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The TM 1517 odontoskeletal assemblage from Kromdraai B, South Africa, and the maturational pattern of *Paranthropus robustus*

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The holotype of *Paranthropus robustus* was discovered by R. Broom in 1938 in an outcrop of bone breccia at the cave site of Kromdraai B, in Gauteng, South Africa [1]. It consists of the left half of a cranium (TM 1517a) and an associated right mandibular corpus (TM 1517b), both bearing teeth, and of seven isolated teeth (a LLP3, a LLP4 and the series URP3-M3 labelled as TM 1517c). A few weeks later, close to the block containing the cranial remains, Broom identified four postcranial elements: the distal end of a right humerus (TM 1517g), the partial proximal end of a right ulna (TM 1517e), and two toe bones (TM 1517k and TM 1517o), all at the time attributed to the same young individual represented by the cranial remains. However, the distal foot phalanx TM 1517o was subsequently attributed to a baboon. While the holotype has been variously referred to as a 'young female', a 'young adult', as 'probably male and immature', or as a 'late adolescent', it certainly represents a dentally immature individual. Since these early descriptions, no study has explored the possibility that the associated postcranial remains preserve evidence of active bone growth or recent epiphyseal closure. Clearly, however, such information would either strengthen, or challenge the idea that the craniodental and postcranial remains belong to a single *P. robustus* individual and, importantly, might provide the first evidence about the odontoskeletal maturational pattern of this fossil taxon. Accordingly, we performed a micro-XCT-based study aimed at characterising the inner structure of the distal humerus TM 1517g, the proximal ulna TM 1517e and the distal hallucial phalanx TM 1517k. Our 2-3D analyses show that the distal humerus was likely completely fused, while the proximal ulna still displays a faint remnant of fusion, and the distal hallucial phalanx shows evidence of still growing bone. These findings, as well as the observation that the distal humerus and the proximal ulna fit anatomically and morpho-dimensionally [2], provide support for the original attribution of the cranial and the three postcranial remains from Kromdraai B to a single individual representing the *P. robustus* type specimen. Using extant human dental standards, the age at death estimate of TM 1517 is of 16.5±3 years if based on the LM2 (not fully closed distal apices) and LM3 root developmental stages (root formation stage between half and three-quarters completed). The skeletal age ranges between 14 and 18 years, for a male, and between 11 and 15 years, for a female individual. When a chimpanzee dental growth pattern is considered, TM 1517 fits the c. 10.5 years 'older juvenile' group [3], while chimpanzee skeletal maturity standards place it between 7.95 and 13.5 years. Interestingly, in humans fusion of the distal hallucial phalanx commonly slightly precedes that of the distal humerus. However, a sequence of distal humerus-distal hallucial phalanx-proximal ulna fusion, as displayed by TM 1517, is usually observed in *Pan*. Taken together, this new evidence for TM 1517 more closely resembles the chimpanzee condition for maturational

patterning. This finding is broadly in line with the evidence observed for *Australopithecus sediba* [4] and *Homo erectus* from Nariokotome [5]. Nevertheless, since *P. robustus* seems characterised by sexual bimaturism (with the males experiencing prolonged growth), the uncertain sex attribution of TM 1517 still represents a limiting interpretative factor.

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Significance: We provide the first evidence on anatomical ground of the very likely association of three postcranial elements to the cranial remains of the dentally immature individual labelled TM 1517 representing the holotype of *Paranthropus robustus* Broom, 1938, from Kromdraai B, in Gauteng, South Africa. The identification on the endosteal surface of two of the three postcranial elements of faint traces of incomplete epiphyseal fusion allows the assessment of the still unreported odontoskeletal maturational pattern of this fossil taxon.