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The Australopithecines – An Extinct Group of Human Ancestors: My Scientific Interest in South Africa

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Abstract: I introduce the subject of my research interest in South Africa – the australopithecines – a group of bipedal, small-brained and large-toothed creatures from the Plio--Pleistocene, from which the human genus arose. I then briefly discuss various topics of my research, concerning: (1) Taxonomic status and morphological description of the extinct human relative from the Kromdraai site (*Australopithecus robustus*); (2) Graphic reconstruction of the partial skull from Kromdraai – specimen numbered TM 1517; (3) Assessment of size sexual dimorphism of the South African australopithecines (*Australopithecus robustus* and *Australopithecus africanus*), which, in terms of facial features, was pronounced – being almost gorilla-sized; (4) Social behavior of a fossil hominid species from around 2 million years ago, which, in terms of the social structure, was most likely a multimale--multifemale one; and (5) An event from the history of paleoanthropology, concerning the content of the 1924/25 photographs of the Taung Child (*Australopithecus africanus*) – the first australopithecine skull discovered.

Keywords: paleoanthropology; South Africa; australopiths; human evolution

My scientific interests have for many years been focused on paleoanthropology [1] and, in particular, the early African human ancestors. This interest was already begun by the eighth grade of elementary school when the Polish translation of the book *Man, Time, and Fossils* by Ruth Moore fell into my hands. After spending a few years studying biology at the Faculty of Biology, University of Warsaw, I transferred to Adam Mickiewicz University in Poznań to study biological anthropology. There, I completed my MSc degree writing the thesis entitled "Diversity of the Australopithecines – Taxonomic and Anthropogenetic Consequences" under the supervision of Professor Jan Strzałko.

My interests in South Africa arose from a combination of circumstances. In 1990 I enrolled as a graduate student of reputed paleoanthropologist – Professor Milford H. Wolpoff at the University of Michigan, Ann Arbor, Michigan. After spending over three years furthering my studies there, the opportunity arose to travel to South Africa – the place of the first discovery and a repository of the australopithecine fossils – to study the original collections and to make australopiths the subject of my doctoral thesis. I undertook my first journey there in 1994 – the same momentous year of the first democratic general election and the election of Nelson Mandela as President – and so began my 'adventure' with South Africa.

1. The australopiths – the subject of my interest

The fossil and genetic evidence show that the history of bipedal primates (hominids) goes back about 6-7 million years. At that time in Africa there lived a common ancestor, from which two evolutionary lineages arose – one that led to us – humans (via the now extinct australopithecines), and the other – to our closest living relatives – the chimpanzees. It is among the australopithecines that the direct ancestors of the human genus should be sought.

The term 'australopithecines' refers to a group of the Plio-Pleistocene species (dated from 4.0 to 1.2 million years ago) including the extinct ancestors and relatives of humans, who lived in broad areas of Africa – from Ethiopia (in the East) to the Republic of South Africa (in the South). While the australopithecines were already bipedal, their brains remained small (approximately 500 cc in volume, compared to an average of about 1,350 cc for modern humans). They had powerful jaws and large back teeth adapted for grinding and chewing hard, tough

[1] Paleoanthropology – the study of human ancestors from fossils (fossils are the preserved remains of organisms from the distant past).

Figure 1. Two australopithecine skulls from South Africa: (left) *Australopithecus africanus* from Sterkfontein (gracile form) vs. (right) *Australopithecus robustus* from Swartkrans (robust form) (photos by K.A. Kaszycka)

foods. In relation to the australopithecines two descriptive terms are commonly used – the so-called "gracile" and "robust" forms [2] (see Fig. 1).

2. Historic background

The history of the South African discoveries of early hominids dates to 1924 when Australian-born anatomist – Professor Raymond Dart from WITS University in Johannesburg, obtained the first fossil remains from the Taung site. Dart (1925) named the new species *Australopithecus africanus* – the "man-ape of South Africa."

We now know of a fair number of fossil-bearing sites across the country. The discovered remains are dated at around 3.0-1.5 million years old, and came mainly from the dolomite caves near Johannesburg (see Fig. 2), located in the Cradle of Humankind – a South African National Heritage site. Aside from Taung, South African australopithecines were also recovered (during the period of Broom's and Dart's excavations) from: Sterkfontein (Broom 1936), Kromdraai (Broom 1938), Makapansgat (Dart 1948) and Swartkrans (Broom 1949). In more recent times, several important discoveries were made at Gladysvale (Berger 1992), Gondolin (Menter et al. 1999), Drimolen (Keyser 2000), Cooper's (Steininger et al. 2008), and Malapa (Berger et al. 2010).

[2] Traditionally the "gracile" (lightly built) and "robust" forms of the australopithecines (australopiths) refer to differences in shape of the skull, size of face, jaws and teeth, as well as diet.

Figure 2. Sterkfontein cave site – place of discovery of *Australopithecus africanus* (photo by K.A. Kaszycka)

Apart from the "Taung Child" (a partial skull together with a natural endocast [3] of the brain), other best known australopith individuals, who received nicknames, are: "Mrs. Ples" (complete cranium), found by Robert Broom (1947) at Sterkfontein, and "Little Foot" (a spectacular near-complete skeleton), whose bones were first found in 1994 in a box, and subsequently *in-situ* between 1997-99 by Ron Clarke (1998), also within the Sterkfontein cave system. The most recent discovery included the remains of two individuals (which were given a new species name – *Australopithecus sediba*), found at Malapa by Lee Berger in 2008.

3. Status of the Kromdraai hominids

My doctoral thesis (completed at the University of the Witwatersrand, Johannesburg, under the supervision of Professors Milford Wolpoff and Maciej Henneberg) was entitled "Status of Kromdraai: Cranial, Mandibular and Dental Morphology, Systematic Relationships, and Significance of the Kromdraai Hominids." The chosen subject concerned the taxonomic status of a group of robust australopithecines from the Kromdraai site (from which the type specimen [4] of *Australopithecus robustus* derives), as well their place in human phylogeny. In the paleoanthropological literature there was no then consensus regarding the

[3] Endocast – the internal cast of a braincase.
[4] Type specimen – the original specimen from which a description of a new species is given.

taxonomic status of the robust australopithecines from Kromdraai as they were considered: the same, or a different species than other robust australopiths from the nearby Swartkrans site; a unique ancestor of hominids from Swartkrans; the possible ancestor of Swartkrans hominids and East African *Australopithecus boisei* clade [5]; or even a link with the earliest *Homo*.

Focusing on variation, I tested two null hypotheses, attempting to find answers to some fundamental questions: What is the specific relationship of the hominids from Kromdraai to similar remains from Swartkrans (a single or two species?), and how the Kromdraai australopithecines relate to the origin of the other robust australopiths (including *Australopithecus boisei*) and the earliest *Homo*. The answer to the first question was obtained from analysis of the relevant morphology and adopting the Evolutionary Species Concept: "A species is a single lineage of ancestral descendant populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate" (Wiley 1978: 18). The answer to the question regarding the phylogenetic relationships between the taxa [6] studied was revealed through cladistic [7] analysis using the PAUP (Phylogenetic Analysis Using Parsimony) computational program in attempting to develop hypotheses of ancestor--descendant relationships.

On the basis of the then available evidence, I concluded that Kromdraai is the most closely related sample to Swartkrans, being most likely an earlier, ancestral representative of the same species – *Australopithecus robustus*. At the same time, Kromdraai, being more plesiomorphic [8] (*Australopithecus africanus*-like) than the other robust australopiths (i.e., the Swartkrans sample and *Australopithecus boisei*), fits morphologically as an ancestor of the robust clade (chronologically, however, it might have been too late). Lastly, the Kromdraai sample was already too derived to be a direct ancestor of early *Homo* (i.e., the habiline species).

The above work was published as a monograph in the series Cahiers de Paléoanthropologie of the Centre National de la Recherche Scientifique, in Paris (Kaszycka 2002).

4. Graphic reconstruction of the Kromdraai skull

While working on the morphological description of the Kromdraai hominid fossils at what was then the Transvaal Museum in Pretoria, I wondered how an

[5] Clade – a group that consists of a common ancestor and all its descendant species.
[6] Taxon – any unit of classification of organisms, e.g., species, genus, family, etc.
[7] Cladistics (phylogenetic systematics) – a method of classification in which taxa are categorized based on shared novel traits.
[8] Plesiomorphic – primitive.

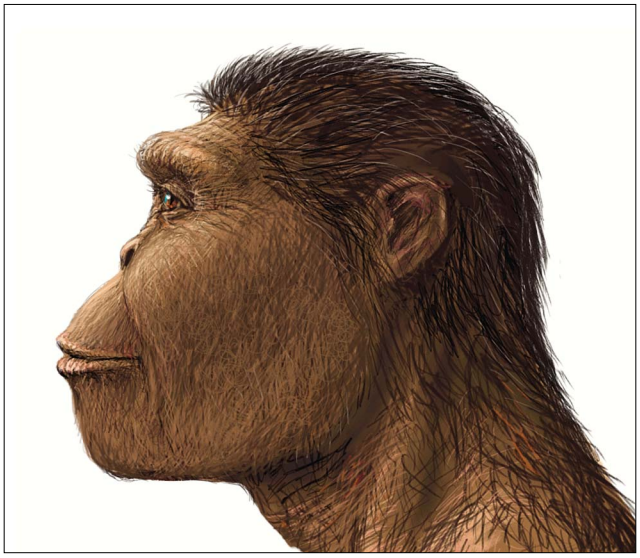

Figure 3. *Australopithecus robustus*. Image of face reconstruction (in profile) based on TM 1517 (Kaszycka 2008)

adult individual from the site (listed under Transvaal Museum catalogue number TM 1517) might have looked in terms of its cranial and facial appearance.

Since its discovery, in the late 1930s, two attempts have been made to reconstruct the Kromdraai skull (Broom 1938; Broom and Schepers 1946; and Krupiński et al. 1958), and one to restore the appearance of the individual's head (Broom 1950) – none of which were satisfactory. At the time of Broom's graphic reconstruction, in 1938, only a few australopithecine fossils were known and none of them complete. Furthermore, the Kromdraai skull was then the only specimen of its species available. Above all, however, Broom's reconstructions were just self-drawn, free-hand sketches.

The other early reconstruction – plaster cast – was made by a team from Wrocław University, and published in a Polish journal in 1958. Krupiński and colleagues based their work on casts sent by Broom, in 1949, of two parts of the TM 1517 skull – facial and mandibular, which they compared with apes and hominids known to date, as well as Broom's data on then published (1946-1952) australopithecines. The authors assessed the cranial capacity of the Kromdraai skull to be as much as 890 cc, and significantly lengthened the back of the reconstructed skull.

A few decades later, a third reconstruction by myself was proposed (Kaszycka 2001), based on the by then broader knowledge of the Kromdraai sample and the other South African robust australopiths. Given its incompleteness, the missing

parts of the TM 1517 skull were reconstructed on the basis of the best-preserved Swartkrans Member 1 individuals (Broom and Robinson 1952) and a new one from Drimolen (Keyser 2000). In preparing the drawings I received immense assistance from two artistically gifted men: Jan Strzałko and Karol Sabath. The image of the newest reconstruction of the Kromdraai robust australopith adult is presented in Fig. 3.

5. Australopithecine sexual dimorphism

In mid 2000 I applied for a grant to conduct research on sexual dimorphism [9] of the australopithecines (the subject of my postdoctoral studies and DSc degree), and being fortunate to receive funding, I, in 2006, again arrived in South Africa.

Why was the subject on sexual dimorphism interesting and important? In primates, sexual dimorphism is a significant phenomenon, being species specific and correlating with patterns of the social behavior. The appreciable enlargement of the South African australopithecine fossil sample (especially *Australopithecus robustus*) from new specimens broadened the range of variability of the species and provided the opportunity to re-examine sexual dimorphism in more representative material. The immediate aim of the research was to ascertain the degree and patterns of size sexual dimorphism of the two southern African australopithecine taxa (*A. robustus* and *A. africanus*) and to relate this to the dimorphism of their closest related species of extant African apes (gorilla and chimpanzee). A further aim was to widen knowledge of the australopithecines and to verify some hypotheses concerning ecological conditions of hominization, including certain aspects of social behavior of our ancestors, thus to deepen the understanding of the evolution of the hominids and, ultimately, ourselves.

The degree of sexual dimorphism for extant apes I assessed directly – as indices of the mean values for males to the mean values for females. The degree of dimorphism in the fossil samples was evaluated by various statistical methods, based on assessment of the parameters of distribution of the variables. For the first time in a single study several different statistical methods for determining dimorphism on material of indeterminate sex were used (Kaszycka 2009). These were: the Mean method, Median method, Coefficient of Variation [CV] method, Finite Mixture Analysis, Method-of-Moments [MoM], Assigned Resampling Method [ARM], and Binomial Dimorphism Index.

Data on African apes (of known sex) were used to assess the goodness-of--fit (effectiveness) for each method estimating sexual dimorphism in the fossil

[9] Sexual dimorphism – morphological differences in appearance between sexes of the same species e.g., size or shape.

samples. Thus, in case of the teeth, the CV method provided the best estimates of sexual dimorphism. In regard to the cranium, at high levels of true dimorphism (as observed in the gorilla skulls), the MoM method gave the best estimates (and for the face alone – the ARM method), while at low levels of true dimorphism (as observed in chimp skulls), the CV method provided the best estimates (Kaszycka 2009).

These studies revealed that the South African australopithecines possessed a combination of small (10%) canine size dimorphism (compared to 30% canine dimorphism in chimpanzees and 50% in gorillas) and marked facial sexual dimorphism, and thus overall body size. *Australopithecus robustus*, with its estimated index of facial sexual dimorphism of 1.13, was significantly more dimorphic than the chimpanzee (with its male to female ratio of 1.06), being almost gorilla-sized (male to female ratio of 1.15) (Kaszycka 2009).

An additional approach taken to assess sexual differences in a sample where the data were measurements of individuals of indeterminate sex, was the use of Cluster Analysis [10] to partition the individuals into two groups (putatively sexes). The accuracy of this technique was tested on samples of African apes of known sex. Thus by applying Cluster Analysis for the apes, I obtained accurate results for highly dimorphic gorillas, while for the much less dimorphic chimpanzees, the method was not accurate. Since the degree of size sexual dimorphism for *Australopithecus robustus* corresponded with that for gorillas, it seemed reasonable to use the clustering technique in categorizing this fossil species into two groups – putatively "males" and "females" (Kaszycka 2009, 2016).

Using the knowledge gained about the sexual dimorphism of australopithecines, I then extrapolated how this could be employed in ecological interpretations.

6. Fossil hominid social structure

As mentioned above, in primates, sexual dimorphism provides clues for reconstructing social behavior (mating systems). As a general rule, size dimorphism is lacking among monogamous primate species, while in polygynous [11] species males are commonly larger than females. This difference in size between the sexes at adulthood can be attained in two ways – males may grow faster than females, or males may mature later than females.

[10] Cluster analysis – a multivariate analysis technique, which, from the standpoint of the calculation, is a "reversal" of analysis of variance.
[11] Polygyny – a form of polygamy in which one male lives and mates with multiple females, but each female mates only with a single male.

While conducting my research on the australopithecines' sexual dimorphism, Charles Lockwood published an article in which he and his co-workers (Lockwood et al. 2007) suggested an uneven sex ratio (4:1 in favor of the males) for the known individuals of *Australopithecus robustus*, and put forward a hypothesis of an extended maturation for males of this extinct South African hominid. Combining this with estimates of a high degree of size sexual dimorphism, those authors used the results to reconstruct the social behavior of this fossil species. They concluded that *A. robustus* had a polygamous social system similar to that of gorillas (i.e., one-male harems).

I reasoned that Lockwood et al.'s (2007) hypothesis warranted re-examination. On doing so (Kaszycka 2016) I discovered their line of thinking to be speculative, and their interpretation questionable in regard to several items – above all, "sexing" australopithecine specimens and the suggested sex ratio in the available *A. robustus* sample. Other disputable items included: relation between sex and body size, between sex and range of variation, as well as the hypothesized evidence for bimaturism and its implications. So although *Australopithecus robustus* exhibited a high, almost gorilla-like level of facial dimorphism, I was able to show that Lockwood's et al. (2007) arguments regarding the polygynous social structure of these early hominids were dubious. I concluded that the typical one--male–multifemale structure of forest-dwelling gorillas is not a particularly good model for interpreting the ecology and social life of the savannah-dwelling robust australopiths, and that the more likely social system of these hominids was a multimale–multifemale one.

7. History of paleoanthropology: The question of the photos

I had occasion to discuss the content of some historical photographs, kept at the University of the Witwatersrand Archives, with colleague Goran Štrkalj, whose interest at the time was the history of South African paleoanthropology. The photographs showed Raymond Dart (the man who described and named the first australopithecine fossil) holding the skull (see Fig. 4).

In the light of conflicting evidence, both for and against, we asked ourselves the question – were the photos those of the first cast of the Taung Child (made for the 1925 British Empire Exhibition in London), or were they some of the earliest photos of the original fossil? Against the background of the historical events of those times, when one of the most important events in paleoanthropology was first unfolding, we (Štrkalj and Kaszycka 2012) concluded that the object on the archival photographs was the fossil itself and not the cast. By this, we "shed light" on what was an old mystery.

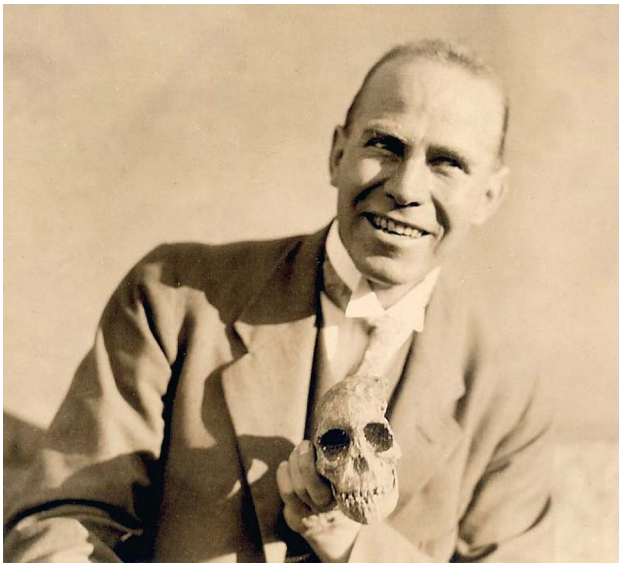

Figure 4. Archival photograph of Raymond Dart holding the Taung skull (courtesy of WITS University Archives)

Having been to South Africa a few times, the above endeavor was more than just research, but an 'adventure' into the distant past – something which I had aspired to since a young age.

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