

# JASs cover story

## The life histories of fossil hominins

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*In recent years a number of research projects concerning the evolutionary history of South African Plio-Pleistocene Hominins have been devoted to the reconstruction of specific aspects of the biology of these species. The increased number of fossil remains recovered and the use of new methods and new technological analyses have made it possible to extract a relevant amount of new information which until recently was completely unknown. One example of this, for instance, regards the lifestyle, the diet and the ecology of these fossil species. My research interest in the life histories of fossil hominins was sparked by the study of the fossil hominins from the Drimolen site. This rich and diverse sample offers tremendous potential for the study of many aspects of the biology of the early South African hominins. The analysis of the most complete skull,*

*DNH7, which led us to infer some details of the biology of Paranthropus, is an example of this kind of research. Similarly, another aspect of the biology of a fossil species which has become possible to investigate is the analysis of the patterns and the rate of somatic development. The study of the dental development of infant and subadult specimens (where the developing dentition can be examined directly or through CT scans to assess stages of development of permanent teeth still in the jaws) can provide information concerning their growth processes. This cover story is also a tribute to Charles Lockwood, a colleague and friend who died tragically, at 38, in July 2008, and whose inspired work formed the basis for this research.*

When studying the earliest phases of human evolution, we are often intrigued by the daunting task of inferring some aspects of the biology and the lifestyle of a fossil hominin species on the basis of the available skeletal evidence and in a comparative framework. This is especially difficult for those biological features that do not leave any direct fossil trace, such as, for example, social behaviour or life history variables (e.g. growth and development). In some cases, however, under special conditions, (mostly related to the abundance and the good state of preservation of the fossils) a careful analysis of the available fossil sample can help formulate testable hypotheses that can predict how some of these features evolved in our lineage.

Sexual dimorphism is the only skeletal evidence for the evolution of human social behaviour, and as such it is routinely analysed and debated for extinct hominin species. Almost without exception, prior research supports high levels of dimorphism in skull size in the early hominins, including well-sampled species such as *Australopithecus afarensis*. Alone, dimorphism is a limited instrument for

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dissecting social structure. Together with analysis of demography and taphonomy, however, it indeed offers the possibility to examine the behavioural ecology of extinct species in greater detail. An excellent example in this respect comes from our recent re-analysis of sexual dimorphism in the south African fossil hominin species *Paranthropus robustus* (Lockwood *et al.*, 2007).

For *P. robustus*, and indeed for South African early hominins in general, Drimolen is the most important site to have been discovered recently. It is located in the same context as the Witwatersrand cave sites such as Swartkrans, Kromdraai, and Sterkfontein (Keyser *et al.*, 2000). Drimolen contains fossils of *P. robustus* and early Homo, as well as abundant faunal remains suggesting a geological age of 1.5 to 2.0 million years ago, similar to Swartkrans Members 1-2. The most complete specimen is DNH 7 (see cover photo), a small skull preserving most of the cranium and mandible, whose morphology indicates affinities to *P. robustus* (Keyser, 2000).

Prior to the discovery of DNH 7, some of the smaller skulls from Swartkrans had been considered females, which, if true, would suggest a low degree of dimorphism in *P. robustus*. The obvious and substantial size difference between DNH 7 and specimens from Swartkrans raises several questions. Are there comparably sized individuals to DNH 7 at Swartkrans? Are the large but less robust skulls from Swartkrans and Kromdraai actually young adult males? Finally, if the complete specimens from Swartkrans are in fact biased towards males, what does this say about social structure in *P. robustus*?

The large available fossil sample of *P. robustus* allowed us to carry out a detailed comparative analysis. The first step involved the identification of all individuals with sufficient parts of the face and mandible to enable a size comparison and which also preserved postcanine teeth well enough to compare relative degrees of tooth wear. Individuals were then ranked by size and by age (based on tooth wear). This was done to determine whether the size range is comparable at Drimolen and Swartkrans (i.e., whether the samples can legitimately be pooled), and whether maximum (presumably male) size increases from young adulthood to full adulthood. Young adults are considered to be those individuals with M3 recently erupted.

The analysis comparing size to age suggests that maximum (presumably male) size was greater among old adults than young adults. Minimum size, on the other hand, occurs throughout the age range, with the oldest specimen in the sample also being the smallest. In other words, young adults consist of small and medium to large sized individuals, while old adults are either small or very large. Based on the ontogeny of sexual dimorphism in modern primates, we interpreted this pattern as continued growth in males between early skeletal adulthood and full maturity. Nonetheless, due to the fact that small individuals can occur at every age, we concluded that females have reached full skeletal size by the time M3 has erupted or soon thereafter. In contrast, male development continues well after the M3 has erupted, in both quantitative and qualitative terms.

It is common in anthropoid primates for males to reach maturity later than females, and this pattern is exaggerated in species with high levels of dimorphism. Extended male growth is thought to occur in sexually dimorphic primates because their reproductive success is concentrated in a period of dominance resulting from intense male-male competition. Given a pattern where *P. robustus* is strongly dimorphic and demonstrates a shift in male size and robusticity well after the M3 has erupted, it is apparent that males dominate the cranial remains attributed to *P. robustus*.

An abundance of males is perhaps not surprising in a fossil sample that that was subjected to predation. Direct evidence of carnivore activity is present on several hominin specimens at Swartkrans,

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and Member 1 of this site is among the most definitive examples of a predator-accumulated assemblage of hominins. In dimorphic primates, non-dominant males spend more time alone, on the periphery of a social group, or in small all-male bands. For a species that was clearly under threat of predation, solitary or peripheral behaviour would put males at high risk.

The picture that seems to emerge for the species *Paranthropus robustus* is of a strongly dimorphic species with an accompanying shift in size and robusticity between young adult and fully adult males. These two pieces of evidence support the conclusion that sex ratios within groups were relatively high. We also inferred that male transfer occurred between groups, and that there was a relatively short period of male dominance, as indicated by the apparently high risk of predation for young adult and fully mature males.

Analysis of sexual dimorphism, demography, and taphonomy of *P. robustus*, combined with a relatively large sample size, show a striking example of what could be possibly inferred about social structure in an extinct hominin species.

Keyser A.W. 2000. The Drimolen skull: the most complete australopithecine cranium and mandible to date. *S. Afr. J. Sci.*, 96: 189-193.

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Lockwood C., Menter C., Moggi-Cecchi J. & Keyser A. 2007. Extended Male Growth in a Fossil Hominin Species. *Science*, 318: 1443 – 1446.

