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The enigmatic molar from Gondolin, South Africa: Implications for *Paranthropus* paleobiology

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ABSTRACT

The specific attribution of the large hominin M_2 (GDA-2) from Gondolin has significant implications for the paleobiology of *Paranthropus*. If it is a specimen of *Paranthropus robustus* it impacts that species' size range, and if it belongs to *Paranthropus boisei* it has important biogeographic implications. We evaluate crown size, cusp proportions and the likelihood of encountering a large-bodied mammal species in both East and South Africa in the Early Pleistocene. The tooth falls well outside the *P. robustus* sample range, and comfortably within that for penecontemporaneous *P. boisei*. Analyses of sample range, distribution and variability suggest that it is possible, albeit unlikely to find a M_2 of this size in the current *P. robustus* sample. However, taphonomic agents - carnivore (particularly leopard) feeding behaviors - have likely skewed the size distribution of the Swartkrans and Drimolen *P. robustus* assemblage. In particular, assemblages of large-bodied mammals accumulated by leopards typically display high proportions of juveniles and smaller adults. The skew in the *P. robustus* sample is consistent with this type of assemblage. Morphological evidence in the form of cusp proportions is congruent with GDA-2 representing *P. robustus* rather than *P. boisei*. The comparatively small number of large-bodied mammal species common to both South and East Africa in the Early Pleistocene suggests a low probability of encountering an herbivorous australopith in both. Our results are most consistent with the interpretation of the Gondolin molar as a very large specimen of *P. robustus*. This, in turn, suggests that large, presumptive male, specimens are rare, and that the levels of size variation (sexual dimorphism) previously ascribed to this species are likely to be gross underestimates.

Introduction

Fossils of *Paranthropus robustus* are known from five sites situated within a 5 km radius of one another in the Bloubank Valley of South Africa (Fig. 1). All represent clastic sediment infillings of karst caves that formed in the Precambrian Malmani dolomitic limestones of the Monte Cristo Formation. A small, albeit significant collection, including the type specimen, is known from Kromdraai (Broom, 1938; Grine, 1982), but the species is best represented at Swartkrans (e.g., Broom and Robinson, 1952; Grine, 1989) and Drimolen (Keyser et al., 2000; Moggi-Cecchi et al., 2010). Several molars attributed to *P. robustus* have also been recovered from Sterkfontein Member 5B (Kuman and Clarke, 2000), and a badly crushed facial skeleton and a few teeth have been found at Cooper's (Berger et.al., 2003; Steininger et al., 2008; de Ruiter et al., 2009).

The geochronological ages of these *Paranthropus*-bearing deposits have been the subject of prolonged investigation. Ignoring the spectacularly bizarre range - 4.38 Ma–0.36 Ma - derived from ESR dating of tooth enamel (Blackwell, 1994; Curnoe et al., 2001, 2002), most faunal estimates indicate accumulation between about 1.9 Ma and 1.5 Ma (Vrba, 1985; Delson, 1988; McKee et al., 1995; Keyser et al., 2000; Kuman and Clarke, 2000). Palaeomagnetic determinations (Thackeray et al., 2002; Herries et al., 2009) are, of course, concordant because they are grounded by these biochronological estimates. The U–Pb determinations from speleothems at Cooper's and Swartkrans (de Ruiter et al., 2009; Pickering et al., 2011) do not contradict the faunal estimates.

Gondolin

In 1997, two hominin teeth were discovered in a "breccia" dump at Gondolin, some 20 km northwest of the other *Paranthropus*-bearing sites (Menter et al., 1999) (Fig. 1). The Gondolin cave

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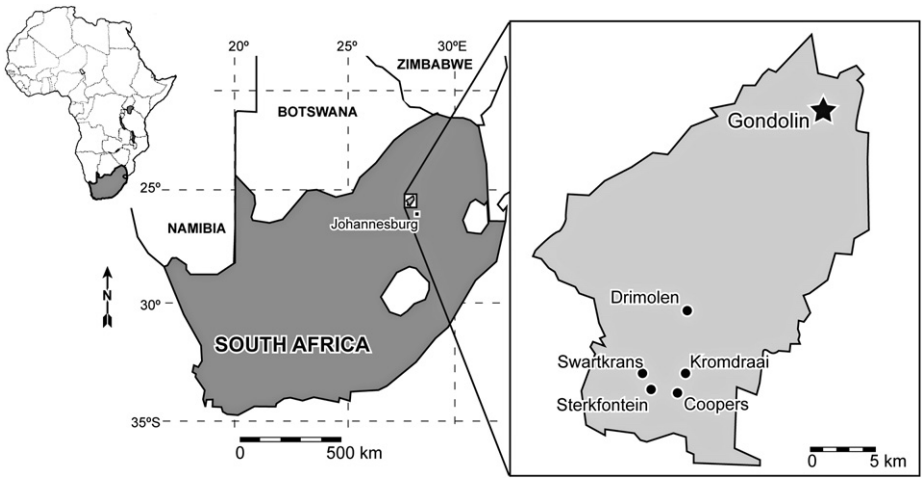

Figure 1. Location of Early Pleistocene *Paranthropus*-bearing sites in South Africa.

system, which developed in Eccles Formation dolomites, is surrounded by greater topographic relief than those in the Bloubank Valley (Herries et al., 2006). Gondolin presents a number of "breccia" dumps created by lime-mining activity, and two in-situ fossiliferous deposits. In 1979, E.S. Vrba conducted a brief excavation of one of the in-situ deposits, designated GD 2, which yielded a number of vertebrate fossils, but no primates (Watson, 1993).

The fossils from Vrba's excavations include "stage III" *Metridiochoerus andrewsi*, which suggests an age of between 1.9 and 1.5 Ma (Watson, 1993). Using this species as a basis for interpolation, Herries et al. (2006) argued that the normal geomagnetic polarity of GD 2 indicates deposition during the Olduvai (C2n) subchron between 1.95 and 1.78 Ma (Cande and Kent, 1995). Subsequent excavation of the in-situ GD 1 deposit produced a vertebrate fauna equivalent to that from GD 2, but these sediments preserve a wholly reversed polarity signature. This has been interpreted as suggesting deposition either just prior to or immediately following the Olduvai subchron (Adams et al., 2007). Adams et al. (2007) argued that GD 1 is the likely source for the "breccia" blocks in Dump GDA that yielded two hominin teeth (Menter et al., 1999).

Thus, the Gondolin (GD 1 = GDA) fossils might be ca. 2.0 Ma (or older), or perhaps 1.7–1.5 Ma. Neither estimate places them outside the probable range of the Bloubank Valley *Paranthropus*-bearing deposits. These dates also fall comfortably within the geochronological range of *Paranthropus boisei* in East Africa, which extends from about 2.3 Ma in lower Member G of the Shungura Formation (Suwa, 1988) to some 1.4 Ma at Konso (Suwa et al., 1997; Katoh et al., 2000).

The Paranthropus *molar from Gondolin*

The first hominin recovered from Gondolin (GDA-1) consists of the distolingual third of a lower molar. Menter et al. (1999) concluded that although it was not possible to attribute this fragment to any taxon, it was unlikely to belong to *Paranthropus*.

The second hominin specimen (GDA-2) is a very large mandibular left second molar crown lacking roots (Fig. 2). Its size and the presence of a large tuberculum sextum (C6) led Menter et al. (1999) to attribute it to *Paranthropus* sp. indet. Although its mesiodistal (MD) and buccolingual (BL) diameters were observed to be substantially larger than those of known *P. robustus* homologues, because of the geographic proximity of Gondolin to the Bloubank Valley sites, Menter et al. (1999: 305) were "content to conclude only that this tooth is a surprisingly large-sized specimen representing a population of South African robust hominids", and that it "would probably be acceptable to attribute this tooth to *P.* cf. *robustus*".

Tobias (2000) quickly enumerated the three possibilities entailed by this molar: 1) it is indeed a very large specimen of *P. robustus*, 2) it is the first indication of *P. boisei* in South Africa and, his least favorite, 3) it attests to the presence of a novel species of "robust australopithecine". Each of these possible interpretations has significant implications for our appreciation of *Paranthropus* paleobiology.

Some workers have likened *P. robustus* size variation to a chimpanzee-like level of dimorphism, whereas others have inferred higher (e.g., gorilla-like) levels for it (e.g., Steudel, 1980; McHenry, 1991; Lockwood et al., 2007). If GDA-2 is attributable to *P. robustus*, the degree of size variation (possibly sexual dimorphism) ascribed to this species is likely to be notably underestimated. The resultant substantial increase in its size range would have significant biological consequences (Calder, 1984).

On the other hand, if GDA-2 is attributable to *P. boisei*, it would have major implications for Early Pleistocene hominin biogeography (Strait and Wood, 1999). Fossils attributable to *P. boisei*, or the presumptive *P. aethiopicus* - *P. boisei* lineage are known from sites that extend from southern Ethiopia to northern Malawi (Suwa et al., 1997; Kullmer et al., 1999) (Fig. 3). The discovery of the *Paranthropus* maxilla at Malema more than doubled the previously known North–South range of *P. aethiopicus* - *P. boisei*. Malema is nearly 2000 km from Konso, Ethiopia, and another 2000 km separates Malema from the South African *Paranthropus*-bearing localities.

If the GDA-2 molar attests to the presence of either *P. boisei* or a novel species of *Paranthropus* in South Africa, this might have paleoecological implications (Giacominia et al., 2009). The notion that the *Paranthropus* specimens from Kromdraai and Swartkrans represent two species, namely *P. robustus* and *Paranthropus crassidens*, as proposed by Broom (1938, 1949), gained some support from cranial and especially deciduous dental comparisons (Howell, 1978; Grine, 1982, 1985), but subsequent discoveries at Drimolen (Keyser et al., 2000; Moggi-Cecchi et al., 2010) have blurred these apparent differences. Even though there is scant evidence for the recognition of two species of *Paranthropus* in the Bloubank Valley deposits, this should neither cloud nor preclude such interpretations for the Gondolin fossils.

Because of the significant implications that follow from the specific attribution of the Gondolin *Paranthropus* molar, we