characterised as morphologically similar to *I. striatus* but similar in size to the African weasel *P. albinucha*. KW 7359 fits with this description. As a consequence we assign KW 7359 to the extinct weasel *Prepoecilogale bolti*.

Firstly described as an *Ictonyx* species (based on a skull description from Bolt's Farm) (Cooke 1985), *Ictonyx bolti* was reassigned to the genus *Prepoecilogale* based on the comparative analysis of the Laetoli sample (Petter 1987). *Prepoecilogale* is a monospecific genus, which is represented by *Prepoecilogale bolti* (Cooke 1985). This species is poorly known and identified in a few localities including Ahl Al Oughlam in Morocco (Geraads 1997), Laetoli in Tanzania (Petter 1987; Werdelin & Dehghani 2011), Bolt's Farm (Cooke 1985) and Cooper's D (O'Regan *et al*. 2013) in South Africa. However, this distribution suggests that the species was widespread from the North to the South of Africa.

Genus *Mellivora* *Storr, 1780*

Mellivora sp.

Material examined
NISP = 1; MNI = 1

Left navicular (KW 6849)

Description and remarks
A complete left navicular (KW 6849) fits well in term of size (L = 10.0, W = 13.2, H = 6.5) and morphology to a large mustelid that could be the honey badger *Mellivora capensis*, excluding at the same time large lutrine such as *Aonyx capensis*. According to the scarcity of comparative datasets for this kind of postcranial element, it is reasonable to assign KW 6849 to *Mellivora* sp.. Further morphological and metrical analysis will probably help to refine this identification.

Mellivora have been recognised in several localities from the Cradle of Humankind. The most recent published find comes from Cooper's D (O'Regan *et al*. 2013). The honey badger has been also identified at Swartkrans Member 2 (Brain 1981) and a distal portion of a humerus from KB has been reassigned to *Mellivora* (Gommery *et al*. 2008).

Honey badger and related species are not rare in African fossil record and have a wide distribution, from Morocco to South Africa (Werdelin & Peigné 2010). However, it appears that pylogenetic relationships between the known *Mellivora* species (mainly *Mellivora benfieldi* from Langebaanweg defined by Hendey 1974b and *M. capensis*) are not clear (Werdelin & Peigné 2010).

Genus *Aonyx* *Lesson, 1827*

Aonyx capensis (Schinz, 1821)

Material examined
NISP = 3; MNI = 1

Left humerus shaft (KW 6931); right maxillary fragment including P3 and alveolus of P4 (KW 7181); maxillary and premaxillary including right C, P1 and left isolated I3 (KW 7219)

Description and remarks
Three specimens are identified as a large mustelid and precisely to an otter: two cranial remains (KW 7181 and KW 7219) and a postcranial one (KW 6931).

The right maxillary fragment including the upper third premolar and the carnassial alveolus (KW 7181) presents mustelid features. According the size of P3 (L = 7.8, W = 5.2), this specimen could be related to a large mustelid such as *Mellivora* or a large lutrine mustelid such as *Aonyx*. In the extant honey badger *Mellivora capensis*, P3 is characterised by a high protocone flanked by a well-developed posterior denticle; the tooth is wide and robust. In the African clawless otter *Aonyx capensis*, P3 is characterised by a prominent protocone covering the crown length. Posteriorly, the cingulum is well developed and runs along the lingual surface of the base of the crown. Compared to *M. capensis,* P3 in *A. capensis* is less wide and robust. KW 7181 P3 fits very well with *A. capensis* P3 features, excluding *Mellivora* sp.

KW 7219 is a right fragmentary maxillary and incisor bone including the upper permanent canine and the first premolar. Associated to this fragment, we have

collected a left third upper incisor which could belong to the same individual. The most interesting aspect, which allows us to relate this specimen to the clawless otter, is the presence and location of the first premolar. In the honey badger *M. capensis* this tooth is absent, while in the large African civet *Civettictis civetta* there is a first premolar which located just behind the canine along the maxillary in the same alignment as the rest of the dentition. On KW 7219 the small rounded premolar is towards the lingual surface of the canine. The same tooth morphology and location can be seen in extant otters, represented in South Africa by the African clawless otter *Aonyx capensis* and spotted-necked otter *Hydrictis maculicollis*. According to the size of the KW 7219 specimen (including canine and premolar metrics (respectively C L = 8.7, C W = 8.5; P1 L = 2.7, P1 W = 2.5) and morphology, the attribution to *H. maculicollis* is excluded, and it fits with *A. capensis*.

The shaft of the left humerus KW 6931 is the only postcranial specimen that can be related to a large lutrine mustelid. The main feature that identifies this specimen as Lutrinae is the important transverse compression of the diaphysis, which is typical of this group. According to the size and metrics of the diaphysis (Bs = 8.2, Ls = 14.5) KW 6931 is tentatively related to the African clawless otter.

Based on the Kromdraai remains morphology and metrics, we referred these specimens to the clawless otter *Aonyx capensis*. This is the third site record of *A. capensis* in the Cradle of Humankind after Bolt's Farm (identification of *Aonyx* cf. *capensis* in Pit 3, according Cooke, *cited in* Brain 1981), and Swartkrans Lower Bank, Member 2 and Member 3 (de Ruiter 2003).

The African clawless otter *Aonyx capensis* has been recognised in fossil context since ca. 4.3 Ma in East (Ethiopia, Kenya, Tanzania) and southern (South Africa) Africa (Werdelin & Peigné 2010). An Aonyxini gen. et sp. nov. have been recently identified at Laetoli (Werdelin & Dehghani 2011). Compared to the fossil record, the current distribution of the extant species is quite large, from Kenya to South Africa; the species is also found is West Africa, in Niger, Nigeria and the Central African Republic (Larivière 2001).

Mustelidae incertae sedis
Material examined
NISP = 1

Left first upper premolar (KW 6855f)

Description and remarks
KW 6855f is a small left upper P1. The round shape indicates that it may be a mustelid.

Family Viverridae Gray, 1821
Genus Civettictis *Pocock, 1915*
Civettictis **cf.** *civetta* (Figure 5.4, I-J)

Material examined
NISP = 1; MNI = 1

Partially-complete right edentulous mandible (KW 7351)

Description and remarks
KW 7351 is a partially-complete right edentulous mandible (only the ascending ramus is missing).

The most interesting aspect is the morphology of the marked subangular lobe on the mandible located at the junction of the horizontal and the ascending ramus. This feature appears as characteristic of genus *Nyctereutes*. Moreover, the raccoon dog have already been identified at KA with the type specimen of *Nyctereutes terblanchei* (KA 1290 *in* Ficcarelli *et al.* 1984) and the almost complete mandible of the type specimen presents similar measurements than those of KW 7351. From the condyle to infradental, the length (122.2 mm) is comparable to *N. terblanchei* (125.3 mm, personal measurements of the right mandible).

However, the number and morphology of the alveoli exclude *N. terblanchei*, as they suggest the presence of a diastema between each tooth. This feature is not so marked in *Nyctereutes* while it is present in African civet *Civettictis civetta*. The overall tooth raw length is also clearly smaller in KW 7351 (53.2 mm) than in KA 1290 (right = ~70 mm; left = 63.8 mm). If the subangular lobe is present in *Nyctereutes*, we have also observed its presence in the African civet *C. civetta*.

The African civet was identified at KB, based on the presence of a distal end of an humerus (Brain 1981), but this specimen has been reassigned to the honey badger *Mellivora* sp. (Gommery *et al.* 2008). However, it is confidently identified at Cooper's D (O'Regan *et al.* 2013).

According to these points we exclude an assignation as a raccoon dog and consider that this specimen is indicative of the presence of an African civet (or a related extinct species). The lack of teeth precludes a confident specific identification, hence we have recorded it as *Civettictis* cf. *civetta*.

Family Herpestidae Bonaparte, 1845

Herpestes sp.

Material examined

NISP = 1; NMI = 1

Horizontal ramus of a right mandible including carnassial and alveoli of p4 and m2 (KW 7283)

Description and remarks

A small herpestid has been recognised based on the presence of a right mandible (KW 7283). This fragment of horizontal ramus includes the alveoli of p4 and m2 and the carnassial m1, which reveals an advanced wear stage indicating an old individual.

The m1 morphology is similar to the overall morphology of medium-sized herpestids of genera *Herpestes* and *Atilax* with a trigonid covering about half of the total length of the tooth and a paraconid inwardly-directed. The metaconid is well developed and high, up to the level of the protoconid.

Herpestids have been already mentioned at Kromdraai: *Atilax mesotes* (firstly described as *Herpestes mesotes* by Ewer 1956c) at KA and *Herpestes* sp. (intermediate size between *Herpestes ichneumon* and *Galerella sanguinea*, syn. = *Herpestes sanguineus*) at KB by Hendey (1973).

KW 7283 is comparable to *A. mesotes* and *Herpestes* sp. from Kromdraai based on their tooth length (KW 7283 L = 8.0; *A. mesotes* L = 8.4 and 8.6, personal measurements; *Herpestes* sp. L = 8.3). However *A. mesotes* m1 is wider (W = 5.2 and 5.0) than the two specimens from KB (KW 7283 W = 3.9; *Herpestes* sp. = 4.2). KW 7283 trigonid is also smaller than *A. mesotes* m1 trigonid (KW 7283 trigonid length = 5.2; *A. mesotes* trigonid length = 6.2 and 6.2).

As there is only one very worn specimen, it seems reasonable to assign KW 7283 to the genus *Herpestes* without any specific attribution.

Viverridae or Herpestidae

Material examined

NISP = 9

Horizontal ramus of a right mandible with p4 to m2 alveoli (KW 7036); proximal radius with shaft (KW 7088); left lower canine (KW 7090); right first upper premolar (KW 7091); acetabulum and ilium of a left innominate (KW 7330); left upper canine (KW 7371); olecraneon of a left ulna (KW 7396); right lower carnassial (KW 7450); horizontal ramus of a right mandible with p2 to p4 alveoli (KW 7559)

Description and remarks

These nine specimens are from small carnivores, which could be either of Viverridae or Herpestidae. Further analysis is needed to refine their identification and they are not discussed further here.

Family Hyaenidae Gray, 1821

Genus Parahyaena (Hendey, 1974)

Parahyaena brunnea (Thunberg, 1820) (Figure 5.4, K)

Material examined

NISP = 1; MNI = 1

Left mandible including p2, p3, p4 and m1 (KW 8248)

Description and remarks

Recently we found an almost complete left mandible of a hyena. The specimen KW 8248 includes four teeth, p2, p3, p4 and m1, but the mandible is partially deformed and compressed because of sedimentary pressure, so it is impossible to measure the ramus. The dental metrics are presented in Table 5.8 and compared to extant species.

Several morphological features allow us to identify KW 8248.

The upper and lower edges of the horizontal ramus are nearly parallel. This feature is observed in *Hyaena* and *Parahyaena*, while these edges are not parallel in *Crocuta* in which we notice an important convexity under the carnassial m1 (Fourvel & Lateur 2015).

In *Crocuta*, the p2 is comprised of two or three cusps including a high and robust protoconid flanked posteriorly by a well-developed cusp, while in *Parahyaena* the p2 is characterised by a large proconid covering two-thirds of the crown length, a small posterior cusp, and a well-marked cingulum all along the base of the crown on the lingual surface and disappearing on the distal surface. In *Hyaena*, the p2 is formed of three cusps, the tooth is less robust than in *Crocuta* and *Parahyaena* and the cingulum is less-developed.

The third lower premolar p3 is a heavy tooth, conical shaped and high, used for bone breakage. Protoconid covers the almost complete tooth length and is flanked posteriorly by a heavy cusp. There is no real morphological difference between *Crocuta* and *Parahyaena*, while in *Hyaena* the strong anterior

cingulum formed regularly a reduced anterior denticle which is not observed in KW 8248.

The lower p4 is a quite long tooth comprising a high and well-developed protoconid flanked by an anterior and a posterior cusp. This tooth is robust in *Crocuta* and *Parahyaena* while it is slender in *Hyaena*. The anterior cusp is smaller and inwardly-directed in *Parahyaena* while it is well developed, individualised from the protoconid and directed in the crown main axis in *Hyaena*. In *Crocuta* this anterior cusp is clearly reduced compared to *Parahyaena* and *Hyaena*.

The carnassial m1 is characteristic in each genus. *Crocuta* is excluded based on the elongated trigonid (composed of paraconid and protoconid) and reduced talonid. The m1 in KW 8248 is similar than the general m1 feature observed in *Hyaena* and *Parahyaena* mainly characterised by a strong talonid. The exclusion of *Hyaena* is mainly the result of the global size of the carnassials, which is larger in extant *Parahyaena* than in *Hyaena*.

The raw teeth p2, p3, p4 and m1 of KW 8248 are clearly different than those from *Crocuta* and *Hyaena* and much more similar to *Parahyaena* feature. According to the morphological features and the metrics presented above, we consider that specimen as a brown hyena *Parahyaena brunnea* mandible.

cf. *Parahyaena brunnea*

NISP = 1; MNI = 1

Proximal end with shaft of a right radius (KW 7095)

Description and remarks

KW 7095 is the proximal portion of a right radius with shaft fragment. The oval-shape of the proximal articular surface is typical of hyenids. According to the proximal end metrics (Bp = 18.9; Lp = ~12.7), KW 7095 is clearly smaller than the extant *Crocuta* specimen we observe (Bp = 29.4–31.1; Lp = 19.1–19.6), which seems to exclude the species. However, the Kromdraai specimen is also smaller than the extant brown hyena (Bp = 24.3–25.7; Lp = 17.9–18.1). Considering that *P. brunnea* is confidently identified, it seems reasonable to assign KW 7095 to a possible brown hyena cf. *Parahyaena brunnea*.

Hyaenidae gen. et sp. indet.

NISP = 6

Proximal end with shaft of a right fifth metatarsal (KW 6892); left mandibular condyle (KW 6954); left third lower incisor (KW 7094); proximal end with shaft of a right fourth metatarsal (KW 7182); fragment of right incisor bone (KW 7249); fragment of a right third upper incisor (KW 7496)

Table 5.8   *Lower raw teeth measurements. Data in millimetres. Min-Max; Mean (N Individuals).*

	Kromdraai	Extant species		
	KW 8248	***P. brunnea***	***C. crocuta***	***H. hyaena***
p2 L	15.2	13.9–15.8; 15.0 (34)	13.0–16.0; 14.8 (7)	11.0–16.0; 14.0 (30)
p2 W	9.8	10.4–12.8; 11.2 (34)	9.5–11.0; 10.1 (7)	8.0–10.5; 9.0 (30)
p3 L	19.8	19.4–22.0; 20.7 (36)	20.0–22.0; 20.7 (7)	17.5–21.0; 19.1 (31)
p3 W	13.6	13.0–15.6; 14.3 (36)	14.0–15.0; 14.4 (7)	10.9–13.5; 12.1 (29)
p4 L	21.1	21.6–24.0; 22.9 (37)	20.5–24.5; 22.6 (7)	19.0–22.5; 20.4 (30)
p4 W	13.2	12.7–15.0; 13.8 (37)	13.0–13.5; 13.2 (7)	10.5–13.5; 11.9 (29)
m1 L	24.2	22.6–25.7; 24.1 (33)	25.5–29.5; 26.8 (9)	19.0–23.0; 20.9 (30)
m1 W	11.1	11.5–13.3; 12.5 (35)	11.0–12.5; 11.7 (9)	10.0–12.5; 11.0 (30)
m1 Paraconid L	11.0	9.9–12.2; 10.9 (31)	11.4–15.0; 13.1 (9)	8.0–10.0; 9.1 (30)
m1 Protoconid L	9.3	7.9–9.9; 8.8 (35)	9.0–12.0; 10.8 (9)	6.0–8.3; 7.0 (30)

Description and remarks

Six specimens, including both cranial and postcranial remains, have been collected and identified as hyenids. Dental remains (KW 7094, KW 7249 and KW 7496) are too fragmented to be referred to a genus or a species and the metapodials (KW 6892 and KW 7182) need further morphological analysis and metrical comparison to identify them.

Based on to the size and morphology of each specimen, the small aardwolf *Proteles* sp. is excluded. Nevertheless, there is a high variability in terms of size and morphological features in the large species genera *Hyaena, Parahyaena, Crocuta* or even the hunting hyena *Chasmapothetes* or the large-bodied *Pachycrocuta*. We need to collect more comparative data on extant species in order to produce a detailed analysis. According to those points, it seems reasonable to assign these specimens to the Hyaenidae family without more precision.

Family Felidae Fischer, 1817
Genus Dinofelis Zdansky, 1924
Dinofelis cf. barlowi (Figure 5.4, L-M)

Material examined
NISP = 1; MNI = 1

Left fourth lower premolar (KW 6594)

Description and remarks
KW 6594 is a left lower fourth premolar of a large felid. This tooth presents the same characteristics as described from other p4 referred to the genus *Dinofelis* (i.e. KA *in* Ewer 1955; Bolt's Farm *in* Cooke 1991; Drimolen, *cited in* O'Regan & Menter 2009). The main cusp (protoconid) is surrounded by two well-developed accessory cusps, which are with a height half of the protoconid height. Just behind the posterior accessory cusp, the cingulum forms a strong ridge. Two species are currently recognised in the 'Cradle of Humankind': *Dinofelis barlowi* and *Dinofelis piveteaui*. The features of KW 6594, particularly the large anterior accessory cusp (the same size as the posterior accessory cusp), which is set slightly lingually, and the almost rectangular outline of the tooth when seen in occlusal view all suggest it is closer to *Dinofelis barlowi* than *D. piveteaui*. The measurements of the tooth fall within the range of the two species (L = 23.5, W = 11.1). With only one tooth it is difficult to be certain of the specific designation, hence the identification as *Dinofelis* cf. *barlowi*.

Dinofelis is a machairodont of intermediate size between leopard and lion. At KA, Ewer (1955) had described a medium-sized machairodont which was identified as a new form *Therailurus piveteaui* nov. sp. (genus *Therailurus* synonym of genus *Dinofelis*; revision of their phylogenic relation in Hemmer 1965). Morphological features of the type specimen KA 61 and two other mandibles (KA 62 and KA 63) are different to *Dinofelis barlowi* from Sterkfontein, which is a more primitive form. The identification of *D*. cf. *barlowi* at KB, and *Dinofelis piveteaui* at KA indicates that there may be some considerable time difference between the two Kromdraai deposits.

Genus Panthera Oken, 1816
Panthera pardus (Linnaeus, 1758) (Figure 5.4, N-Q)

Material examined
NISP = 13; MNI = 3

Proximal end of a right third metatarsal (KW 6332); complete sacrum (KW 6344 + KW 6505); proximal end of a left tibia (KW 6346); left upper canine (KW 6365); left upper canine (KW 6421); left second metatarsal (KW 6498); partially-complete left innominate (KW 7039 + KW 7110); proximal end with shaft of a left fourth metatarsal (KW 7092); distal end of a left tibia (KW 7451); left first upper incisor (KW 7575); right upper canine (KW 7611)

Description and remarks
The upper canines KW 6421, KW 6365 and KW 7611 present typical felid features. The permanent canine is characterised by transverse flattening and recurrent presence of two grooves, located on the crown, which are directed lengthwise. The measurements, including length (L = 13.0, 10.8 and 12.4) and width (W = 9.8, 9.3 and 9.4) are closely related to extant leopard and fossil specimens from Europe (i.e. Spanish sites *in* Sanchis *et al.* 2015) and Africa (i.e. Swartkrans *in* Ewer 1956b). These remains are referred to two individuals, one old adult and one senile. Size difference could be related to sexual dimorphism.

The first upper incisor KW 7575 is referred to a medium-sized felid and attributed to the leopard.

We have identified an almost complete left innominate (KW 7039 + KW 7110) as a leopard.

KW 6344 + KW 6505 is an almost complete sacrum which is morphological similar to an extant leopard. Published comparative data (including measurements) are rare. The main values recorded on this remain are GL = 71.29; max W = 53.81.

KW 6346 is a proximal end of a left tibia. The morphology of the articular surface and tibial crest attribute it to a felid. Osteometry suggests that it could be referred to a leopard (Bp = 47.03; Lp = 46.08). KW 7451 is a distal end of a left tibia, which could be also referred to a leopard according to the morphology and osteometrical data (Bd = 30.24, Ld = 22.65).

Metapodials, here including a second (KW 6498), a third (KW 6332) and a fourth metatarsal (KW 7092), are related to a medium-sized felid: main axis presents a more-or-less pronounced dorso-palmar curvature which is typical of felid; distal end has a kind of globular aspect. Identification of these specimens as a false dirk-tooth cat *Dinofelis* is excluded. Indeed, osteometrical data are too small to correspond to this felid (KW 6498 Bp = 9.66; Lp = 17.9; KW 6332 Bp = 15.58; Lp = 19.3; KW 7092 Bp = 10.9; Lp = 15.93) and are more similar to the leopard.

Leopard is a common species in South African Plio-Pleistocene sites. Its taphonomical implication on bone accumulation processes is well known for both fossil (i.e. Swartkrans *in* Brain 1981) and modern (i.e. Brain 1981; de Ruiter & Berger 2000) context. The implication of the presence of this predator in KB should be explored further.

Panthera sp. cf. *P. pardus*

Material examined

NISP = 13; MNI = 1

Proximal end of a right fourth metatarsal (KW 6138); first phalange (KW 6195a); first phalange (KW 6195b); left fifth metatarsal (KB 6501); proximal end of a left fourth metacarpal (KB 6503); second phalange (KW 6934); partially-complete lumbar (KW 7017); distal end of a metapodial (KW 7018); right third cuneiform (KW 7020); second phalange (KW 7031); patella (KW 7040); cuboid fragment (KW 7093); left fifth metacarpal (KW 7211)

Description and remarks

Thirteen specimens have not been specifically identified. These elements present typical felid features. Specimens (particularly the metapodials) appear too small to be clearly identified as leopard. However, their robustness excludes any attribution to a smaller felid (i.e. *Caracal caracal* or *Leptailurus serval*).

A more detailed analysis of these remains, including a more important comparative dataset of extant and extinct leopard, should help us to precise their identification. Actually, based on the general size, the remains are considered as leopard-size felid and tentatively related to *Panthera* sp. cf. *P. pardus*.

Genus Caracal *Gray, 1843 or genus* Leptailurus *Severtzow, 1858*

Caracal sp. or *Leptailurus* sp.

Material examined

NISP = 6; MNI = 2

Horizontal ramus, masseteric fossa of a left mandible (KW 7277a); horizontal ramus, masseteric fossa of a right mandible (KW 7277b); horizontal ramus, masseteric fossa of a right mandible (KW 7345); second phalange (KW 7447); left radius shaft (KW 7602a); right radius shaft (KW 7602b)

Description and remarks

In modern Africa, there are two species of medium-sized felid: caracal *Caracal caracal* and serval *Leptailurus serval*. These extant species share a wide distribution covering sub-Saharan Africa (Nowell & Jackson 1996). *C. caracal* and *L. serval* are nearly the same size with a serval body mass of 9 to 18 kg, a caracal body mass of 7 to 18 kg, a serval shoulder height of about 0.6 m and a caracal shoulder height of 0.5 m (Stuart & Stuart 2008). Even if the two species are easily distinguishable in a modern context based on their morphology (elongated limbs in serval, fur differences, etc.), they are largely indistinguishable in a fossil context because of overall similarity of felid cheek teeth and their scarcity in the fossil record (Werdelin & Dehghani 2011).

At Kromdraai, six specimens have been identified as medium-sized felids that could represent either caracal or serval.

Three mandible fragments have been collected (KW 7277a, b and KW 7345). Each specimen shows the same portion: end of horizontal ramus including masseteric fossa. According to their general size and shape, these remains belong to a medium-sized felid. The masseteric fossa appears well marked and deeper in serval than in caracal according to the extant specimen that we observed at the Ditsong Museum. This feature is similar on KW 7277a, but beyond this there is not enough information to be confident in a specific attribution of these horizontal rami.

Two radius shafts (KW 7602a and b) came from the same area of the excavation and may be the same individual (one left and one right). Morphologically, these radii show typical felid features (long and straight shaft, triangular section near distal end, and well-developed and oval-shape tuberosity in dorsal view located under the proximal end). Both proximal and distal ends are missing on both. This is the result of carnivore activities, as the shafts present characteristic gnawing marks. Shaft transverse (Bs) and antero-posterior length (Ls) have been recorded

on the left radius KW 7602a: Bs = 15.0, Ls = 9.9. In extant caracal *C. caracal* shaft measurements are comprised between 10.8 and 11.7 (Bs) and 9.1 and 9.6 (Ls) while in extant serval *L. serval* nearly similar metrics are recorded (Bs = 10.3–11.3; Ls = 9.4–9.7). KW 7602a is quite larger than the data we collect on extant medium-sized felid, but at the same time the radius is too gracile to be related to a larger species such as *P. pardus,* and we could not exclude that this specimen could be a large individual or another extinct species.

KW 7447 is a complete second phalange. According to its size (smaller than a leopard but bigger than a wildcat) and morphology (asymmetric distal end), the specimen is referred to a medium-size felid which could be *Leptailurus* or *Caracal*.

Caracal has previously been identified at KA. Based on the morphology and size of the left upper carnassial KA 1544, Turner (1986) considered that this specimen is confidently referred to the caracal *Caracal* sp. We have personally observed an almost complete

Figure 5.4 *Carnivores from Kromdraai B (South Africa). (A–D)* Lycaon *sp., left ulna KB 6411: (A) medial view, (B) lateral view; right mandible KW 6970, (C) lingual view, (D) buccal view; (E–F)* Vulpes *sp., left mandible KW 6500: (E) lingual view, (F) buccal view; (G–H)* Prepoecilogale bolti*, right mandible KW 7359: (G) lingual view, (H) buccal view; (I–J)* Civettictis *cf.* civetta*, right mandible KW 7351: (I) lingual view, (J) buccal view; (K)* Parahyaena brunnea*, left mandible KW 8248, buccal view. (L–M)* Dinofelis *sp., left lower fourth premolar, KW 6594: (L) buccal view, (M) lingual view; (N–Q)* Panthera pardus*: (N) left upper permanent canine KW 6365, lingual view, (O) left upper permanent canine KW 6421, lingual view; (P–Q) right third metatarsal KW 6332, articular surface and dorsal view. The scale bar represents 1 cm.*

horizontal ramus of right mandible (KD 1023) including p4 and m1 of a medium-sized felid from KD (KA, mining dump), which could be eventually related to *Caracal* sp. However, this specimen needs further analysis to confirm the attribution.

Werdelin and Dehghani (2011) described several specimens of a medium-sized felid, including a horizontal ramus of left mandible with p3 to m1 LAET 75-991A and concluded that they could not assign specifically this material.

Concerning KB material, it seems reasonable to assign the fragmentary specimens to a medium-sized felid, which could be either *Caracal* sp. or *Leptailurus* sp. pending further revision.

Felidae gen. et sp. indet.

Material examined

NISP = 1

Distal end of a tibia (KW 6531)

Description and remarks

This distal end of a tibia presents felid features. However, its actual state of preservation does not allow any precise identification. A comparative analysis of its particular morphological aspects should help refine this.

Canivora indet.

Material examined

NISP = 3

Sesamoid (KW 6896); right talus (KW 7239); proximal end with shaft of a third or fourth metacarpal (KW 7431)

Description and remarks

Three bone remains have been tentatively referred to Carnivora.

KW 6896 is a complete sesamoid. According to its general morphology (quite long and tranversally compressed) this specimen could be possibly related to a felid. It is always difficult to assign a sesamoid to a species, mainly in carnivores, because those elements are rarely described in detail.

According to the poor preservation of the right talus KW 7239 and the metacarpal KW 7431 it appears difficult to make a precise identification. Considering the overall morphology of each specimen, we suppose that canid and hyenid are excluded.

Moreover, the identification of these specimens as felids is uncertain. Consequently, we assign the remains to undetermined Carnivora.

Ecological and biochronological implications

The identification of the carnivores has numerous implications for both biochronology and palaeo-environmental reconstruction at KB. Palaeonto-logical research on Kromdraai material are essential for biochronological purposes, characterisation of the predator guild and for species palaeoecology understanding (i.e. behavioral specialisation, inter- and intra-specific relations, competition, including Hominin-Carnivore interactions).

Canids

The canid guild from KB is represented by one, or potentially two species. As previously discussed, Hendey (1973) identified two small canids referred to *Canis* sp. (considering that seven specimens could be related to a jackal-sized canid and the two others to a larger species which could be the raccoon dog). The new material allows us to extent the canid guild. The presence of the wild dog *Lycaon* sp. could be an interesting biochronological element. The recent description of the extinct *Lycaon sekowei* from Gladysvale and Cooper's D (Hartstone-Rose *et al.* 2010) provides information about site biochronology and further analysis will help us in the wild dog identification. According to the specialised meat-cutting teeth of the wild dog, it appears as a primary hunter, which could provide carcasses to other predators (scavengers) such as the smaller jackal-sized canids. Jackals, *Canis* cf. *mesomelas*, are also recognised at KB. Foxes are also represented. At present, we could not identify it to a specific level but the recent publication on Plio-Pleistocene fox *Vulpes skinneri* (Hartstone-Rose *et al.* 2013) provides new datasets and morphological description, which will be used to assign the Kromdraai assemblage in the future.

Felids

The felid guild presents the highest species diversity in the first part of the Pleistocene, including small and medium felines, large pantherines and dirk-tooth cats. Prior to this work, the felid guild from KB was composed of one pantherine (*Panthera pardus*) and three machairodonts (including *Megantereon whitei*, *Megantereon* sp. and *Dinofelis* sp.). The identification of the false dirk-tooth cat *Dinofelis* is indicative in term of biochronology. There are at least two species

of *Dinofelis* in the Cradle, including *D. barlowi* and *D. piveteaui*. Werdelin & Lewis (2001) consider *D. piveteaui* as the most evolved form in southern Africa, which is generally younger than 1.6 Ma. The KB *Dinofelis* material reported by Vrba (1981) has here been identified as possibly *Dinofelis piveteaui* (see above). We also identified *Dinofelis* cf. *barlowi* from the most recent excavations. It is very unusual to find two *Dinofelis* species at the same site, and the presence of these two taxa may indicate that there is considerable time difference between the two KB deposits, as well as KA. We have also identified the presence of a medium-sized feline *Caracal* or *Leptailurus* and future work may help us to refine these identifications.

Hyaenids

The hyaenid guild from Plio-Pleistocene sites could reveal a high diversity including specialised species such as the hunting hyena *Chasmaporthetes* or the giant hyena *Pachycrocuta bellax* (syn. *Pachycrocuta brevirostris*). At Kromdraai, several hyena species have been identified in previous researches, including three distinct genera at KB (*P. brunnea, H. hyaena, Proteles* sp.). The material coming from the new excavations confirm the presence at KB of the brown hyena. The species is an ubiquitous hyena with scavenging behaviour. No biochronological data or palaeoenvironmental precision could be deduced from the brown hyena identification.

Mustelids

Since Broom's original research, no mustelids were found at Kromdraai. Gommery *et al.* (2008) reassigned a distal humerus from KB, which was previously identified as *Civettictis,* to the honey badger *Mellivora* sp.. A new identification of honey badger has been presented here and confirms its presence at KB. Moreover, here we present the first record of the African clawless otter *Aonyx capensis* at KB. This is the third record of this lutrine in the Cradle of Humankind after its potential presence at Bolt's Farm (Brain 1981) and its presence at Swartkrans (de Ruiter 2003). This species provides interesting information related to palaeoenvironment and the presence of rivers, swamps or lakes in Kromdraai vicinity. Finally, the identification of the small extinct weasel *Prepoecilogale bolti* at KB is one of the most interesting finds. According to Werdelin & Peigné (2010), the species evolved in Africa between 3.7 and 2.6 Ma. The recent find from Cooper's (1.5–1.4 Ma) seems to extend the species time span, but the morphological features there may represent a further evolutionary step (O'Regan *et al.* 2013). *P. bolti* from KB appears much more similar to the specimen described from the Laetoli Upper Unit (Werdelin & Dehghani 2011), which could be indicative of an older age than Cooper's.

Viverrids and Herpestids

Viverrids and Herpestids are diverse and our knowledge of their phylogeny and evolutionary trend is quite limited, even if some palaeontological sites provide numerous specimens and various genera and species (e.g. Laetoli *in* Werdelin & Dehghani 2011). Hendey (1973) identified one herpestid (*Herpestes* sp.) and one viverrid (*Viverra* sp., syn. = *Civettictis* sp.) at KB. The revision of the second one reassigned it to a large mustelid, the honey badger (Gommery *et al.* 2008). The presence of a small herpestid is confirmed. The specimen is quite similar in size and shape to *Herpestes ichneumon* but we could not exclude a potential relation with the KA herpestid *Atilax mesotes*. The African civet *Civettictis* cf. *civetta* is also recognised within KB carnivora spectrum.

CONCLUSION

The carnivora spectrum from KB is greatly extended with the new data collected and presented in this paper. Some species could provide biochronological information (e.g. *Prepoecilogale bolti, Dinofelis* cf. *barlowi*, *Lycaon* sp.) and further analysis will refine these aspects. The high diversity of carnivore species (families and genera) is similar to the high carnivore diversity regularly recorded in these Plio-Pleistocene contexts (e.g. Malapa, Gladysvale, Cooper's D, Swartkrans and Sterkfontein). Even if the majority of the carnivores recognised at KB are ubiquitous and inhabit a broad spectrum of habitats, several species provide interesting data to help refine aspects of the environment (e.g. *Aonyx capensis*).

The identification of this range of carnivores has implications for trophic chain understanding and the role of predators in hominin evolution. Taphonomical analysis of the complete bone sample (including carnivore, bovid, bird, primate,...) will provide quantity of information to precise inter- and intra-specific relation and the palaeoecological status of each species (e.g., predator, prey, primary hunter, scavenger and secondary collector).

Finally, the further fossil sample and carnivore spectrum from KB provide a new insight of the Plio-Pleistocene palaeoenvironment and palaeoecology in the Cradle of Humankind.

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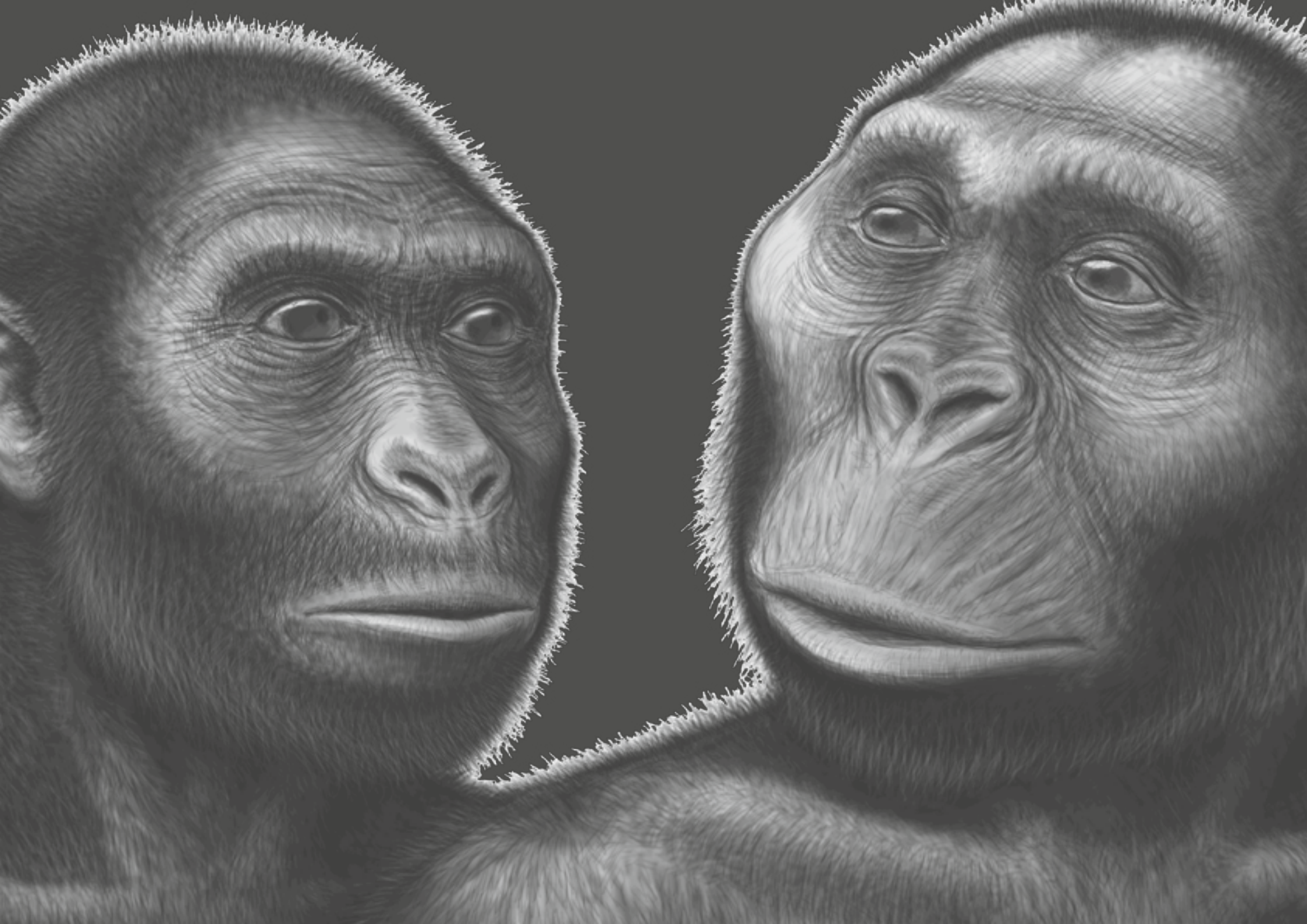
Kromdraai: A preliminary hypothetical evolutionary scenario

José Braga and John Francis Thackeray

HYPOTHESES TO BE TESTED

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? Given that the small size of several *Paranthropus* dental, cranial and post-cranial 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 (including at KB) has 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 derived from distinct site assemblages have been explored. At this stage, we do not know whether the Kromdraai assemblages accumulated during at least three distinct periods can be described either as natural death traps, carnivore lairs or accumulations due to hominin opportunistic scavengers or hunters. The two main Kromdraai faunal assemblages yet fully described and successively recovered by Brain (1955–1956) and Vrba (1977–1980) have been taphonomically interpreted in variable ways that led to spectacularly distinct reconstructions of the Kromdraai hominin behaviours (Brain 1975, 1978, 1981; Vrba 1981, Vrba & Panagos 1982).

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), after controlling for body size, used phylogenetic simulations to predict 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 shifts with an increase of molar area relative to body size along the *Paranthropus* lineage (see Figure 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 proportionally 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 measure-ments of phylogenetic signals combined with ancestral reconstructions (e.g., Braga *et al*. 2015), will also 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 *A. 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 generalised 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 may potentially be very informative to document the locomotor repertoire of this genus. New postcranial and cranial hominin specimens from Kromdraai may also help us to portray several as yet unknown features of the juvenile and adult skeleton of early *Homo*.

CONCLUSIVE REMARKS AND PERSPECTIVES

Fieldwork undertaken since 2014 by the KRP, as well as laboratory work initiated on 2 200 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 *A. prometheus* represented both at Sterkfontein Member 2 and 4, and Makapansgat) to a *Paranthropus* paraphyletic one. More hominin discoveries at Kromdraai may also help to clarify the early stages of the genus *Homo* in southern Africa.

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 not only an earliest Member 1 of the *P. robustus* lineage but also with its co-occurrence with a pre-2 Ma South African form of

early *Homo*. 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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index

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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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.

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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

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.
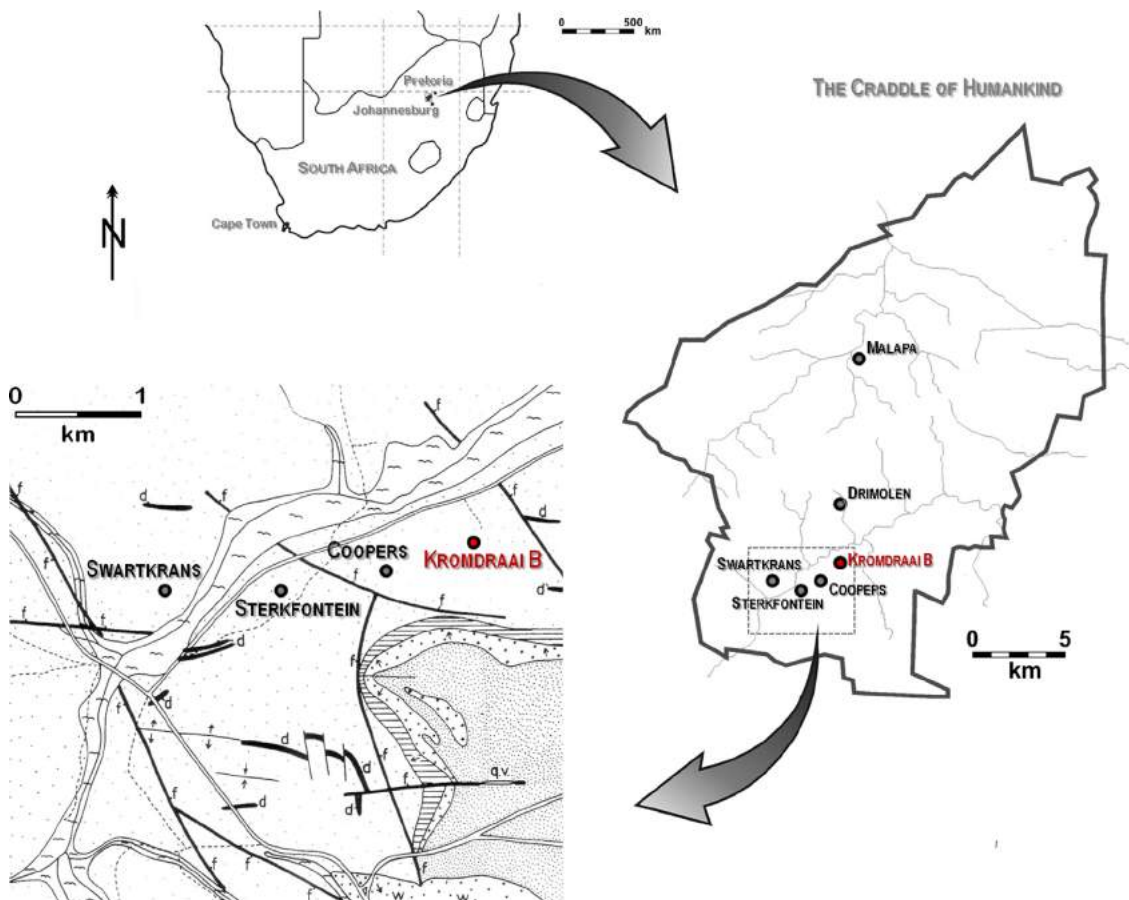

Fig. 1. Map showing the location of the site of Kromdraai (Gauteng, South Africa).
Fig. 1. Carte de localisation du site de Kromdraai (Gauteng, Afrique du Sud).
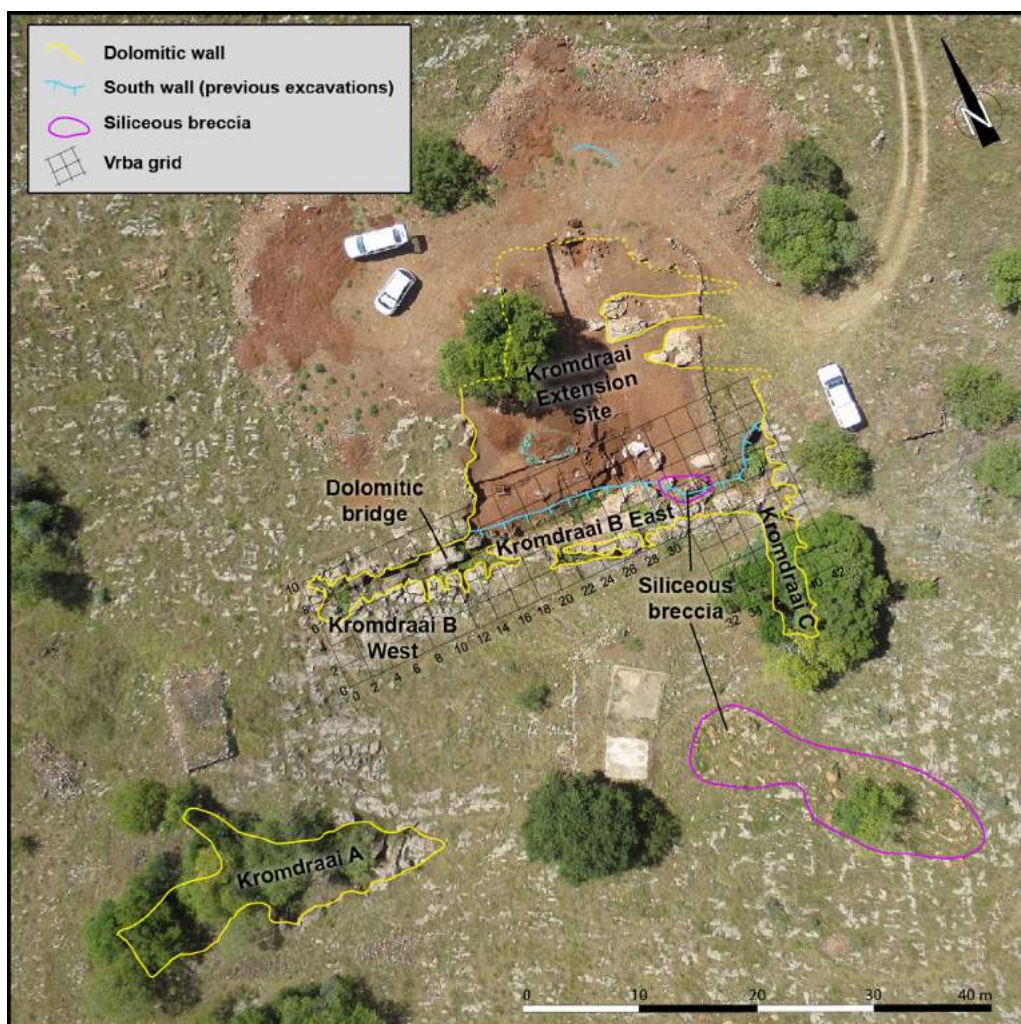
Fig. 2. Aerial view of the Kromdraai site with locations of its main features.
Fig. 2. Vue aérienne du site de Kromdraai et localisation de ses principaux éléments.

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 m² 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 m² (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 m². Not even a single bone was found during this phase. When the sediments became darker, less than one unidentifiable bone fragments per m² 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 $\delta^{13}C$ 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 $\delta^{13}C$ 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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Taphonomic interpretations of a new Plio-Pleistocene hominin-bearing assemblage at Kromdraai (Gauteng, South Africa)

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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.

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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

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

Small rodents (NISP = 40), lagomorphs (NISP = 35), reptiles and amphibians (NISP = 32) are also excluded. Our study focuses on 1889 identified macro-mammal bones (carnivores, bovids, non-hominin primates and unidentified remains) from Member 2, discovered up until May 2016. These newly discovered specimens are curated at the Evolutionary Studies Institute of the University of Witwatersrand in Johannesburg. They represent at least 35 non-hominin species identified by one of us (JBF), associated with a comparative study of fossil specimens from the nearby sites of Swartkrans, Sterkfontein and Cooper's D (Table 2). The preliminary description of the Kromdraai Member 2 faunal assemblage was published by Fourvel et al. (2016) and Fourvel (2017a). With its 5 families, 18 genera and at least 22 species, the Kromdraai carnivore assemblage described here (Table 2) highlights the richness and high specific diversity of the bone accumulation. The ungulate sample is dominated by Alcelaphini, with some Caprini and Antilopini (Table 2). The four main taphonomic criteria used in this study (mortality profiles, representation of skeletal parts, bone fragmentation and surface modifications) are described below.

2.1. Quantification units

We use three quantification units (see Lyman, 1994 for more details) in order to describe the faunal assemblage investigated in this study: NISP (number of identified specimens), MNE (minimum number of elements) and MNI (minimum number of individuals). Moreover, we use the MAU (minimum animal unit) and "%MAU" parameters (Binford, 1981, 1984; Lyman, 1994) in order to discuss the absolute and relative representation of bodyparts. Considering the fact that the taphonomic analysis is focused on carnivore-prey interactions (including bovid and non-hominin primates), all the frequencies (such as tooth marks) are based mainly on the macro-mammalian remains considered here (carnivores NISP = 197; ungulates NISP = 1127; non-hominin primate NISP = 284). Some indices can be used to assess the taxonomic diversity at Kromdraai Member 2 and to compare them with faunal spectra from other Plio-Pleistocene sites in the Cradle of Humankind. We used the Shannon diversity index (H′), and its evenness (E), associated with Simpson's index (D) (Magurran, 1988).

2.2. Prey size classes

Brain (1980, 1981) distinguished the following four size classes of bovids: "Class I" (less than 20 kg), "Class II" (medium-sized bovids ranging from 20 to 100 kg), "Class III" (large-sized bovids up to 300 kg), "Class IV" (species larger than 300 kg). In order to consider a larger sample of both identified and unidentified bone remains, we simplify Brain's classification by merging class III and class IV into one size class ("large-sized") and by considering the three following groups: "small-sized" bovids (including Antilopinae), "medium-sized" bovids (including the majority of Alcelaphinae), and "large-sized" bovid. In addition to the bovids, we also consider the large-bodied (baboon-like) cercopithecoids as another category of prey.

2.3. Age classes and mortality profiles

The prey age classes used to reconstruct mortality profiles are also important taphonomic indicators (e.g., Stiner, 1990; Cruz-Uribe, 1991; Steele, 2003, 2005; Bunn and Pickering, 2010; Val et al., 2014; Fourvel et al., 2015). The three main mortality models, as proposed by Stiner (1990), have been recognized: "attritional" (a U-shape profile with high proportions of both juvenile and old individuals, corresponding to the natural mortality of a living population); "prime-dominated" (representing potential selection by a predator); "catastrophic" (with a high representation of juveniles). Following Stiner (1990), we distinguish three age classes based on tooth eruption and replacement, and degree of wear: "juvenile" (individuals with deciduous teeth only), "prime adult" (from the eruption of the first permanent tooth and before heavy wear of the raw teeth), and "old" (all permanent teeth heavily worn). According to this method, only cranial remains with teeth (such as maxilla and mandible fragments) and isolated teeth are considered in our analysis. Consequently our sample differs from the MNI presented in Table 2 which includes both cranial and post-cranial remains. However we provide a more detailed age classification of both cranial and post-cranial remains in Supplementary 1. In order to compare the mortality structures observed for bovids (according to size classes) and non-bovid species, we illustrate our results in a ternary plot.

2.4. Representation of skeletal parts

We investigate the representation of skeletal parts in order to detect and quantify their potential selection according to as yet unknown biological or non-biological processes (cf. the allopodial versus autopodial hypothesis developed by Vrba, 1981 who considered "two modes in which bones may be transported to final resting sites by animals: autopod accumulation involves arrival on the animals' own feet [natural bone accumulation in a death trap]; allopod accumulation on the feet of others (predators, scavengers, collectors) [bone accumulation resulting of carnivore denning]" Vrba, 1981, p.47). We first consider the possibility that some post-depositional processes have biased our bone sample, particularly because of the differential bone mineral density of different skeletal elements. We therefore investigate, for each prey size class, the relationship between the bone preservation rate and its mineral density (Lyman, 1984; Pickering and Carlson, 2002; Carlson and Pickering, 2004; Lam and Pearson, 2004). We then examine the relative proportions of each skeletal part for each prey size class according to frequencies of NISP, MNE and MAU. Since the relative abundance of the skeletal elements of an animal's body is usually regarded as indicative of its introduction into the faunal assemblage (e.g., the introduction by a hominin or a carnivore; or a death trap, as exemplified for example by the work of Vrba in 1981), we consider separately the cranial, axial and appendicular parts. Each skeletal element is also considered separately. In order to avoid over-representation of some parts due to post-depositional processes (e.g., sedimentary compaction), we excluded unidentified long bones (i.e., shaft fragments generally less than 3 cm and with no diagnostic morphological features) and isolated teeth from this analysis. Indeed, the inclusion of the isolated teeth (durable elements most frequently recovered due to good preservation) in our analysis would bias the representation of other skeletal elements. Isolated teeth represented almost 50% of the large bodied primate samples at Kromdraai.

2.5. Long bone fragmentation

Carnivore involvement, hominin exploitation and non-biological processes that played a role in bone accumulation usually imply variable bone fragmentation, depending on the intensity of each taphonomic process (Brain, 1981; Bunn, 1983). We examined the degree of fragmentation of particular elements (humerus, radius, femur, tibia and metapodials). Because of their smaller size, we excluded cercopithecoid metapodials for comparative purposes.

We considered the degree of fragmentation for both "meaty" (humerus, radius, femur, tibia) and "non-meaty" (metapodial) bones as well as their relative representation by using the following five categories: "complete", "epiphysis with shaft" (both proximal

Table 2
Faunal spectrum (including NISP, MNE, MNI and related frequencies) from Kromdraai Member 2.

Order	Family	Sub-family	Genus	Species	Size class	NISP	%NISP	MNE	%MNE	MNI	%MNI
Carnivora	Felidae	Machairodontinae	*Dinofelis*	*D. cf. barlowi*	Large	1	<1%	1	<1%	1	1%
		Pantherinae	*Panthera*	*P. pardus*	Medium	53	2%	50	4%	6	5%
		Pantherinae	*cf. Panthera*	*cf. P. pardus*	Medium	4	<1%	4	<1%	1	1%
		Felinae	*Leptailurus / Caracal*	*L. serval / C. caracal*	Small	8	<1%	8	1%	3	3%
		indet.	*gen. indet.*	*sp. indet.*	?	2	<1%	2	<1%	-	-
	Canidae	Caninae	*Lycaon*	*cf. Lycaon*	Large	10	<1%	10	1%	3	3%
		Caninae	*Canis*	*Canis sp.*	Large	1	<1%	1	<1%	1	1%
		Caninae	*Canis*	*Canis cf. mesomelas*	Small	13	1%	13	1%	2	2%
		Caninae	*Canis*	*sp. indet.*	Small	2	<1%	2	<1%	1	1%
		Caninae	*Vulpes*	*V. chama*	Small	6	<1%	5	<1%	3	3%
		Caninae	*gen. indet.*	*sp. indet.*	?	4	<1%	4	<1%	-	-
	Hyaenidae	Hyaeninae	*Crocuta*	*cf. Crocuta*	Large	1	<1%	1	<1%	1	1%
		Hyaeninae	*Parahyaena*	*P. brunnea*	Large	2	<1%	2	<1%	1	1%
		Hyaeninae	*Hyaena*	*H. hyaena*	Large	1	<1%	1	<1%	1	1%
		Hyaeninae	*gen. indet.*	*sp. indet.*	Large	6	<1%	6	<1%	1	1%
		Protelinae	*Proteles*	*P. cf. amplidentus*	Small	1	<1%	1	<1%	1	1%
	Mustelidae	Mustelinae	*Mellivora*	*cf. M. capensis*	Small	1	<1%	1	<1%	1	1%
		Mustelinae	*Prepoecilogale*	*P. bolti*	Small	3	<1%	3	<1%	1	1%
		Lutrinae	*Aonyx*	*A. capensis*	Small	8	<1%	7	1%	1	1%
		indet.	*gen. indet.*	*sp. indet.*	Small	1	<1%	1	<1%	-	-
	Herpestidae	Herpestinae	*Herpestes*	*sp. indet.*	Small	4	<1%	4	<1%	1	1%
	Viverridae	Viverrinae	*Civettictis*	*Civettictis cf. civetta*	Small	4	<1%	4	<1%	1	1%
		Viverrinae	*Civettictis*	*Civettictis braini*	Small	2	<1%	2	<1%	2	2%
	Viverridae / Herpestidae	indet.	*gen. indet.*	*sp. indet.*	Small	14	1%	11	1%	-	-
	indet.	indet.	*gen. indet.*	*sp. indet.*	?	39	2%	-	-	-	-
Artiodactyla	Bovidae	Bovinae	*Taurotragus*	*T. oryx*	Large	1	<1%	1	<1%	1	1%
		Alcelaphinae	*Megalotragus*	*sp. indet.*	Large	6	<1%	6	<1%	2	2%
		Alcelaphinae	*Connochaetes*	*C. taurinus*	Medium	6	<1%	5	<1%	2	2%
		Alcelaphinae	*Connochaetes*	*sp. indet.*	Medium	23	1%	21	2%	3	3%
		Alcelaphinae	*cf. Numidocapra*	*cf. N. crassicornis*	Medium	3	<1%	3	<1%	1	1%
		Alcelaphinae	*Damaliscus*	*cf. D. lunatus*	Medium	1	<1%	1	<1%	1	1%
		Alcelaphinae	*Damaliscus / Parmularius*	*sp. indet.*	Medium	5	<1%	5	<1%	2	2%
		Caprinae	*gen. indet.*	*sp. indet.*	Large	4	<1%	4	<1%	1	1%
		Antilopinae	*Ourebia*	*O. ourebi*	Small	1	<1%	1	<1%	1	1%
		Antilopinae	*gen. indet.*	*sp. indet.*	Small	10	<1%	8	1%	1	1%
		indet.	*gen. indet.*	*sp. indet.*	Small	324	13%	241	18%	11	9%
		indet.	*gen. indet.*	*sp. indet.*	Medium	478	20%	376	29%	13	11%
		indet.	*gen. indet.*	*sp. indet.*	Large	50	2%	44	3%	3	3%
		indet.	*gen. indet.*	*sp. indet.*	?	181	7%	136	10%	-	-
	Suidae	Suinae	*gen. indet.*	*sp. indet.*	Medium	10	<1%	6	<1%	3	3%
	Hippopotamidae		*Hippopotamus*	*sp. indet.*	Large	1	<1%	1	<1%	1	1%
Perissodactyla	Equidae		*gen. indet.*	*sp. indet.*	Large	2	<1%	2	<1%	2	2%
Proboscidea	Elephantidae		*gen. indet.*	*sp. indet.*	Large	21	1%	5	<1%	2	2%
Primates	Cercopithecoidae	Cercopithecinae	*Papio / Parapapio*	*sp. indet.*	Large	284	12%	243	19%	14	12%
	Hominidae	Homininae	*Paranthropus*	*P. robustus*	Large	23	1%	23	2%	-	-
Lagomorpha	Leporidae		*? Lepus*	*sp. indet.*	Small	35	1%	29	2%	15	13%
Hyracoidea	Procaviidae		*? Procavia*	*sp. indet.*	Small	4	<1%	4	<1%	3	3%
Tubulidentata	Orycteropidae		*gen. indet.*	*sp. indet.*	Large	1	<1%	1	<1%	1	1%
Rodentia	Pedetidae		*Pedetes*	*sp. indet.*	Small	1	<1%	1	<1%	1	1%
	Hystricidae		*Hystrix*	*sp. indet.*	Large	2	<1%	2	<1%	2	2%
	indet.	indet.	*gen. indet.*	*sp. indet.*	Small	39	2%	-	-	-	-
Chelonii	Testudinoidea	indet.	*gen. indet.*	*sp. indet.*	Small	6	<1%	-	-	-	-
Squamata	Serpentes	indet.	*gen. indet.*	*sp. indet.*	Small	2	<1%	-	-	-	-
	Sauria	indet.	*gen. indet.*	*sp. indet.*	Small	7	<1%	-	-	-	-
Amphibia	indet.	indet.	*gen. indet.*	*sp. indet.*	Small	17	1%	-	-	-	-
Aves	indet.	indet.	*gen. indet.*	*sp. indet.*		415	17%	-	-	-	-
			Undetermined	Undetermined		284	12%	-	-	-	-
			Coprolite	Coprolite		6	<1%	-	-	-	-

and distal), "isolated epiphysis", "shaft cylinder", and "shaft fragments". This classification can be used to determine the degree of bone exploitation/consumption according to the quantity of meat and fat available (e.g., Brain, 1981; Binford, 1981; Fourvel and Mwebi, 2011; Fourvel et al., 2012).

2.6. Tooth marks

Tooth marks are bone surface modifications that result from a particular agent (Sutcliffe, 1970; Binford, 1981; Brain, 1981; Fernandez-Jalvo and Andrews, 2016). In past decades,

taphonomists have focused on bone surface modifications associated with either non-biological (e.g., Behrensmeyer, 1978; Hill, 1979; Coumont, 2009) or biological (e.g., Capaldo and Blumenschine, 1994; Selvaggio, 1998) factors. Since carnivore involvement in the bone accumulations is now well demonstrated, there is a need to identify the species responsible for bone surface modifications observed on prey remains (e.g., Haynes, 1983; Blumenschine, et al. 1996; Delaney-Rivera, et al. 2009; Njau and Blumenschine, 2006, 2012; Baquedano, et al. 2012). In this study we record the bone surface modifications following the tooth marks characterization as defined in previous studies (Sutcliffe, 1970; Maguire et al., 1980; Binford, 1981; Brain, 1981; Haynes, 1983). We focus our observations on seven features: pitting marks (Binford, 1981), punctures (Maguire et al., 1980; Binford, 1981), scoring and furrowing (Sutcliffe, 1970; Maguire et al., 1980; Binford, 1981), gnawing marks (Sutcliffe, 1970; Brain, 1981), fracture scars (Maguire et al., 1980; Brain, 1981; Binford, 1981), crenulated edges (Maguire et al., 1980; Brain, 1981; Binford, 1981) and ingested remains (Sutcliffe, 1970; Maguire et al., 1980).

3. Results

3.1. The Kromdraai species diversity

The analysis of the Kromdraai Member 2 assemblage of macro-mammals highlights a remarkably high taxonomic diversity (with 8 orders and 16 families) relative to the sample size (NISP = 2444; MNI = 119; see Table 2). This diversity is similar to that observed at Drimolen including 9 orders and 14 families (Adams et al., 2016) and Cooper's D with 7 orders and 15 families (Berger et al., 2003). The faunal assemblage as yet sampled at Kromdraai Member 2 is quite diverse, as indicated by H′ and E values (1.963 and 0.557 respectively; Table 3). However, Simpson's index (D = 0.312) suggests that the species were not equally represented.

3.1.1. Herbivores species diversity

The bovid spectrum covers a high diversity of species and size classes (Table 2), including one of the smallest Antilopini (e.g., Ourebia ourebi) and some of the largest ones (e.g., Taurotragus oryx) as well as a buffalo-sized bovid. The sample is dominated by Alcelaphini, with some Caprini, Antilopini, one oribi specimen, O. ourebi, and one eland, T. oryx. The Alcelaphini include at least five taxa. The largest is a species of Megalotragus. The most commonly represented taxon is an ancestor of the blue wildebeest, Connochaetes taurinus prognu, followed by a slightly smaller wildebeest-like alcelaphine species, probably Connochaetes gentryi known from theTurkana basin and the oldest deposits of the Olduvai sequence (Harris, 1991; Gentry, 2010). We also observed postcranial evidence for the occurrence of Numidocapra

crassicornis, a species with an Early Pleistocene record in North and East Africa (Gentry, 2010). Medium-sized alcelaphines may belong to either the tsessebe or to an as yet unidentified Damaliscus-like alcelaphine. A small number of caprine specimens appear to be of the same size as Makapnia broomi (Gentry, 2010), but the specimens as yet recovered are not sufficient to allow a more accurate diagnosis. Given the marked diversity of Alcelaphini and the absence of Reduncini and Hippotragini, the palaeoenvironment reflected by the Kromdraai Member 2 bovid sample is a semi-arid grassland.

3.1.2. The carnivore palaeoguild

Confirming preliminary results (Fourvel et al., 2016; Fourvel, 2017a), here we expand the carnivore spectrum from the oldest deposits at Kromdraai, as represented by Members 1 to 3 (Braga et al., 2016, 2017). Some carnivore species could represent reliable biochronological indicators (e.g., Prepoecilogale bolti, Dinofelis cf. Barlowi, Civettictis braini n. sp.), but this will be investigated in detail in a separate study. The high diversity of carnivore species observed at Kromdraai Member 2 (based on 152 specimens) is similar to that which is recorded from nearby Plio-Pleistocene assemblages (e.g., Malapa, Gladysvale, Cooper's D, Swartkrans and Sterkfontein).

The felid guild (small and medium feline, large pantherine and dirk-tooth cat) is one of the most important and diverse large carnivore guilds known in the early Pleistocene (Turner and Antón, 1997; Werdelin and Lewis, 2005; Werdelin and Peigné, 2010). The best-represented felid from Kromdraai Member 2 is the leopard Panthera pardus (NISP = 59; MNI = 6) (Table 2), a species well-known as a primary hunter and a bone accumulator, in particular when its remains are associated with bones that have tooth marks (e.g., Brain, 1981; De Ruiter and Berger, 2000, 2002). We have recently recovered 28 bones representing both left and right feet (tarsals, metatarsals, phalanges) and a tail (caudal vertebras), all associated with one individual (Fig. 1). A small-sized feline, Caracal or Leptailurus, is also present. These are known to be specialized in the predation and consumption of rodents, but they are also predators of small antelopes such as Gazella dorcas (Nowell and Jackson, 1996).

We have also identified the wild dog cf. Lycaon, a primary hunter that could provide carcasses to other predators (scavengers) such as the smaller jackal-sized canid (jackals, Canis cf. mesomelas, and foxes, Vulpes chama). The occurrence of this large-sized and cursorial canid at Kromdraai Member 2 suggests an open habitat. The Cape fox and the jackal (both species recognized at Kromdraai Member 2) occupy open, semi-arid to arid ecosystems (Kingdon and Hoffmann, 2013).

Several hyena species, including at least three genera (Parahyaena brunnea, Hyanea hyaena, Proteles cf.amplidentus), previously

Table 3
Shannon (H′ and E) and Simpson (D) diversity indices for the Kromdraai Member 2 and comparative South African fossil assemblages. The * indices are calculated from MNI.

| Site	Reference	N (NISP)	S (n taxa)	H′ (Shannon)	E (evenness)	D (Simpson)
Kromdraai m2	This study	525	34	1.963	0.557	0.312
Kromdraai B3E	Vrba and Panagos 1982	22 (*)	8	1.859	0.894	0.143
Kromdraai B	Brain 1981	183	18	1.903	0.658	0.267
Kromdraai A	Brain 1981	541	40	2.590	0.702	0.134
Cooper's D	De Ruiter et al. 2009	174 (*)	41	3.322	0.894	0.043
Swartkrans m1	Brain 1981	543	35	2.778	0.781	0.097
Swartkrans m2	Brain 1981	878	38	2.484	0.683	0.165
Drimolen	Adams et al. 2016	426	29	1.646	0.489	0.392
Gladysvale	Berger 1993	84 (*)	48	3.700	0.956	0.018
Gladysvale ED	Lacruz et al. 2002	226	30	2.704	0.795	0.101
Gondolin GD-2	Adams 2010	1193	19	1.777	0.604	0.277
Malapa	Val et al. 2015	128	17	2.030	0.716	0.184
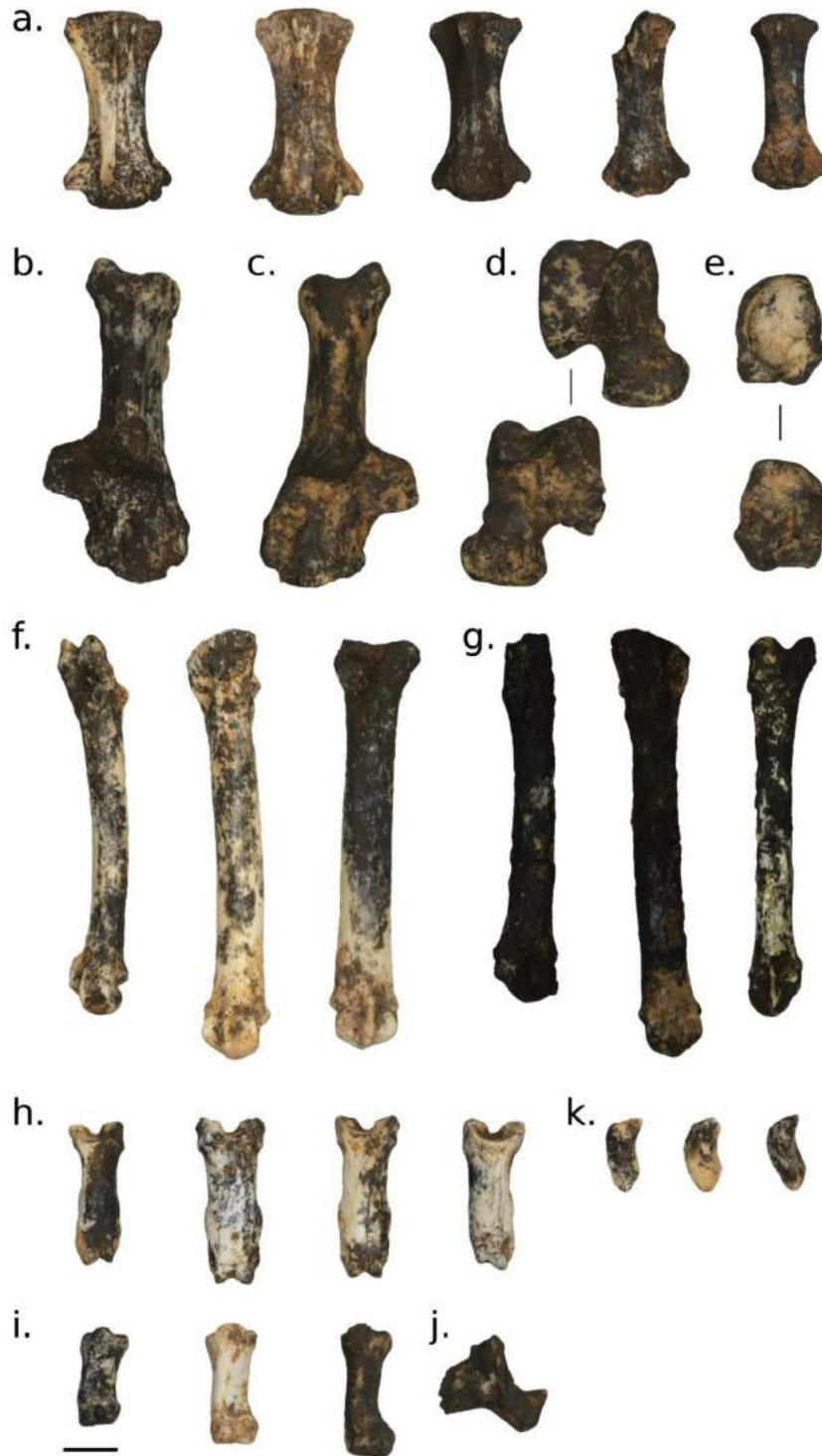
Fig. 1. Feet and tail of the leopard *Panthera pardus* KW81616. a. caudal vertebrae; b. left calcaneus; c. right calcaneus; d. right talus; e. right navicular; f. left fifth, fourth and third metatarsals; g. right second, fourth and fifth metatarsals; h. first phalanges; i. second phalanges; j. third phalange; k. sesamoids. Bar scale: 10 mm. Photo. R. Hautefort.

identified at Kromdraai (Ewer, 1954, 1955; Hendey, 1973; Turner and Antón, 1997, Turner, 1986), have been identified (Table 2; Fig. 2). One specimen (KW7665) suggests the presence of a "crocutoid" hyenid, tentatively referred to cf. *Crocuta* (Table 2). The spotted hyena (*Crocuta crocuta*) should be considered as the primary predator within the hyenid guild, whereas the brown (*P. brunnea*) and the striped (*H. hyaena*) hyaenas are scavengers and

secondary collectors (Kruuk, 1976; Rieger, 1981; Mills and Hofer, 1998). The association of these hyena species reflects an ecological balance which has also been recognized recently at Cooper's D (Kuhn et al., 2016). We should notice that we recovered six coprolites. Because of their specific rounded morphology, these bioglyphes are typical of a hyenid (Larkin et al., 2000; Brugal, 2010; Sanz et al., 2015). Having recovered only six coprolites in close

Fig. 2. Left mandible of brown hyena *Parahyaena brunnea* KW8248. Vestibuar view, occlusal view, lingual view. Bar scale: 10 mm. Photo. J.-B. Fourvel. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Fig. 3. Ternary plot of the mortality profiles (%MNI) according to each type of prey (small-, medium-, large-sized bovid and cercopithecoid).

Table 4
Age classes representation (MNI and related frequencies) for cranial remains (maxilla, mandible and isolated tooth) according to each type of prey (small-, medium-, large-sized bovid and cercopithecoid).

Prey size class	Quantification	Juvenile	Prime adult	Old	Total
Small-sized bovid	MNI	2	3	2	7
	%MNI	29	42	29	100
Medium-sized bovid	MNI	2	5	1	8
	%MNI	25	63	12	100
Large-sized bovid	MNI	1	2	0	3
	%MNI	33	67	0	100
Cercopithecoid	MNI	3	6	2	11
	%MNI	27	55	18	100

association at Kromdraai Member 2, we do not interpret them in terms of a latrine area.

The mustelids are represented by at least three species. A single navicular has been identified as honey badger (cf. *Mellivora capensis*). The extant species is an ubiquitous carnivore which occupies a wide geographic range from southern Africa to south-western Asia (Vanderhaar and Hwang, 2003) and fossils are known from at least three other sites in the Cradle (Swartkrans Member 2, Kromdraai B and Cooper's D). Secondly, the small extinct weasel *Prepoecilogale bolti* has also been identified to supplement identifications from Bolt's Farm and Cooper's D. Overall, this species is poorly known, but it has a wide distribution across Africa (Fourvel et al., 2016). Thirdly, the Cape clawless otter *Aonyx capensis* is known to live in the vicinity of water (Larivière, 2001); it is represented in the Kromdraai Member 2 assemblage. This suggests the vicinity of a wet-land or a riverine area, as also indicated by the occurrence of the African civet *Civettictis* cf. *civetta* (Stuart and Stuart, 2008).

3.2. Taphonomy and palaeoecology

3.2.1. Mortality profiles

Even though our analysis of the mortality profiles is based only on maxillary and mandibular remains and isolated teeth, we nevertheless provide detailed data on age classes that include both cranial and post-cranial remains (Supplementary Materials 1). The MNI in each group is small (small, medium, large-sized bovids and cercopithecoids represented by 7, 8, 3 and 11 individuals, respectively).

The mortality profiles for each of the three size classes of bovids and the cercopithecoids are represented in Fig. 3 and Table 4. According the relative abundance of each age class (juvenile, prime-adult and old), the prime adult dominates in each prey classes.
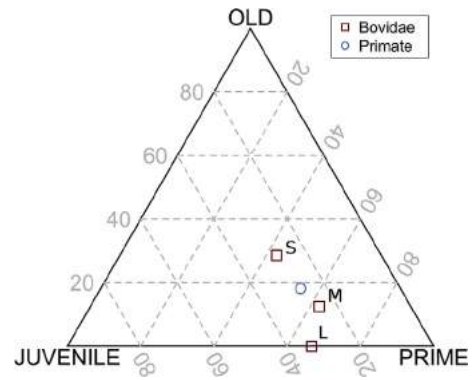
This representation is typical of an adult-dominated profile that could be interpreted in terms of a particular selection of adult individuals by a predator.

3.2.2. Representation of skeletal parts

The preservation of most of the bones is exceptional. Moreover, the presence of some of the most fragile bones (e.g., the hyoid) and the relative abundance of ribs, support the idea that biological and non-biological alterations were relatively low. The positive correlation with the bone mineral density of the skeletal parts for each prey classes (small-sized, medium-sized and large-sized bovid and cercopithecoid) is not significant here (Fig. 4). Moreover, small bones or juvenile remains with a low density are also represented. These observations support the fact that the non-biological and post-depositional processes have played a minimal role in the damage to bones.

For each prey class, the %NISP, %MNE and %MAU for each skeletal part are given in Fig. 5 and Supplementary Materials 2. According to %NISP and %MNE, the appendicular skeleton dominates each bone sample for each prey size class while the cranial remains of small-size and medium-sized bovid are represented by a high frequency of skulls (Supplementary Materials 2). Axial remains are relatively equally distributed for both size classes. In terms of %MAU, each prey size class is represented by distinct skeletal elements (Fig. 5). Both small- and medium-sized bovid are mostly represented by girdle and long bones. Large-sized bovid skeletal distributions differ among small- and medium-sized bovids with a higher representation of cranial elements. However, this could be related to the small sample size that biases the representation of skeletal parts. The %NISP and %MNE observed in cercopithecoids reveal a similar representation of skeletal parts in relation to small- and medium-sized bovids (Fig. 5; Supplementary 2), even though (as illustrated by the %MAU) the cercopithecoid limb bones are
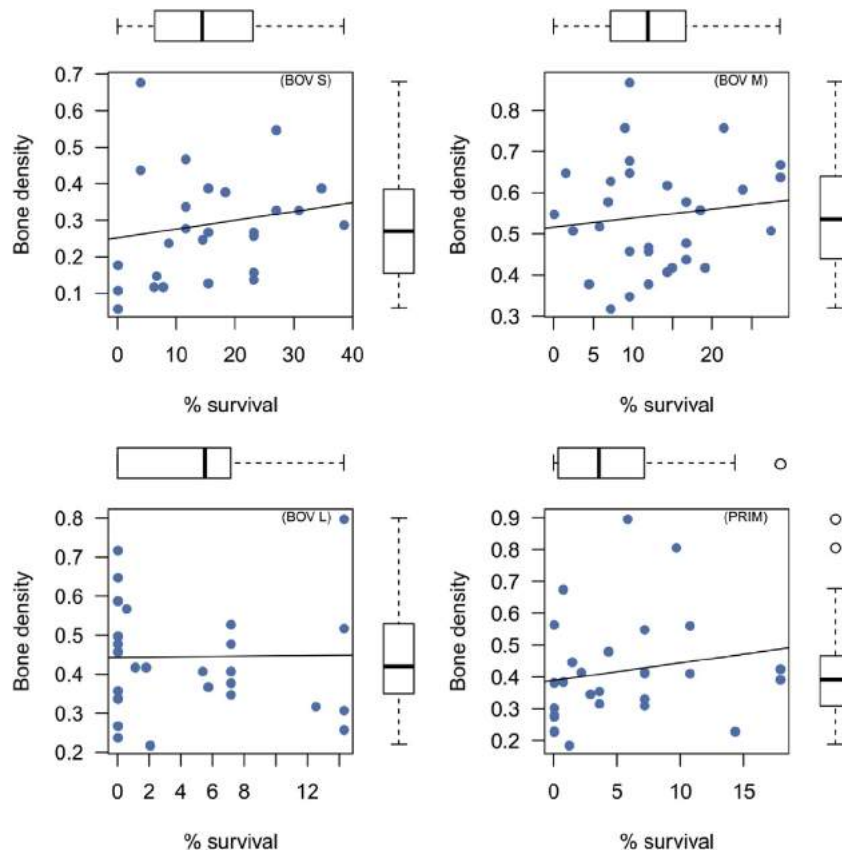
Fig. 4. Scatterplots of survival percentages for small-sized, medium-sized and large-sized bovids and cercopithecoids from Kromdraai (Bovid S: rs = 0.27; P = 0.18 > 0.05; Bovid M: rs = 0.07; P = 0.71 > 0.05; Bovid L: rs = −0.04; P = 0.85 < 0.05; Primates: rs = 0.34: P = 0.08 > 0.05).

common and their cranial remains are overrepresented.

We compare our results to those of bone accumulations associated with spotted, striped and brown hyenas (Fourvel, 2012) and leopards (Brain, 1981). We observe certain similarities (Fig. 5). Even if there is some degree of variability in the distribution of skeletal parts observed in extant hyena dens and leopard lairs, the pattern observed for each prey size class is similar to the Kromdraai Member 2 bone sample. The main difference is the distribution of bovid cranial and axial remains from leopard lair. There are no major differences in the distribution patterns of cercopithecoid remains associated with leopard lairs and the Kromdraai Member 2 assemblage. This result highlights the predator influence in the latter bone accumulation.

3.2.3. Bone fragmentation

In small-sized bovids, the fore- and hind-limbs are almost equally represented, while the "meaty" bones are most frequent (Fig. 6, Supplementary 3). With the exception of one complete radius, fully preserved long bones are absent, while shaft cylinders and ends with shafts are most common. Shaft fragments are rare and proximal ends with shafts are scarce in "meaty" bones. Among metapodials, the proximal extremities dominate and are generally less fragmented than other long bones. The hind-limbs are more fragmented than the fore-limbs, with a higher proportion of shaft fragments. The medium-sized bovid long bone fragmentation is similar to that of the small-sized bovids. The fragmentation pattern is characterized by a high proportion of extremities with shafts. The isolated extremities are more frequent than in the small-sized bovids, a pattern suggesting a more intense reduction of shaft portions. The large-sized bovid sample is too small to provide reliable

results (NISP = 18; Fig. 6, Supplementary 3). We may just note the absence of complete bones in this category.

The cercopithecoid sample is also small (NISP = 25; Fig. 6, Supplementary Materials 3). We nevertheless observe a distinct pattern of fragmentation with a higher proportion of shaft cylinders. The lack of extremities could be the result of post-depositional processes as well as consumption by carnivores.

Analyses of bone fragmentation by carnivores have been conducted mainly on bone accumulations associated with hyena activities (Cruz-Uribe, 1991; Pickering, 2002; Kuhn, 2006, 2011; Fourvel, 2012). The degree of fragmentation observed in bovid limb bones from modern hyena dens is comparable to that observed at Kromdraai Member 2. In modern contexts, the bovid bones rich in meat and marrow are more fragmented than those of metapodials, while one third of the bone accumulation is composed of parts of epiphyses (Fourvel, 2012; Fourvel et al., 2012). About 10% are composed of shaft fragments.

3.2.4. Tooth marks

Although we have identified remains of porcupines (NISP = 2), we have not observed a single typical rodent gnawing mark. We therefore assume that porcupine involvement in the bone accumulation was very low (or even null). Moreover, not a single bone displays marks due to butchering or hammerstone percussion. The carnivore tooth marks are commonly observed in the assemblage, with 107 macromammalian remains (6% of the total sample, Table 5) being associated with a total of 129 tooth marks. Five different types of bone surface modification have been recorded (Table 5). The gnawing marks are the most frequent and are followed by the punctures and pits. Modifications due to digestion
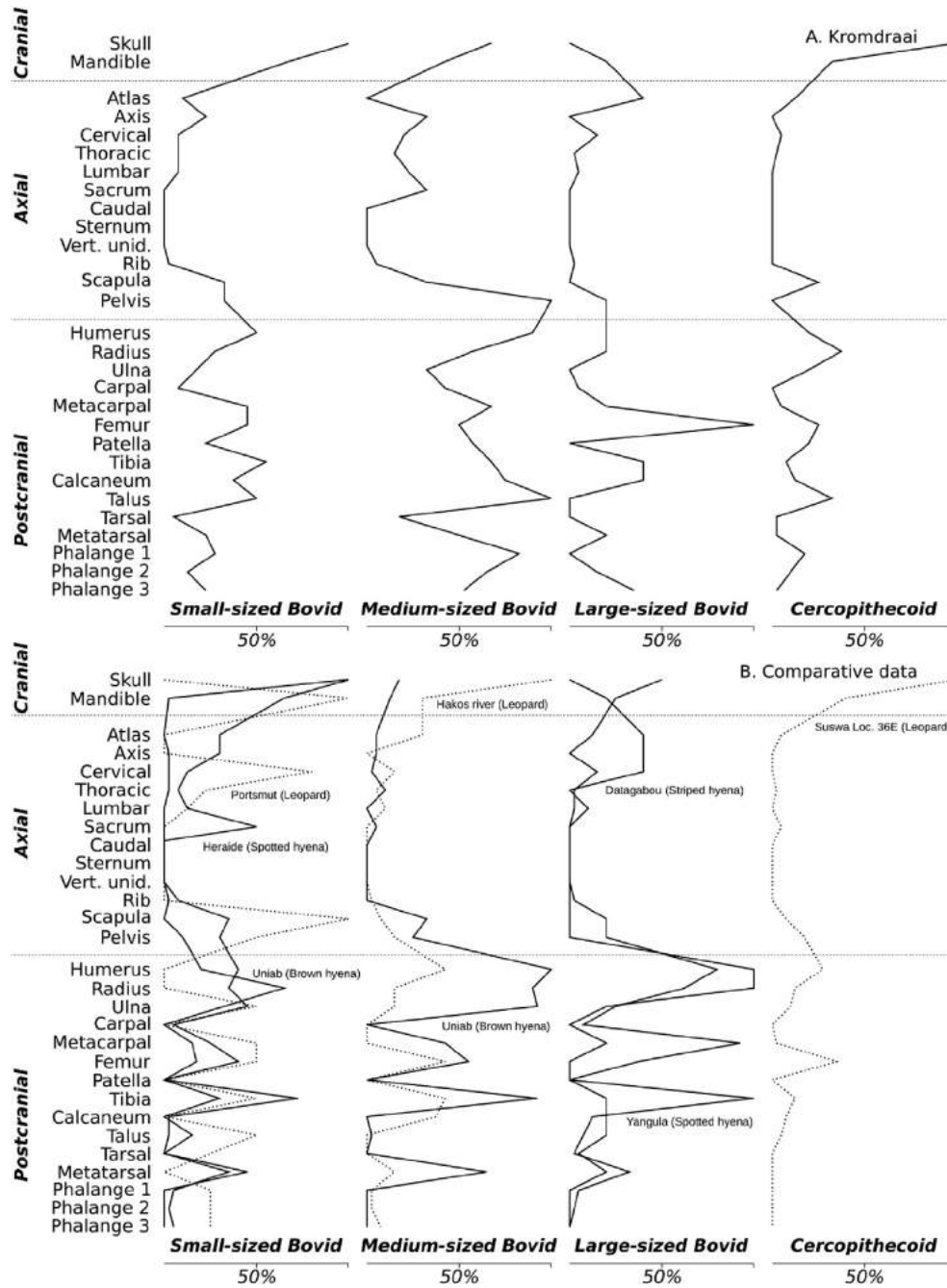
Fig. 5. Skeletal part representation %MAU), excluding unidentified long bones and isolated teeth, according to each type of prey (small-, medium-, large-sized bovid and cerco-pithecoid) from Kromdraai (A) compared to modern predators (B): hyena dens (full line) *in* Fourvel, 2012; Fourvel et al., 2015 and leopard lair (dotted line) *in* Brain, 1981.
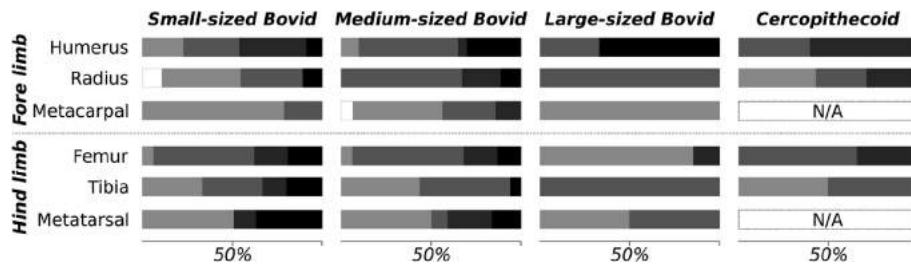

Fig. 6. Cumulative histogram (%NISP) of bone fragmentation according to prey size, long bone type and portion (white = complete; light grey = end with shaft; grey = end; dark grey = cylinder; black = shaft fragment).

Table 5
Carnivore mark diversity (altered NISP and number of tooth marks) according to each type of prey (small-, medium-, large-sized bovid and cercopithecoid).

		Puncture	Pit	Notch	Gnawing	Ingested	Total	%
Small-sized bovid	NISP	15	2	11	17	8	53	50%
	N tooth marks	18	3	16	17	8	62	–
Medium-sized bovid	NISP	8	2	7	20	2	39	36%
	N tooth marks	11	5	8	20	2	46	–
Large-sized bovid	NISP	4	–	–	–	–	4	4%
	N tooth marks	9	–	–	–	–	9	–
Cercopithecoid	NISP	3	–	1	5	2	11	10%
	N tooth marks	4	–	1	5	2	12	–
Total	NISP	30	4	19	42	12	107	100%
	N tooth marks	42	8	25	42	12	129	–

Fig. 7. Bovid remains damaged by carnivores. Upper line, left to right: Small-sized bovid right pelvis KW8874; small-sized bovid pelvis KW8829; Small-sized bovid left mandible KW8425; Lower line: Medium-sized bovid femur shaft fragment KW8661; medium-sized bovid thoracic vertebra KW9096. Arrows indicate carnivore damage. Bar scale: 10 mm. Photo. R. Hautefort.

Fig. 8. Cercopithecoid remains damaged by carnivores. Right calcaneus KW8800c (left) and left humerus KW8800b (right). Arrows indicate carnivore damage. Bar scale: 10 mm. Photo. R. Hautefort.

damage occur in small durable bones (e.g., carpal, tarsal, patella; NISP = 12). The small-sized bovid bones are the most frequently damaged (NISP = 53, 50% of the marked sample), and are followed by medium-sized bovid bones (NISP = 39, 36%) (Fig. 7). In total, four large-sized bovid remains show punctures, a result suggesting that the occurrence of this group in the assemblage could also result

from carnivore consumption and accumulation. The cercopithecoids have also been consumed by carnivores (11 elements have been modified, including evidence of digestion, Fig. 8).

The role of the medium and large felids has been questioned for a long time and numerous studies demonstrate their bone collecting habits and bone consumption capacities in both modern (e.g. Brain, 1981; Martin and Borrero, 1997; De Ruiter and Berger, 2000; Arriaza et al., 2016; Borrero et al., 2016) and fossil contexts (e.g. Brain, 1969, 1981; Pickering, et al., 2004; Sauqué et al., 2014, 2017). Although carnivore diversity in fossil sites suggests that several species could play a role in bone accumulation/consumption processes, this topic has been rarely questioned. Several carnivore species identified at Kromdraai Member 2 could represent an agent that consumed bones and left some tooth marks on them. The large (*Dinofelis*) and medium felids (*P. pardus*), the large canid (cf. *Lycaon*), and all the large hyenids could produce tooth marks. In terms of their behavior, extant wild dogs are cursorial predators and primary hunters and therefore have privileged access to meat (Creel and Creel, 2002), with some degree of osteophagy, as indicated in recent neo-taphonomical studies (Yravedra et al., 2014; Fourvel et al., 2017). The capacities of bone consumption and accumulation of the three large extant hyenas, also represented at Kromdraai Member 2, are well known (e.g.,

Brain, 1981; Kuhn 2011; Fourvel, 2012; Fourvel et al., 2015). Even though the tooth marks could not be attributed to any of these felids, canids and hyenids in particular, we can exclude some carnivore species such as the small-sized felids (caracal and serval) which are also represented in the assemblage. Indeed, the caracal is specialized in bird and mesomammal (hyrax, springhare, leporid) hunting (Cohen and Kibii, 2015). We did not record tooth marks on birds and mesomammals (represented by Procaviidae and Leporidae in Kromdraai Member 2). The caracal (or the serval) is likely to have had little influence on the bone deposition processes in this assemblage.

4. Discussion

4.1. Species richness

The diversity observed at Kromdraai Member 2 is close to that from Kromdraai B sampled during Brain's excavations (H' = 1.903, E = 0.658; Brain, 1981) and Malapa (H' = 2.030, E = 0.716; Val et al., 2015). The assemblages from all three Swartkrans Members, as well as from Kromdraai A (Brain, 1981) and Gladysvale External Deposit (Lacruz et al., 2002) show higher diversity indices (H' between 2.5 and 2.7). However, the values for Cooper's D (De Ruiter et al., 2009), Kromdraai B 3 East (Vrba and Panagos, 1982) and Gladysvale (Berger, 1993) should be considered with extreme caution because they are based on MNI and not NISP. Therefore, the observed differences between sites could be due to variable levels of taxonomic identification. Since the herbivore megafauna also comprises one proboscidian and probably one Hippopotamidae, the Kromdraai Member 2 faunal list reflects a high environmental richness, another clue for the interpretation of the accumulation processes of this assemblage.

Carnivores and bovids are highly diverse in the new Kromdraai Member 2 assemblage with its high carnivore-ungulate MNI ratio (40:60). The carnivore-bovid MNI ratio is 44:56. The ungulate and bovid diversity is clearly related to the environmental context and represents the available of prey species (Fourvel and Mwebi, 2011; Fourvel et al., 2015). It is usually argued that a carnivore/bovid sample from a typical carnivore lair should contain at least 20% carnivores (MNI) (Cruz-Uribe, 1991; Pickering, 2002). Since the occurrence of carnivores at Kromdraai Member 2 represents almost twice this 20% threshold value, our result fits well with the hypothesis of a carnivore lair. This occurrence of carnivore species is much higher than that reported for both Swartkrans Members 1 and 2 (respectively, 10,6% and 11.7% MNI), probably the most relevant example of carnivore involvement in bone accumulation processes reported so far for the Plio-Pleistocene in South Africa. When compared to the 22:78 carnivore-bovid MNI ratio reported for Kromdraai A (Brain, 1981), an accumulation also regarded as a carnivore lair, the relative occurrence of carnivores at Kromdraai Member 2 appears to be higher.

The carnivore-ungulate ratio differs significantly in extant leopard and hyena dens. In modern contexts, hyenas and leopards are known to be important bone collectors/accumulators. Hyena dens are well known examples of agents of bone accumulation (270 modern cases are as yet published; see Fosse et al., 2010), even though some variability has been recorded between assemblages (Kuhn, 2006, 2011; Fourvel et al., 2015). Brain (1981) noted that carnivores were usually represented by very few individuals in a leopard lair, a situation that likely results from the leopard strategy of avoiding inter- and intra-specific competition. The leopard is specialized in small-to-medium-sized prey, while hyenas are more opportunistic and access a greater variety of prey-species, including carnivores (e.g., Kruuk, 1972; Mills, 1990; Mills and Hofer, 1998; Hayward, 2006; Hayward et al., 2006). According to Brain (1981),

leopards can accumulate partial skeletons and isolated elements of mostly adult specimens representing large species such as zebra, kudu and oryx (weight range 150–300 kilos). The Kromdraai Member 2 data fit better with a "hyena model", according to the criteria given by Cruz-Uribe (1991) and Pickering (2002) with its high representation and diversity of both carnivores and ungulates.

The abundance of leopard remains (NISP = 53; MNI = 6) as well as the high representation of small- and medium-sized bovids indicate both hyenas and felid involvement in the Kromdraai Member 2 bone deposition processes. According to felid ecomorphology and dental specialization, leopards may represent a primary predator that preyed upon both small-to-medium-sized bovids and cercopithecoids. In terms of hyena bone consumption and collecting habits, this group may represent both a primary accumulator and a secondary scavenger that used the Kromdraai cave as a den, also accessing food remains already accumulated by the leopard.

The most parsimonious hypothesis is that several occupation events (by hyenas and leopards) occurred at Kromdraai (as represented by the Member 2 assemblage), corresponding to modern contexts (Bountalis and Kuhn, 2014).

4.2. Predator-prey interactions

As stated in the introduction to this study, a bone accumulation should also be discussed in the light of the accumulating habits and the competition pressure between the various predators represented in the assemblage. At least three large hyena species (the brown and striped hyenas as well as a "crocutoid") have been identified in Kromdraai Member 2. The association between a primary hunter (spotted hyena) and scavengers (brown and striped hyenas) suggest differences in their palaeoecological status (hunter versus scavenger) as well as their involvement in the bone deposition process. According to the foraging and collecting behaviors in extant hyena species, bone accumulations in modern dens are highly variable. We recorded a mean NISP value of 205 for 33 spotted hyena dens, with 22 dens containing less than 100 remains (Fourvel, 2012; Fourvel et al., 2015). This is due to a low degree of competition, the spotted hyena often being the primary predator (e.g., Djibouti in Fourvel and Mwebi, 2011). By contrast, bone accumulations in striped hyena dens are huge (mean NISP of 605 for 12 dens; Fourvel, 2012) and result from their avoidance of predator competition (strictly scavenger). In brown hyena dens the mean NISP value is 576 for 35 dens (Fourvel, 2012). Therefore, brown and striped hyenas from Kromdraai Member 2 could be considered as important bone collectors and accumulators which had played an important role in the bone accumulation or modification. The single "crocutoid" specimen could reflect a primary hunter which had a lesser role in the bone deposition process.

All the other taphonomic criteria used in this study lead us to consider the Kromdraai Member 2 assemblage as an accumulation of mainly bovid species here regarded as prey by several carnivore species. Indeed, we observe prime-dominated profiles in small and medium-sized bovid species; an over-representation of their limb bones; the occurrence of bone fragmentation and carnivore damages, as well as the presence coprolites. In the European cave context, the presence of coprolites is a marker of the use of a cavity as a den by a predator (Fosse, 1994; Fourvel, 2012). In modern hyena dens (particularly striped hyenas), faeces are regularly found in bone assemblages but are not numerous (e.g. Kempe et al., 2006; Fourvel, 2012). Latrine areas are known in modern hyenas but they are generally located outside the den (Kruuk, 1972; Mills, 1990). However latrine areas have been already reported within the cave sites (e.g., Berger et al. 2009; Pineda et al., 2017). For each potential prey recorded in the Kromdraai Member 2 assemblage, we observe

an prime-dominated profile (Fig. 3; Supplementary 1) which it is usually regarded as indicative of prey selection by one or more predators such as carnivores and hominins (e.g., Stiner, 1990). In both European and African Pleistocene contexts, some authors argue that the hyena used to prey upon the weakest individuals that are therefore highly represented by both juvenile and old individuals in their dens (Cruz-Uribe, 1991; Discamps, 2011). However we demonstrated a huge variability in the mortality profiles of prey associated with large carnivores such as modern and fossil hyenas (Fourvel, 2012). The same applies to leopards that prey upon sub-adult and even adult baboons (Brain, 1981). In Kromdraai Member 2, the skeletal part distribution of small- and medium-sized bovids is clearly dominated by appendicular elements while cranial and axial remains are less represented. Usually, the appendicular skeleton (including some articulated limbs) is mostly represented in carnivore dens. Moreover, limb bone fragmentation is generally reduced, with a high representation of complete bones and shaft cylinders (e.g., Cruz-Uribe, 1991; Pickering, 2002; Prendergast and Dominguez-Rodrigo, 2008; Fosse et al., 2010; Fourvel et al., 2015). We observe that both the mortality profiles and the distribution of the skeletal parts are very similar in Kromdraai Member 2 (this study) and Kromdraai A (Brain, 1981) assemblages. In Kromdraai A, the adults clearly dominate the medium and the large-sized bovid samples. Moreover, the appendicular skeleton is mostly represented in each size class at Kromdraai A. Kromdraai Member 2 data fit perfectly with the evidence from Kromdraai A, reflecting carnivore lairs.

Tooth marks (including both tooth marks and digestion marks) have been observed on 6% of the Kromdraai Member 2 sample. This frequency is very large compared to other fossil carnivore lairs from the surrounding areas. The Sterkfontein Member 5 West sample contains only 1.6% of chewed bones, 2.3% tooth marks including digested bones (Pickering, 2002) while the Kromdraai A and Swartkrans Member 1 (Brain, 1981) samples contain only 1.6% (NISP = 30) and 1.2% (NISP = 29) respectively. The Swartkrans Member 2 sample shows similar tooth mark frequency when compared to Kromdraai Member 2. The Swartkrans value is 4.9%, NISP = 291 (Brain, 1981). In modern dens, tooth marks are significantly higher, ranging from 39% to 60% of marked bones in extant hyena dens (Kuhn et al., 2008).

The identification of the carnivore species responsible for the tooth marks, according to their diversity, location, morphology and size, is a key question for the interpretation of Quaternary bone assemblages and hominin-carnivore interactions (e.g., Pickering et al., 2004; Saladié et al., 2014; Daujeard et al.,2016). There is abundant literature on carnivore taphonomy and particularly tooth marks. For a decade, studies have focused on tooth mark sizes to make a distinction at a species level but showing the difficulty of relating tooth marks to a carnivore species according to their size (e.g. Dominguez-Rodrigo and Piqueras, 2003; Delaney-Rivera et al., 2009; Andrés et al., 2012; Saladié et al., 2013; Fourvel and Fosse, 2015; Fourvel et al., 2015). The study of the relative abundance of different tooth mark types could assist in this regard. Some research has demonstrated the usefulness of the relative abundance of particular features in tooth marks to distinguish carnivore species (Haynes, 1983; Fourvel, 2012, 2017b; Fourvel et al., 2012). The digested remains and the gnawing marks observed at Kromdraai Member 2 could be related to hyenas (Fourvel et al., 2012). The high proportion of punctures could result from bone consumption by both felids (leopard) and hyenids.

4.3. Non-hominin primates: palaeoecological status

The newly discovered cercopithecoid sample from Kromdraai Member 2 supports the view that at least some of the non-hominin

primate specimens were collected and brought into the cave by large carnivores. Even though the sample of cercopithecoid specimens is small, the data match a carnivore model. Indeed, the mortality curve shows a predominance of adullts (MNI = 4; 36% MNI), followed by juveniles (MNI = 3; 27%MNI); see Fig. 3 (Supplementary Materials 1). The non-hominin primate skeletal representation is characterized by an over-representation of the appendicular skeleton (77%NISP, 82%MNE; Fig. 5; Supplementary Materials 2). The %MAU tends to show an over-representation of cranial remains (excluding isolated teeth). The bone fragmentation is quite low according to the high proportion of shaft cylinders (Fig. 6 ; Supplementary Materials 3). Moreover carnivore damage has been recorded on eleven specimens (3.9%NISP and 7.2%NISP excluding isolated teeth; Table 5). By comparison, the Sterkfontein Member 4, Swartkrans Member 1 and Kromdraai A assemblages are all considered as carnivore lairs. The published taphonomic data from these three assemblages (Brain, 1981) and Cooper's D (Val et al., 2014) are comparable to those obtained from the newly discovered Kromdraai assemblage presented in this study. In all instances, the non-hominin primates are well represented and their mortality profiles are prime-dominated. Their cranial remains are over-represented, even if the carnivore tooth marks are rare. Regarding the Cooper's D sample, its cercopithecoid assemblage was interpreted as partly accumulated by carnivores (with a particular involvement of a hyenid) and partly the result of an occupation by these primates. In modern contexts, primate predation by hyenas is rare (Hayward, 2006). Moreover, as described in several behavioral and ecological studies, leopards do not preferably hunt baboons (Hayward et al., 2006) and, even when they do, leopards do not target only juveniles and adult females. For instance, Jooste et al. (2013) reported an unusual case of high predation (more than 20% of hunted) on chacma baboons by leopards in the Waterberg Mountains (South Africa), but with no distinction in terms of age or sex. Cowlishaw (1994) noticed that leopards prefer hunting on adult baboons rather than on juveniles and, more often, on males than on females. These observations support the idea of skill specialization in leopards, and their hunting and dragging capacities on large-bodied primates such as adult male baboons. Non-hominin primates are regularly found as prey remains in carnivore (particularly leopard) lairs (Brain, 1981). Cranial remains are frequent and represent mainly adults. These data fit well with our taphonomic investigations of the Kromdraai Member 2 cercopithecoid assemblage.

4.4. Plio-Pleistocene hominin remains from the Cradle of Humankind

Plio-Pleistocene hominins from the Cradle of Humankind, including Kromdraai, are found in assemblages mostly interpreted as either carnivore lairs or as natural traps (Table 6). Hominin remains thought to be from a natural trap (e.g., Stw 573 from Sterkfontein Member 2 in Pickering et al., 2004; Clarke, 2007; Bruxelles, et al., 2014; *Australopithecus sediba* from Malapa in Val et al., 2015) are generally relatively complete with little or no damage by carnivores, insects, roots, or post-depositional disturbance such as bone scattering resulting from geological processes. Since the seminal taphonomic study by Brain (1981), hominin remains from important Plio-Pleistocene assemblages (Sterkfontein, Swartkrans, Kromdraai) have often been interpreted in terms of prey hunted, consumed and accumulated by carnivores (e.g., Pickering et al., 2004). Brain (1981) identified carnivore damage on hominins from "Kromdraai B" and observed chewing areas and ragged-edged margins on the TM 1605 isolated pelvis (here re-examined by JBF), conventionally attributed to *Paranthropus robustus* with unknown stratigraphic provenience (see Braga et al., 2017 for more details)

Table 6
Plio-Pleistocene hominin-bearing assemblages related to site function.

Site	Member	Homini species	Hominin remains	Interpretation / Hypothesis	Reference
Kromdraai	B	*P. robustus*	NISP = 8	Carnivore-collecting hypothesis ?	Brain 1981
Kromdraai	B 3E	*P. robustus*	NISP = 5	Natural trap	Vrba 1981; Vrba and Panagos 1982
Swartkrans	Member 1	*P. robustus / Homo sp.*	NISP = 18	Carnivore-collecting hypothesis	Brain 1981; Pickering et al. 2012, 2016
Swartkrans	Member 2/3	*P. robustus*	NISP = 2	Carnivore-collecting hypothesis	Pickering et al. 2016
Swartkrans	Member 3	*P. robustus*	NISP = 3	Carnivore-collecting hypothesis	Pickering et al. 2016
Swartkrans	Talus Cone Deposit	*P. robustus*	NISP = 4	Carnivore-collecting hypothesis	Pickering et al. 2016
Swartkrans	UNE	*P. robustus*	NISP = 1	Carnivore-collecting hypothesis	Pickering et al. 2016
Sterfontein	Member 4	*Au. africanus*	NISP = 87	Carnivore-collecting hypothesis	Brain 1981; Pickering et al. 2004
Sterfontein	Member 2	*Australopithecus sp.*	Stw 573	Natural trap	Pickering et al. 2004; Clarke 2007; Bruxelles et al. 2014
Gondolin	GD 2	*P. robustus*	NISP = 2	Carnivore-collecting hypothesis	Menter et al. 1999; Adams 2010; Grine et al. 2012
Malapa		*Au. sediba*	NISP = 237	Natural trap	Val et al. 2015
Gladysvale		*Au. cf. africanus*	MNI = 1	Carnivore-collecting hypothesis ?	Berger 1993
Cooper's D		*P. robustus / Homo sp.*	NISP = 10	Carnivore-collecting hypothesis	Steininger et al. 2008; De Ruiter et al. 2009; DeSilva et al. 2013
Drimolen	Main Quarry	*P. robustus / Homo sp.*	NISP = 80	Carnivore-collecting hypothesis	Gommery et al. 2002; O'Regan and Menter 2009; Moggi-Cecchi et al. 2010; Adams et al. 2016

Fig. 9. *Paranthropus robustus* innominate TM1605 damages by carnivores. Anterior (left) and posterior (right) views. Arrows indicate carnivore damage. Bar scale: 10 mm. Photo. J.-B. Fourvel.

(Fig. 9).

Since 2014, hominin remains have been recovered from Member 2 at Kromdraai, an older hominin-bearing deposit than Member 3 (Braga and Thackeray, 2016; Braga et al., 2017). These discoveries raise several questions beyond the scope of the present study and addressed in future studies (i) their taxonomic status, recognising that at least some Kromdraai paranthropines have been regarded as representing a more primitive condition for this lineage, with more similarities to some Sterkfontein Member 4 specimens than to Swartkrans *Paranthropus* (see Braga et al., 2013 and Braga et al., 2016, 2017 for more details); (ii) their body size in the context of recent discoveries of relatively large *Paranthropus* specimens at both Gondolin (Grine et al.,2012) and Swartkrans (Pickering et al., 2016); (iii) their paleobiology and paleoecology, recognising

distinct stable isotope signatures between southern and eastern African paranthropines.

4.5. Implications for further studies of paranthropus

The small number of Kromdraai hominins discovered before 2014 has been attributed to *P. robustus* and early *Homo* (Braga and Thackeray, 2003, but see Grine et al., 2009 and Moggi-Cecchi et al., 2010). The new data for the Kromdraai Member 2 hominins may help to determine whether the southern African *Paranthropus* body size and sexual dimorphism was either underestimated due to some taphonomic bias associated with carnivore involvement and selective predation; or whether potential size and other paleobiological differences observed between southern African samples reflect alpha taxonomic and/or evolutionary factors. These data will be published in a separate studyconsisting in a detailed paleobiological interpretation of the Kromdraai Member 2 hominin sample. However, in order to further expand our discussion on the paleoecological status of hominins during the accumulation of Member 2 at Kromdraai, we provide an example of carnivore damage observed in one of the newly discovered hominins from this assemblage.

KW8182 is a hominin left patella showing punctures and a typical tooth notch on the margin (Fig. 10). This nearly complete patella bone will be described and discussed in detail elsewhere. The abrasion marks observed on the KW 8182 upper and lower margins are due to post-depositional processes. The most typical carnivore mark recorded here is a tooth notch located on the lateral side of the patella. This notch is 5 mm in length. KW 8182 represents the first gnawed hominin patella ever observed. This type of damage has been already observed on bovid patellae, inflicted by modern hyenas (Fourvel, 2012). It is generally considered to be a result of femur-tibia disarticulation. Brain (1981) recorded the same kind of damage on a zebra kill. Considering this evidence, there is no reason to not consider KW 8182 as the result of a hominin hind leg dismemberment by a large carnivore such as a leopard or a hyena. This evidence is in line with the hypothesis that hominin
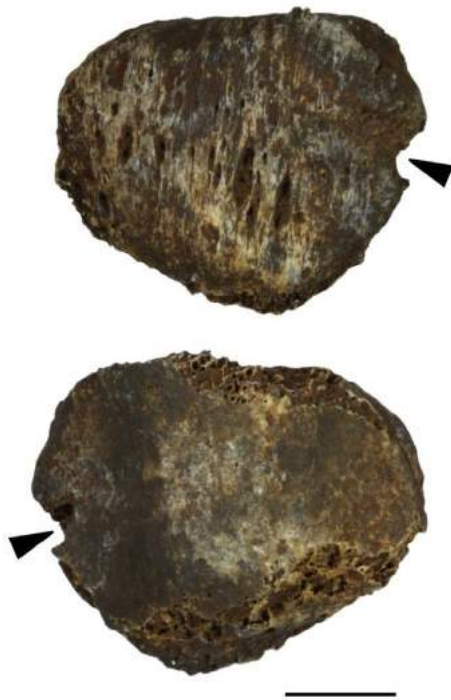
Fig. 10. Newly discovered hominin patella KW8182 damaged by carnivores. Anterior (up) and posterior (down) views. Arrows indicate carnivore damage. Bar scale: 10 mm. Photo. J. Braga.

remains accumulated, at least in part, through carnivore involvement.

5. Conclusions

This paper provides insights into the faunal bone accumulation processes of a newly discovered and stratigraphically seriated assemblage from Kromdraai Member 2, the oldest investigated yet from this site. According to our comparative and taphonomic analyses, the carnivore (felids and hyenids) involvement in the bone deposit process was likely to have been more important than was previously suggested. The faunal spectrum with its high diversity of ungulate and carnivore species, associated with taphonomic indicators such as the distribution of skeletal parts, bone breakage and bone surface modifications, allow us to consider the Kromdraai Member 2 assemblage in terms of a carnivore lair (Table 7).

The trophic chain represented in Kromdraai Member 2 is

Table 7
Taphonomical characterization of Kromdraai Member 2.

Variable #1	Variable #2	KB Member 2
Prey	Diversity	High
	Size classes	Bovid M (+) Baboon-sized
	Mortality profile	Adult-dominated
	Skeletal distribution	Bovid = Limb bone Primates = Cranial
Predator	Diversity	High
	Main predator	Felid (Leopard)
	Potential accumulator	Leopard + Hyena
	Secondary predator	Jackal
Taphonomy	Bone breakage	Moderate
	Rodent marks	NONE
	Hominin marks	NONE
	Carnivore marks	6%NISP
	Ingested remains	+ (n = 12)
Bioglyphe	Coprolithes	+ (n = 6)

complex. Secondary predators (hyenid and small canid) could have been, at least in part, responsible for bone breakage and tooth marks. The absence of large rodent (porcupine) bone surface modifications exclude their involvement. The presence of a significant amount of hominin remains in this palaeoecological context (Braga et al., 2017) is of great interest. Our observations on the newly discovered hominin remains from Kromdraai Member 2 are more in line with Brain's (1981) previous interpretations that considered Plio-Pleistocene hominins from South Africa mainly as prey of large carnivores. Hominins could also be considered as secondary predators who scavenge the carcasses provided by large carnivores such as felids and hyenids, but no marks made by hominins have been observed as yet on bovid remains from Kromdraai Member 2.

Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.quascirev.2018.04.018.

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