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The alpha taxonomy of *Australopithecus* at Sterkfontein: The postcranial evidence

*La taxonomie alpha d'*Australopithecus *à Sterkfontein : le registre postcrânien*

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ABSTRACT

The possibility that the fossils attributed to *Australopithecus africanus* represent more than a single species is of significance because of the pivotal role that *A. africanus* has played in discussions about hominin evolution. The *A. africanus* hypodigm that is currently widely recognized evinces considerable variation in a number of craniodental characters, and this has led to speculation that more than one australopith taxon may be represented among the specimens from Sterkfontein. Although crania, mandibles and teeth have dominated these taxonomic discussions, the Sterkfontein postcranial remains also have been invoked. While several workers have proposed that some of the craniodental remains from Sterkfontein can be partitioned into two groups, there is a notable lack of agreement among them as to their actual sorting. Most of the craniodental observations that have been put forward in support of arguments for taxonomic heterogeneity of the Sterkfontein australopith assemblage have been subjective and anecdotal in nature. So too, the postcranial evidence that has been cited in support of more than one australopith species at Sterkfontein has been largely subjective, and limited to a small number of elements. The results of quantitative statistical analyses of the craniodental and postcranial fossils that have been undertaken to date are not necessarily consistent with the hypothesis of taxonomic heterogeneity.

Mots clés :
Grotte de Silberberg
Caverne de Jacovec
Espèces
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RÉSUMÉ

La possibilité que les fossiles attribués à *Australopithecus africanus* représentent plus d'une espèce est importante à considérer, en raison du rôle crucial qu'a joué *A. africanus* dans les discussions sur l'évolution des homininés. L'hypodigme d'*A. africanus*, qui est largement reconnu à l'heure actuelle, présente des variations considérables au niveau de certains caractères crânio-dentaires, permettant de supposer que plus d'un taxon d'Australopithèque serait représenté parmi les spécimens de Sterkfontein. Si les restes crâniens, mandibulaires et dentaires ont dominé ces discussions taxonomiques, les restes postcrâniens de Sterkfontein ont également été évoqués. Bien qu'un certain nombre de chercheurs aient proposé de séparer une partie des restes crânio-dentaires de Sterkfontein en deux groupes, ils ne s'entendent généralement pas sur leur classement. La plupart des observations

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crânio-dentaires avancées en faveur d'une hétérogénéité taxonomique de l'assemblage australopithèque de Sterkfontein est de nature subjective et anecdotique. De même, les preuves basées sur le matériel postcrânien qui ont été citées en faveur de plus d'une espèce d'Australopithèque à Sterkfontein sont largement subjectives et limitées à un petit nombre d'éléments. Les résultats des analyses statistiques quantitatives réalisées à ce jour sur les fossiles crânio-dentaires et postcrâniens ne sont pas nécessairement compatibles avec l'hypothèse d'une hétérogénéité taxonomique.

1. Introduction

The identification of species in the fossil record is of importance because species are one of the fundamental units of biology. Various species concepts (e.g., biological, evolutionary and phylogenetic) have been advocated by different workers, and these conceptualizations have influenced the methodological problem of species delimitation (de Queiroz, 2007). Because paleontologists deal almost exclusively with morphological characters, most alpha-level taxonomic studies are concerned with their distribution and variation, and the use of morphological traits to define entities that are diagnostically distinct from one another (Nixon and Wheeler, 1990; Wiens and Servedio, 2000).

As such, measures of character variability are commonly employed in the assessment of fossil samples on the assumption that an extinct species was no more variable than the modern ones employed as references. For the most part, extant reference taxa have been chosen based on phylogenetic propinquity, since degree of evolutionary relatedness will potentially serve to constrain morphology. However, this is not a necessary constraint since selection may have engendered elevated levels of variation (e.g., sexual dimorphism) in some species in the past (De Lisle and Rowe, 2015; Plavcan, 2012; Schillaci, 2010). Another potential problem with the use of extant species as models to evaluate paleontological assemblages is their temporal dissimilarity. Although the consequence of time-averaging on phenotypic variation in fossil samples has been examined, observations to the effect that morphometric variance in time-averaged samples may exceed only slightly that of temporally instantaneous samples of closely related extant species (e.g., Hunt, 2004) are not wholly unexpected since the latter are used to establish the boundaries of the former. As an interesting alternative, Wood (1991b) has suggested that one extinct species might be used to model intraspecific variation in other fossil assemblages, where the comparator has a reasonably deep temporal record and there is little disagreement concerning its hypodigm.

Australopithecus africanus exemplifies the problem of defining paleontological species and delimiting the degree to which polymorphisms affect the characters that are employed in its diagnosis. The initial period of discovery of fossils at Taung, Sterkfontein and Makapansgat saw them attributed to three species partitioned between two or possibly three genera (Broom, 1936, 1938, 1947, 1950; Dart, 1925, 1948). This was followed by a period of rationalization, wherein all were regarded as representing a single species, a view that gained ascendency through the work of a number of influential authorities (Le Gros Clark, 1964; Robinson, 1954, 1956; Tobias, 1967; Wolpoff, 1974). This has become conventional palaeoanthropological wisdom (e.g., MacLatchy et al., 2011; White et al., 1981; Wood and Richmond, 2000). Nevertheless, nagging questions persist about the degree and pattern of craniodental variability exhibited by the fossils that constitute its hypodigm (e.g., Clarke, 1985a, 1988a, 1988b, 1994, 2008; Fornai et al., 2010, 2015; Kimbel and White, 1988; Lockwood and Tobias, 2002; Moggi-Cecchi and Boccone, 2007). These same questions also have been raised about certain aspects of the postcranial remains, and particularly those that are held to derive from Sterkfontein Member 4.

Although the possibility that the *A. africanus* hypodigm subsumes more than one species has involved discussion of the fossils from Makapansgat, it revolves largely around those from Sterkfontein Member 4 (Clarke, 1985a, b). According to Clarke (1988a, b, 1994, 2008), there are two australopith species represented at Makapansgat and at Sterkfontein, and one is more closely related to *Homo*, while the other has affinities with *Paranthropus*. Clarke's suggestion harks back to Aguirre's (1970) arguments that the Makapansgat hominin sample comprises fossils of *Australopithecus africanus* and *Paranthropus robustus*. Aguirre (1970) additionally speculated that two species might also be found among the Sterkfontein fossils.

The taxonomic history of *Australopithecus africanus* and the arguments pertaining to the craniodental evidence for its hypodigm subsuming two (or more) species have been reviewed in detail elsewhere (Grine, 2013). In essence, much of the evidence put forward in support of taxonomic heterogeneity has been in the form of subjective, anecdotal observation. Moreover, not a few of the specimens that have been singled out as displaying potentially divergent traits are juveniles, and the ontogenetic changes that may affect the particular features that have been singled out have not been explored fully. Many of the arguments that have been espoused for heterogeneity have been based on variably incomplete, fragmentary and distorted fossils. Among the quantitative analyses that have been undertaken (e.g., Ahern, 1998; Calcagno et al., 1999; Fornai et al., 2010, 2015; Grine et al., 2013; Moggi-Cecchi, 2003; Moggi-Cecchi and Boccone, 2007; Wood, 1991b), very few have concluded that there is any craniodental evidence for more than a single species.

Table 1
Morphological groups recognized among the craniodental fossils that constitute the *Australopithecus africanus* hypodigm from Sterkfontein by different workers.
Tableau 1
Groupes morphologiques reconnus parmi les fossiles postcrâniens qui constituent l'hypodigme *Australopithecus africanus* de Sterkfontein selon les chercheurs.

	Group 1	Group 2
Kimbel and White (1988)	Sts 5	Sts 52 Sts 71
Clarke (1988a)	Sts 5 Sts 52	Sts 71 Stw 252
Clarke (1994)	Sts 17 TM 1511	Stw 505
Lockwood (1997)	Sts 5	TM 1511 Sts 71 Stw 505
Lockwood and Tobias (2002)	Sts 5 Sts 17 Sts 52 Sts 71 TM 1511 Stw 505	? Stw 252 Stw 183

What is perhaps most telling is the significant lack of agreement among the workers who have argued that there may be two (or more) australopith groups represented among the craniodental fossils from Sterkfontein and Makapansgat as to which fossils constitute those groups (Table 1).

In the first instance, Kimbel and White (1988) suspected that the Sterkfontein crania could be divided into two groups, with Sts 5 in one and the comparatively orthognathic Sts 52 and Sts 71 in the second. However, they were hesitant to ascribe these groups to different taxa and, beyond these three fossils, did not elaborate upon other possible constituents. Clarke (1988a, b), on the other hand, opined that the Sts 5 and Sts 52 represent one group, while Stw 252 and Sts 71 sample a "second species" that was ancestral to *Paranthropus*. Clarke (1994) drew favorable comparisons between the isolated occipital from Makapansgat–MLD 1–and the Sts 71 and Stw 252 occipitals, and because Dart (1948b) had designated MLD 1 as the holotype of *Australopithecus prometheus*, Clarke (1994) suggested that this name be used in reference to the "second species."[1] However, the resemblance between Stw 252 and Sts 71 in their "high, gently curved" occipital profiles is open to question in light of the fact that back of the Stw 252 cranium is imaginatively reconstructed and the profile of Sts 71 occiput is owing to taphonomic deformation (Broom and Robinson, 1950; Lockwood and Tobias, 1999). Three of these four specimens – Sts 52, Sts 71 and Stw 252 – possess teeth, and while there are certainly size and morphological differences among them, studies of the Sterkfontein dentitions have failed to identify these differences as being of a taxonomic nature (e.g., Moggi-Cecchi, 2003; Moggi-Cecchi and Boccone, 2007). Clarke (1994) also argued that because the configuration of the frontal bone exhibited by the Taung skull was an ontogenetic precursor of the form shown by Sts 5, the latter represented *A. africanus* at Sterkfontein. However, a 3D geometric morphometric analysis of craniofacial ontogeny by McNulty et al. (2006) found that between Sts 5 and Sts 71, the latter is more likely to resemble the adult form of the Taung child.

While Lockwood (1997) regarded the strongest evidence for distinct "subgroups" within the Sterkfontein Type Site assemblage to be Sts 5 representing one, and TM 1511, Sts 71 and Stw 505 representing another, he noted that they are not necessarily clearly differentiated as there are additional, more fragmentary fossils that blur this division. As a result, he concluded that these cranial remains most likely represent the range of variation attributable to a single species.

Lockwood and Tobias (2002) subsequently considered all of these specimens to represent *A. africanus*, and suggested that Stw 252 (or, at least the Stw 255/Sts 266a temporal fragments that are likely part of the same individual) and the Stw 183 juvenile maxilla may hint at a "distinct phenon." Although they felt that Stw 183 constituted the strongest evidence for a second species, they were hesitant to consider it as definitive evidence because of its ontogenetic immaturity.

While most of the discussion over to the presence of more than one australopith species at Sterkfontein has centered on the craniodental fossils, aspects of the postcranial remains from this site have also featured in such discussions. At least four issues have been involved in these arguments:

- the degree and type of morphological variation that is encountered among the fossils that almost certainly derive from the Member 4 (Type Site) deposit;
- the question of whether the fossils derive from Member 4 or from Member 5;
- the taxonomic ascription of the skeleton from the Silberberg Grotto;
- the species attribution(s) of the fossils from Jacovec Cavern.

Although all four potentially involve the issue geochronological heterogeneity, this is especially relevant to the second. The differentiation of Member 4 from Member 5 relates to the question of whether the fossils, if they are seen to differ from others that are securely identified as coming from Member 4, might represent *Homo* rather than *Australopithecus*. Indeed, this stratigraphic distinction has been involved in taxonomic discussions at Sterkfontein for over half a century (e.g., Hughes and Tobias, 1977; Robinson, 1957, 1958; Tobias, 1965, 1978). The fossils from the repositories in the Silberberg Grotto

[1] Berger and Hawks (2019) have recently proposed that *Australopithecus prometheus* Dart, 1948 is a *nomen nudum* on the basis that the diagnosis was conditional and did not designate the species based on morphological criteria. However, Dart (1948) did cite some morphological evidence, although this related to the occurrence of Wormian bones in MLD 1, and it is unclearwhether their opinion that the Holotype MLD 1 occipital cannot be unambiguously aligned or differentiated from homologues attributed to *A. africanus* is valid.

and Jacovec Cavern may (or may not) be substantially older than those from Member 4.

Each of these issues will be discussed below in relation to the postcranial fossils that have been described as bearing on the issue of australopith heterogeneity. Of course, because these bones are "associated" with craniodental remains – either through rare individual association or because they derive from the same repository – the cranial evidence is of some relevance. Where applicable, the craniodental fossils will be discussed in relation to the postcranial evidence.

2. Does the *Australopithecus africanus* postcranial hypodigm subsume two or more species?

Following Clarke's (1985a) suggestion that the commonly accepted Sterkfontein hypodigm of *A. africanus* includes fossils of two australopith species, several workers have addressed this issue with reference to the postcranial fossils. If the two species posited by Clarke (1985a, 1994, 2013) as represented by the craniodental remains from Sterkfontein Member 4 and Makapansgat Members 3 and 4 are also manifest in the postcranial bones from these deposits, it might be expected that morphological or morphometric differences between at least some homologous elements would be detectable. At the same time, however, if two closely related species were skeletally very similar overall, the vagaries that govern preservation and recovery might make it very difficult to detect any differences that might have existed.

At the outset, it must be recognized that, with very few exceptions, it is not possible to definitively associate postcranial bones with one another or with cranial and/or dental remains within the karst cave deposits of South Africa. The only three instances of undoubted cranial and postcranial association of which I am aware are the Stw 573 skeleton from the Silberberg Grotto (Clarke, 1998), and the juvenile MH 1 and adult MH 2 skeletons from the site of Malapa (Berger et al., 2010).

Proximity of fossils to one another and similarity of preservation might suggest association, and this has been reasonably argued in relation to the postcranial bones that comprise the Sts 14 and Stw 431 partial skeletons (Broom and Robinson, 1947; Kibii and Clarke, 2003; Robinson, 1972; Toussaint et al., 2003). According to its describers, Sts 14 comprises 15 vertebrae, several ribs, two os coxae, a partial sacrum and an incomplete left proximal femur, while Stw 431 is made up of 9 vertebrae, left and right partial os coxae, a partial sacrum, right clavicle, left scapula, distal right radius and proximal right radius and ulna.

In no instance has it been possible to definitely associate craniodental specimens and postcranial bones from Makapansgat or from Sterkfontein Member 4. The pieces that comprise Sts 7 – a crushed mandible, a fragmentary right scapula and a proximal right humerus – were found in close proximity to one another. According to Broom and Robinson (1947: 430), "on June 24 we discovered the nearly complete and fairly well-preserved lower jaw of a large middle-aged male. With it were found part of a maxilla and much of the humerus and scapula." This purported association has persisted in the literature, and it is seemingly based solely on the proximity of the three elements. While the proximity of a right proximal humerus and right scapula might be taken as reasonable evidence of association (Broom and Robinson, 1950), and while this might also be extended to a mandible that was recovered in close proximity, it is noteworthy that the maxilla to which Broom and Robinson (1947) refer was not mentioned subsequently by them in their description of Sts 7 (Broom and Robinson, 1950). It is reasonable to conclude that they no longer considered the maxilla to be associated with the other three specimens. Indeed, the maxilla to which they refer is unknown to me. It is conceivable that it was identified as that of a monkey. If the maxilla was deemed no longer to be associated with the scapula and humerus, it is unclear why the mandible continued to be held in association. Clarke (1994) has assigned the Sts 7 mandible to his "second" species, *A. prometheus*. If the mandible is actually associated with the humerus and scapula, these postcranial elements would then also be attributed to this taxonomic group.

With reference to the Stw 431 skeleton, Toussaint et al. (2003: 219) noted that a number of isolated hominin teeth were recovered from "the same grid squares and from approximately the same depth." While they believed that some of the teeth might well have belonged to the same individual as represented by the postcranial bones, they also observed that "there are a few duplicated dental elements indicating that more than one individual is represented." This highlights the problem of anticipating association through proximity in this and other of the South African palaeokarst cave deposits.

Nevertheless, Thackeray et al. (2002b) proposed that the Sts 5 cranium and the Sts 14 partial skeleton belong to the same individual on the basis of their apparent spatial proximity in Member 4 and their presumed similarity in ontogenetic development. Although the Sts 14 partial skeleton was initially held to represent an adult (e.g., Robinson, 1972), several lines of evidence suggest that the bones derive from a sub-adult individual (Berge and Gommery, 1999; Bonmatí et al., 2008; Häusler and Berger, 2001). Gommery and Thackeray (2006) have posited that their comparatively diminutive sizes are also consistent with this interpretation. At the same time, Thackeray (1997; Potze and Thackeray, 2010; Thackeray et al., 2002a, b) have argued that Sts 5 is a juvenile – a juvenile male to be precise – and could reasonably be interpreted as belonging to the same individual as Sts 14 (Thackeray et al., 2002b). However, several lines of evidence point to the fact that Sts 5 is a fully adult individual, and a reasonably old one at that (Bonmatí et al., 2008; Grine et al., 2012; Villmoare et al., 2013).

3. Postcranial remains from the Sterkfontein Type Site deposit

A large number of postcranial elements have been recovered from Sterkfontein Member 4 (Table 2). Considering that an adult hominin skeleton comprises some 177 separate bones, the number of elements represented by more than two or three specimens is rather impressive. By contrast, a paltry sample of hominin postcranial bones

Table 2
Postcranial elements from the Sterkfontein Type Site and from Makapansgat.
Tableau 2
Eléments post-crâniaux du site type de Sterkfontein et de Makapansgat.

Element	Specimen number
Axial Skeleton	
Cervical vertebrae	Stw 642 ($n = 1$)
Thoracic vertebrae	Sts 14 ($n = 9$); Sts 73 ($n = 1$); Stw 8/41 ($n = 2$); Stw 431 ($n = 5$); Stw 642 ($n = 10$)
Lumbar vertebrae	Sts 14 ($n = 6$); Stw 8/41 ($n = 4$); Stw 431 ($n = 6$); Stw 642 ($n = 2$)
Sacra	Sts 14; Stw 30; Stw 431
Costae	Sts 14; Stw 431; Stw 670
Os coxae	Sts 14; Sts 65; Stw 431; Stw 441; Stw 442; Stw 611; MLD 7; MLD 8; MLD 25
Femora	
Proximal	Sts 14; Stw 99; Stw 367; Stw 403; Stw 479; Stw 501; Stw 522; Stw 610; MLD 46
Head only	Stw 25; Stw 30; Stw 31; Stw 361; Stw 392; Stw 572
Shaft	Stw 121; Stw 448; Stw 614; Stw 615
Distal	Sts 34; TM 1513; Stw 129; Stw 318
Tibiae	
Proximal	Stw 396; Stw 514a
Distal	Stw 181; Stw 358; Stw 389; Stw 514b; Stw 515
Fibulae	
Shaft	Stw 356
Clavicles	Stw 431; Stw 582; Stw 616
Scapulae	Sts 7; Stw 162; Stw 366; Stw 431; Stw 612
Humerii	
Proximal	Sts 7; Stw 328; Stw 517
Distal	Stw 38; Stw 124; Stw 150*; Stw 182*; Stw 339; Stw 431; Stw 2198a; MLD 14
Radii	
Proximal	Sts 68; Stw 105; Stw 139; Stw 431; Stw 516; Stw 2198b
Shaft	Stw 125; Stw 348; Stw 528; Stw 626a; Stw 627
Distal	Stw 46; Stw 354
Ulnae	
Proximal	Stw 108; Stw 113; Stw 125; Stw 380; Stw 390; Stw 398; Stw 431; Stw 571; Stw 613; Stw 632
Shaft	Stw 340; Stw 349; Stw 577; Stw 626b
Distal	Stw 326; Stw 399
Manus	
Carpals	
Capitate	TM 1526; Stw 624
Scaphoid	Stw 618
Metacarpals	
Pollical	Stw 583
2nd	Stw 382
3rd	Stw 27; Stw 64; Stw 68; Stw 394
4th	Stw 26; Stw 65; Stw 292; Stw 330
5th	Stw 63
Manual phalanges	
Proximal	Stw 28; Stw 29; Stw 122; Stw 293; Stw 400; Stw 597
Middle	Stw 331
Distal	Stw 294 (pollex); Stw 617 (pollex)
Pes	
Tarsals	
Talus	Stw 88; Stw 102; Stw 347; Stw 363; Stw 486
Calcaneus	Stw 352; Stw 643
Navicular	Stw 623
Cuboid	Stw 638
Metatarsals	
Hallucial	Stw 562; Stw 595
2nd	Stw 89*; Stw 377; Stw 562
3rd	Stw 387; Stw 388; Stw 435; Stw 477; Stw 496; Stw 595d
4th	Stw 485; Stw 596
5th	Stw 114; Stw 634
Pedal phalanges	
Proximal	Stw 355; Stw 470 (hallucial); Stw 478 (hallucial); Stw 595b (hallucial)

TM, Sts and Stw specimens are from Sterkfontein Member 4; MLD specimens are from Makapansgat Members 3 and 4. The identifications of the Sterkfontein elements largely follow those of Pickering et al. (2004) and Clarke (2013). * Specimens that possibly derive from Sterkfontein Member 5 (see text).
Les spécimens TM, Sts et Stw proviennent du membre 4 de Sterkfontein; les spécimens MLD proviennent des membres 3 et 4 de Makapansgat. Les identifications des éléments de Sterkfontein s'accordent généralement avec celles proposées par Pickering et al. (2004) et par Clarke (2013). * Spécimens qui proviennent probablement du membre 5 de Sterkfontein (voir texte).

has been recovered from Makapansgat. Three of the four or five postcranial elements from Makapansgat are from young juvenile individuals (Dart, 1949a, b, 1958), and the adult femur exhibits severe marginal osteophytosis (Reed et al., 1993). Although Boné (1955a, b) described an additional five fragments from Makapansgat, his recognition of MLD 15, MLD 16, MLD 17 and MLD 20 as hominin has not withstood scrutiny (e.g., Hooijer, 1975; Senut, 1978; Wolpoff, 1973). Only one of the distal humeral fragments described by Boné as hominin (MLD 14) seems to have been accepted as such (Lague and Menter, 2017; Senut, 1978). This severely limits meaningful comparisons with homologous elements from Sterkfontein.

Analyses of the postcranial fossils from Sterkfontein of relevance to the question of possible taxonomic heterogeneity in the Member 4 assemblage take two forms. The first entails comparisons between two (or more) specimens that might suggest discrete morphological dissimilarities that transcend sexual dimorphism and attest to possible functional differences in postural or locomotor abilities. The second considers the spectrum of morphometric variability exhibited by a series of homologous elements in relation to the ranges of intraspecific variation found among extant primate species. For example, one might ask whether the coefficient of variation (CV) in a given parameter in the fossil assemblage exceeds the CVs of living great apes and humans.

Despite the reasonable number of homologous elements that are preserved in the postcranial assemblage from Sterkfontein Member 4 (Table 2), very few have been directly compared with one another where the comparisons have led to the conclusion that two comparatively discrete morphs are represented. To put this into context, nearly 75 cranial and mandibular fossils from this same deposit have been assigned to one or another "species" group by various workers on the basis of such intra-assemblage comparisons (see Grine, 2013 for a review). About a third of these craniodental specimens have been attributed to the "second species," or *A. prometheus*, by Clarke (1988a, 1994, 2008).

Among the postcranial bones from Sterkfontein Member 4 that have been compared with one another, five elements – sacrum, ilium, tibia, first metatarsal and second metatarsal – reveal morphological differences that have been surmised to perhaps attest to a taxonomic distinction. In each instance, the assessment has entailed comparisons between two homologues, and in those cases where a taxonomic distinction may be warranted it is unclear that the two taxa are species of *Australopithecus*. In another two instances – the distal humerus and proximal femur – comparisons among multiple homologues have concluded that the variation encountered among them could reasonably be sampled in a single species.

3.1. Discrete morphological differences between two homologous elements

Sacrum. Sacral comparisons have juxtaposed Sts 14 vs. Stw 431. In their description of the Stw 431 skeleton, Toussaint et al. (2003) noted several differences with the sacrum of Sts 14, including the degree of ventral concavity, the extent of the auricular surface, and the ratio of the heights of the bodies of S1 and S2. However, they suggested that the differences are likely related to their interpretation of Sts 14 as female and Stw 431 as a male. As such, it would seem unlikely that the differences between them necessarily relate to a taxonomic distinction.

Ilium. Comparisons of the ilium have juxtaposed Sts 14 vs. Stw 431. In their description of Stw 431, Toussaint et al. (2003) were not able to differentiate the ossa coxae from that of Sts 14. Reconstruction of the Stw 431 pelvis led Haeusler (2002) to conclude that there are "many similarities" between it and Sts 14, whereas he was struck by the "conspicuous differences" between the Sterkfontein pelves and that of *A. afarensis* (A.L. 288-1). Subsequently, Kibii and Clarke (2003) produced a second reconstruction of the Stw 431 pelvis based on additional pieces of the left os coxae. In that reconstruction, the iliac blade flares laterally to a greater extent than in Sts 14 (it was noted that they resemble more closely A.L. 288-1). However, Kibii and Clarke (2003: 226) also noted that in the Sts 14 ossa coxae, "the upper part of the left iliac blade is incorrectly aligned with the lower part by a large area of plaster. It is thus probable that slight adjustments to these reconstructed areas would result in a more lateral pelvic blade orientation." Nevertheless, they remained uncertain whether Stw 431 and Sts 14 belong to a single species, or if either of them necessarily represents *A. africanus*.

Berge et al. (2007) undertook a multivariate morphometric assessment of the Stw 431 pelvis as reconstructed by Kibii and Clarke and concluded that it "shared the majority of ilium traits" with specimens of *Paranthropus robustus* from Kromdraai (TM 1605) and Swartkrans (SK 50 and SK 3155) in contrast with Sts 14. They took these results as confirming that Stw 431 represented a "robust species" that was contemporaneous with *A. africanus* and probably related to the origin of *P. robustus*. Subsequently, however, Berge and Goularas (2010) reconstructed the Sts 14 pelvis from digital models created with CT images, and found that it conformed largely to Haeusler's, with the exception that the iliac blades were more transversely flattened, resulting in a greater lateral flare. Although this would conform more closely to the reconstruction of the Stw 431 iliac blades by Kibii and Clarke (2003), Berge and Goularas (2010) were curiously silent on the subject of Stw 431. It would seem that the purported differences between the ossa coxae of Sts 14 and Stw 431 no longer pertain.

Tibia. Tibial comparisons have juxtaposed Stw 396 vs. Stw 514. In their description of Stw 514, Berger and Tobias (1996) stressed the primitive, ape-like morphology of the proximal plateaus, which was seen as implying a "less stable and more mobile" knee joint than evident even in *A. afarensis*. Although they did not compare Stw 514 directly with any other Sterkfontein specimen, they assumed that it belonged to *A. africanus* inasmuch as it had been excavated from *in situ* hard breccia near the areas from which Sts 5, Sts 14 and Stw 505 had been recovered. Subsequently, Zipfel and Berger (2009) compared Stw 514 with the proximal tibial fragment, Stw 396, which also derives from Member 4, but from partially decalcified deposits at a greater depth. Zipfel and Berger (2009) assessed Stw 396 as having a much more-human-like morphology, with greater stability at the

knee. They (2009: 74) concluded that the four differences they observed between Stw 396 and Stw 514 "indicate a degree of morphological variability that may represent the extremes of intraspecific variability or even exceed what one would expect from intraspecific variation alone." The possibility that these morphologies may relate to different functional adaptations led Zipfel and Berger (2009) to suggest support for the presence of two species of australopith in this deposit.

Earlier, Berger and Tobias (1996) had alluded to the compatibility of the highly mobile, medially divergent first metatarsal that had been inferred for the foot of Stw 573 from the Silberberg Grotto (Clarke and Tobias, 1995) with their interpretation of a mobile, ape-like knee in Sts 514. However, as discussed below, the purported ape-like nature of hallucial tarsometatarsal joint of Stw 573 has been questioned by several experts (Harcourt-Smith and Aiello, 2004; Kidd and Oxnard, 2005; McHenry and Jones, 2006; Stern, 2000; R.L. Susman, pers. comm.).

A recent study of trabecular bone orientation in distal tibiae from Sterkfontein (Barak et al., 2013) examined three specimens from Sterkfontein (Stw 358, Stw 399 and Stw 567) and found them all to possess a similar pattern. Unfortunately, they did not include the distal end of Stw 514 in their study.

Hallucial metatarsal. Comparisons of the hallucial metatarsal have juxtaposed Stw 562 vs. Stw 595. In her description of the foot bones from Sterkfontein, Deloison (2003: 195–196) concluded that Stw 595 presents morphology that is characteristic of an abductable toe, indicating a "prehensile foot and probable arboreality" and that Stw 562, although larger, is very similar. She viewed both as evincing many features of ape homologues, indicative of a non-bipedal foot ("donc de pied non bipède").

By contrast, Zipfel et al. (2010: 125) suggested that these two bones differ from each other "to an extent unlikely to fall within the range of intraspecific variability." They observed that the distal articular surface of the more robust Stw 562 extends onto the dorsal surface of the head, which would have permitted human-like metatarsophalangeal dorsiflexion at toe-off, whereas Stw 595 possesses a "more ape-like" distal articular face. Clarke (2013: 114) has reiterated these statements. Multivariate analyses undertaken by Zipfel et al. (2010) suggested an affinity of Stw 562 with *Homo* and *Pan*, and for Stw 595 a closer affinity with *Pongo*. This was taken to suggest that individuals possessing these toes were unlikely to have had the same mode of bipedality, and that neither would have been identical to modern humans. Proctor's (2010) multivariate analysis of the proximal surface of Stw 562 reinforces its morphological intermediacy between extant chimpanzees and humans.

DeSilva et al. (2012) have stated that the Stw 595 first metatarsal is "quite similar" to that of the Burtele foot (BRT-VP-2/73) from Ethiopia based on the description of the latter by Haile-Selassie et al. (2012: 566) as lacking the "dramatic dorsal doming" of the head that typifies the genus *Australopithecus* – or perhaps more precisely, *A. afarensis*. On the other hand, according to the Proctor's (2010) study, the base of Stw 562 would appear to differ substantially from the "deeply concave, sigmoidal configuration" that was described for the Burtele hallucial metatarsal and which is seen in extant African apes and *Ardipithecus ramidus* (Haile-Selassie et al., 2012). The Burtele foot, which is dated at approximately 3.4 Ma and is thus contemporaneous with *A. afarensis* in the Afar region of Ethiopia (range between ca. 3.6–2.9 Ma), could represent a separate species with a more primitive, opposable hallux, as suggested by Haile-Selassie et al. (2012). Perhaps it is attributable to *Au. deyiremeda* (Haile-Selassie et al., 2015)? If this is the case, then it is feasible that the Stw 595 first metatarsal also signifies a species-level difference at Sterkfontein, although it must be stressed that the base of the Stw 595 does not conform to the deeply concave, sigmoidal configuration in feet with opposable big toes.

Thus, the notion that there are two separate early Pleistocene pedal adaptations in the Afar does not necessarily extend to Sterkfontein. Certainly, Deloison (2003) did not view the two hallucial metatarsals from Member 4 as differing substantially from one another, and Drapeau and Harmon (2013) recorded low head torsion values for Stw 562 and Stw 595 indicative of a lack of opposability of the hallux in both specimens.

Second metatarsal. Comparisons of the second metatarsal have juxtaposed Stw 89 vs. Stw 377. In her description of pedal remains from Sterkfontein, Deloison (2003: 197) suggested differences between the Stw 89 and Stw 377 second metatarsals, although she did not specifically refer to one when discussing the other. Thus, with reference to Stw 89, she drew attention to characters shared with modern humans (e.g., the straightness and form of the shaft, and the form of the base), noting that its head (l'épiphyse distale) possesses "une forme particulière" differentiating it from humans and chimpanzees. The Stw 377 metatarsal was seen by her as being manifestly ape-like ("cet os présente des caractères simiens"), and she noted that its owner could have belonged to the same taxon, if not having been the same individual to which the Stw 477 and Stw 485 third and fourth metatarsals belonged (Deloison, 2003: 197).

By contrast, Zipfel et al. (2010: 125) described Stw 89 as possessing a head with morphology indicative of human-like metatarsophalangeal joint dorsiflexion during toe-off, and a base that is "triangular in shape unlike that of both extant apes and humans." They noted that its base is "quite gracile" in comparison to the dorsoplantar height of Stw 377, and surmised that the "unusual morphology" of Stw 89 could represent "an extreme in intraspecific variability" or a species other than *A. africanus*.

DeSilva et al. (2012) reiterated the difference in the dorsoplantar heights of the Stw 89 and Stw 377 bases, with the latter falling within the range of modern humans and resembling homologues attributed to *A. afarensis*. The dorsoplantar gracility of the Stw 89 base was suggested to indicate greater midfoot laxity. Although DeSilva et al. (2012) described Stw 89 as possessing internal torsion of the head, a condition "decidedly unlike" that exhibited by humans, Drapeau and Harmon (2013) noted that their measurement of torsion in Stw 89 (−4.7°) and estimation of it for Stw 377 (−1.0°) are very similar to one another with both falling within the range predicted for a foot that lacked a human-like arch but also lacked grasping ability.

DeSilva et al. (2012) went on to note that Stw 89 is similar to the morphology described for the pedal skeleton from Burtele by Haile-Selassie et al. (2012). Haile-Selassie et al. (2012) described the BRT-VP-2/73b second metatarsal as possessing a base with a triangular outline and a compressed dorsoplantar height. Here, too, DeSilva et al. (2012) suggested that the difference between the *A. afarensis*-like Stw 377 and the Burtele-like Stw 89 could reflect the sort of distinction recognized by Haile-Selassie et al. (2012) among the Ethiopian fossils.

In light of these comparisons, the provenience of Stw 89 – specifically, whether it derives from Member 4 or from Member 5 – is of relevance. Initially, Clarke (1985b) indicated that Stw 89 derived from Member 5, and noted that flaked lithic artifacts were found in close proximity to it; as such, he provisionally attributed Stw 89 to *Homo habilis*. Subsequently, however, Kuman and Clarke (2000) argued that these deposits represent Member 4, even though they and Partridge (2000) observed significant differences in environmentally sensitive fauna between this deposit and Member 4 (e.g., in the preponderance of grazing antelopes and the presence of *Theropithecus oswaldi*). Despite Kuman and Clarke's (2000) reassignment of Stw 89 to Member 4, Partridge (2000) clearly continued to regard the unit from which it came as being distinct from Member 4, aligning it with the artifact-bearing units of Member 5.

Thus, if it becomes more apparent that Stw 89 and Stw 377 do actually represent distinct locomotor adaptations and possible taxonomic differentiation, it is not clear that Stw 89 should be attributed to *Australopithecus* rather than *Homo*. Of course, even if Stw 89 is relatively gracile in comparison to OH 8 (DeSilva et al., 2012), a specimen that has been attributed to *Homo habilis* by some workers (Leakey et al., 1964; Susman, 2008; Susman and Stern, 1982; Susman et al., 2011; but see also Day and Napier, 1964; Gebo and Schwartz, 2006; Weiss, 2012; Wood, 1974), there are reasons to suspect that the species of *Homo* that is represented in Sterkfontein Member 5 is not necessarily the same as found in Bed I of Olduvai Gorge (e.g., Grine, 2001; Smith and Grine, 2008). As such, there is little reason to presuppose identical pedal morphologies among the representatives of early *Homo* in eastern and southern Africa.

In sum, Stw 89 would appear to be a second metatarsal with a head whose morphology indicates human-like metatarsophalangeal joint dorsiflexion during toe-off, a head whose degree of internal torsion falls within the range predicted for a foot that lacked a human-like arch but also lacked grasping ability, and a base whose dorsoplantar gracility is perhaps indicative of greater midfoot laxity than in modern human. This combination is perhaps not unexpected for early *Homo* in light of the mixture of derived and primitive postcranial attributes that have been described for other early Pleistocene *Homo* specimens (Jashashvili et al., 2010; Lordkipanidze et al., 2007; Pontzer et al., 2010) and the foot of the late Pleistocene *Homo floresiensis* (Jungers et al., 2009).

3.2. Comparisons among multiple homologous elements

Distal humerus. Analyses of the distal humerus have juxtaposed Stw 38, Stw 124 and Stw 431 vs. Stw 150 and Stw 182. Lague (2015) has undertaken a geometric morphometric analysis of the cross-sectional shape of the distal diaphysis of a number of early hominin humeri, and has demonstrated the utility of this feature for taxonomic identification. Unfortunately, he was able to include only a single specimen (Stw 431) from Sterkfontein in his study. Lague and Menter (2019) have expanded the Sterkfontein sample with the addition of five other specimens. They observed that three (Stw 38, Stw 124 and Stw 431) are very similar to one another, and exhibit similarities to *A. afarensis* and *Paranthropus* (*P. robustus* as well as *P. boisei*) homologues. On the other hand, they found that two of the Sterkfontein specimens (Stw 150 and Stw 182) are much more similar to *Homo erectus* humeri. This could suggest the presence of two distal humeral morphs, and perhaps two australopith taxa (one of which diverged towards the *Homo erectus* condition) if all of the fossils actually derive from Member 4.

However, Senut and Tobias (1989) described Stw 150 as having derived from either Member 4 or Member 5 and Stw 182 as having derived from Member 5. Unfortunately, they did not undertake any comparative analysis of the humeral fragments described by them because of their "poor state of preservation," but they recognized that *Homo* rather than *Australopithecus* is represented in Member 5. Because Kuman and Clarke (2000: table 1) did not include either of these humeral fragments in the list of hominin associations for their revised interpretation of Sterkfontein stratigraphy, it would appear reasonable to conclude that they regarded the provenance of Stw 182 as Member 5. However, Pickering et al. (2004: table 3) and Clarke (2013: table 7.1) subsequently list both Stw 182 and Stw 150 as having derived from Member 4. One must presume, therefore, that this revision is based on the reassignment of part of Member 5 – specifically the region described as the stony "Stw 53 Infill" – to Member 4 by Kuman and Clarke (2000), even though the two fossils in question were not included in that revision. Despite Clarke's reassignment of Stw 182 to Member 4, Partridge (2000) clearly continued to regard the unit from which it came as being distinct from Member 4. Similarly, it is uncertain whether Stw 150 should continue to be regarded as having derived from Member 4, since the morphology of both Stw 150 and Stw 182 aligns them with *Homo erectus* rather than *Australopithecus* (Lague and Menter, 2017).

In addition to the differences noted above with regard to the comparison of Stw 150 and Stw 182 to the three distal humeri from Member 4 (Stw 38, Stw 124 and Stw 431), Lague and Menter (2019) have also observed that a fourth distal humerus from Member 4 (Stw 339) differs somewhat from the others, resembling the MLD 14 fragment as well as the MH 1 and MH2 distal humeri of *A. sediba*. Although the morphology shared by the Makapansgat, Stw 339 and *A. sediba* specimens is somewhat unusual by comparison with the other Sterkfontein Member 4 specimens, it is not possible to reject the null hypothesis that all could be accommodated within a single species on the basis of resampling (bootstrapping) analysis (Lague and Menter, 2019). Thus, the variation encountered among all of the distal humeri that are undoubtedly from Sterkfontein Member 4 (i.e. Stw 38, Stw 124, Stw 339 and Stw 431) and from

Makapansgat (MLD 14) could reasonably be sampled in a single species of *Australopithecus*.

Proximal femur. Analyses of the proximal femur have included MLD 46, ten specimens from Sterkfontein Member 4 (Sts 14, Stw 25, Stw 99, Stw 311, Stw 392, Stw 403, Stw 479, Stw 501, Stw 522, Stw 527) and one from Jacovec Cavern (Stw 598). Harmon (2009a) undertook a multivariate analysis based on a series of linear measurements and angles of the proximal femur and noted that the *A. africanus* femora do not form a "cohesive group." According to her analysis, "*A. africanus* varies quite a bit in neck cross-sectional shape. . ., where Stw 99 is elliptical, and others, such as Stw 311 and Stw 501, are human-like" (Harmon (2009a: 168). At the same time, however, she concluded that the range of variation among these (and other australopith) femora is comparatively low, but may still be meaningful. Rather than variation within the *A. africanus* sample, the differences appear to have been primarily between her *A. afarensis* and *A. africanus* samples.

Harmon's (2009b) study of a larger sample of proximal femora found the degree of size variation in the Sterkfontein sample to be consistent with that of a single species, being most similar to the distributions of modern humans and chimpanzees. Similarly, a study of 18 femoral heads – the most plentiful element from Sterkfontein (and Makapansgat) – by Grabowski et al. (2015) found a distribution that is indistinguishable from that of modern humans, with an average estimate of some 30.5 kg.

While Harmon (2009b) claimed that some, but not all shape variables of the proximal femora from Sterkfontein showed more variation than her extant reference samples, the variables that she reported pertain to size rather than shape (i.e. femoral neck length as considered by her is a size variable because it was not corrected for femoral head size). She concluded that size variation among the Sterkfontein proximal femora is lower than that among *A. afarensis* homologues, whereas shape variation at Sterkfontein is greater. Harmon (2009b) noted that Stw 99 is phenetically "very similar" to Stw 598 from Jacovec Cavern in that both possess a longer neck in combination with a somewhat smaller head than other Sterkfontein femora.

3.3. Other analyses of the range of postcranial variation

In addition to the studies of the distal humerus proximal femur discussed above, other analyses have considered morphometric variation among the postcranial elements from Sterkfontein. In some instances, these have involved estimates of body size dimorphism; in other instances, the comparisons have been between upper and lower limb elements with a view to establishing whether there is evidence for a consistent pattern of intermembral proportions.

McHenry's (1992) study of hind limb joint size found a pattern consistent with a single species that exhibited moderate sexual dimorphism (e.g., *Pan troglodytes*). Plavcan's (2003) analysis also revealed body mass estimates for the Sterkfontein fossils that were consistent with a single species that displayed only slight to moderate dimorphism. As noted above, Harmon's (2009a, b) study of proximal femora found the degree of size variation in the Sterkfontein sample to be consistent with that of a single species, being most similar to the distributions of modern humans and chimpanzees, and Grabowski et al. (2015) found a distribution that is indistinguishable from that of modern humans. Similarly, W.L. Jungers (pers. comm.) has found a unimodal, if somewhat platykurtotic distribution of femoral head size for a somewhat larger sample that included estimates taken from acetabular diameters – the resultant average is smaller than any small-bodied modern human group (e.g., African and Andamanese pygmies and the Khoesan).

McHenry and Berger (1998) found evidence of relatively large upper compared to lower limb elements in the Sterkfontein assemblage. A more comprehensive study by Green et al. (2007) of fore- and hindlimb joint sizes found comfortable matches for the Sterkfontein bones within the ranges of humans and chimpanzees. Neither study found any evidence for more than a single species. The impression from these studies of morphometric variation is that there is little, if *any*, evidence to refute a single species hypothesis for the postcranial assemblage from Sterkfontein Member 4. In this regard, they are in keeping with the results of studies of morphometric variation in the large dental assemblage from this same deposit (e.g., Fornai et al., 2015; Grine et al., 2013; Moggi-Cecchi, 2003; Moggi-Cecchi and Boccone, 2007; Moggi-Cecchi et al., 2006).

4. Do other Sterkfontein repositories sample another species of *Australopithecus*?

As noted previously, three of the four issues that pertain to the question of the presence of more than a single species of *Australopithecus* at Sterkfontein potentially involve the issue of geochronological heterogeneity. In these instances, the questions relate to the derivation of fossils from the Member 4 Type Site deposit or from Member 5, the attribution of the hominin remains from the Silberberg Grotto, and the assignment of the fossils from the Jacovec Cavern.

As discussed above, the differentiation of Member 4 from Member 5 involves the question of whether the fossils – if they are seen to differ from others that are securely identified as coming from Member 4 – might represent *Homo* rather than *Australopithecus*.

The issues that relate to the fossils from the Silberberg Grotto and Jacovec Cavern are almost certainly colored to some degree by the possibility that they substantially predate those from Member 4. A single hominin specimen in known from the Silberberg Grotto, and five postcranial elements have been recovered from Jacovec Cavern (Table 3).

4.1. The Silberberg Grotto skeleton

A single hominin specimen, Stw 573, is known from the Silberberg Grotto (formerly known as the Daylight Cave). The skeleton was discovered *in situ* in 1997, following the description of the foot bones by Clarke and Tobias (1995). Assessment of Stw 573 involves not only its morphology, but also its geochronological relationship to specimens from Member 4. In the first instance, let us consider its geochronological age, which has been a matter of prolonged discussion and debate, with proposal ranging from

Table 3
Postcranial elements from the Silberberg Grotto and Jacovec Cavern.
Tableau 3
Éléments post-crâniaux de la grotte de Silberberg et de la caverne de Jacovec.

Silberberg Grotto	
Element	Specimen number
Various associated bones	Stw 573
Jacovec Cavern	
Element	Specimen number
Axial skeleton	
Lumbar vertebra	Stw 600 (5^{th})
Femur	
Proximal	Stw 598
Clavicle	Stw 606
Humerus	
Distal	Stw 602
Manus	
Manual Phalanx	Stw 605

1.07 Ma (Berger et al., 2002) to 4.17 Ma (Partridge et al., 2003).

This specimen derives from a deposit designated as Member 2 (Partridge and Watt, 1991), which was initially argued to be considerably older than the Member 4 Type Site breccia (Clarke, 2008; Clarke and Tobias, 1995; Muzikar and Granger, 2006; Partridge et al., 1999, 2000, 2003). In large measure, this was inferred from the depth of the Silberberg Grotto in relation to the Type Site deposit (Protsch von Zieten and Clarke, 2003). Initially, Clarke and Tobias (1995: 522) surmised that "Member 2, which is much deeper and older than Member 4. . . could not be less than 3.0 million years ago (Ma) and is more likely about 3.5 Ma." In this, they followed Partridge (pers. comm.), who argued that Member 3, which overlies Member 2 is "of considerable thickness (averaging about 6.5 m)," and that "it is probable that Member 4 predates 2.6 Ma" (Clarke and Tobias, 1995: ref. # 27). Thus, the comparative antiquity of Stw 573 and the Member 2 breccia was inferred from its presumed stratigraphic depth below the base of Member 4, with an estimated faunal age of ca. 2.7–2.5 Ma. Partridge et al. (1999) later stated that a minimum of 10 m separated the Stw 573-bearing Member 2 talus cone from Member 4; Protsch von Zieten and Clarke (2003) gave a figure of 19 m. Protsch von Zieten and Clarke (2003) elaborated further that since the skull of Stw 573 was sealed beneath a thick travertine that separates Members 2 and 3, and Member 3 has a depth of 6.5 m, a "great span of time" must have elapsed between Member 4 and Member 2.

The fauna from the same stratigraphic unit (Member 2) that produced Stw 573 in the eastern end of Silberberg Grotto includes a number of primate taxa which, together with carnivores, dominate the assemblage (Pickering et al., 2004). With the possible exception of the hunting hyaena, *Chasmapothetes nitidula,* which Turner (1997) observed to have affinities with the Pliocene species *C. australis* from Langebaanweg (primarily owing to the presence of a metaconid on the carnassial), none of the other species identified thus far appear to differ from those recovered from Member 4. Indeed, the presence of *C. nitidula* in Member 4 and especially at Swartkrans (Berger et al., 2002; Turner, 1997) would appear to negate its use by Clarke (1998, 2002), Partridge et al. (1999) and Protsch von Zieten and Clarke (2003) to suggest considerable antiquity. McKee (1996) noted that all the faunal species from Member 2 occur in Member 4 but that some are absent from Makapansgat Member 3, which indicated to him that Member 2 does not appear to be as old as Makapansgat Member 3 (at ca. 3.0 ma), but "falls closer in time" to Sterkfontein Member 4 (at ca. 2.6–2.5 Ma) – he placed it as later than Taung and Makapansgat and "just prior" to Sterkfontein Member 4. Tobias and Clarke (1996) took issue with the temporal sensitivity of some of the taxa employed by McKee in his seriation, and observed that the absence of taxa from Makapansgat may be related to ecological and/or taphonomic issues rather than time. As noted above, Berger et al. (2002) argued that the Sterkfontein Member 4 fauna indicated a time range of 2.5–1.5 Ma, and in an unexplained leap of logic, proclaimed that the minimum "bracketing" age for Stw 573 "should be set at 1.5 Ma (Berger et al., 2002: 194)." They go on to state that this specimen "may be as young as 1.07–1.95 Ma (Berger et al., 2002: 195)." These age estimates have been soundly criticized by Clarke (2002).

Given the apparent silence of the fauna as to the age of Member 2 in the Silberberg Grotto, other methods, including magnetostratigraphy, U–Pb dating of speleothems, and the use of cosmogenic nuclides have been applied in attempts to ascertain the geochronology of this deposit.

The Stw 573 skeleton is sandwiched among four thin flowstone layers that are interbedded conformably within the deposits that constitute the debris cone, with a fifth speleothem layer that comprises Unit A of Member 3 (Partridge, 2000) some 4 m above it. Partridge et al. (1999) analyzed core samples from these five flowstones and recorded a series of reversed and normal signals. These were interpreted by Partridge et al. (1999) as indicating an age of between 3.58–3.22 Ma (i.e. between the Mammoth subchron [C2An.2r] and the Gauss chron [C2An.3n] above it) for the skeleton. These dates were further refined by Partridge et al. (2000: 112), who placed Stw 573 more precisely between 3.33–3.30 Ma. Herries and Shaw (2011) proclaimed the paleomagnetic results obtained by Partridge et al. (1999) to be invalid as they were influenced by recent overprinting resulting from mining activity; they argued that the "short" normal polarity observed in the flowstone that caps Ste 573 correlates rather with the Réunion or even the Huckleberry Ridge events at 2.16 or 2.04 Ma. This, of course, speaks to the uncertainty that surrounds palaeomagnetic correlations – especially those based on stratigraphically very limited samples from karst caves.

Cosmogenic nuclide age determinations of 3.78 and 4.72 Ma for two cave wall sediment samples that bracketed the skeleton, and an age of 4.17 ± 0.14 Ma for a sample adjacent to Stw 573 were taken to confirm the antiquity of the specimen (Partridge et al., 2003). However, Partridge et al. (2003: 608) noted that this age exceeds the earlier paleomagnetic estimate of Partridge et al. (1999) by "nearly four standard errors of analytical uncertainty and 1.7 standard errors in absolute age uncertainty." As a result, they concluded that the previous matching of reversals in the Silberberg Grotto with the geomagnetic

polarity time scale was incorrect, and that the Sterkfontein sequence had been placed two reversals too young. This speaks to the uncertainty that surrounds palaeomagnetic correlations – especially those based on limited samples from karst caves. Although it was not commented upon by Partridge et al. (2003), it is rather worrisome that the $^{26}Al/^{10}Be$ burial ages they obtained from above and below the skeleton are chronostratigraphically inverted.

Subsequent U–Pb determinations for these same flowstones suggested a much younger age for the skeleton (Herries and Shaw, 2011; Pickering and Kramers, 2010; Walker et al., 2006). In particular, the U–Pb determinations suggested ages of 2.2 Ma (Walker et al., 2006) and 2.35 Ma (Pickering and Kramers, 2010), which would make it contemporaneous with the specimens from Member 4. This date would correspond to the faunal age estimate provided by Berger et al. (2002). In concert with him, Herries and Shaw (2011) interpreted the paleomagnetic excursion in a flowstone overlying the skeleton as representing the Réunion at 2.16 Ma. Coupled with reversed polarity for the sediments below Stw 573, they determined that the fossil must postdate 2.58 Ma. Once again, supposed palaeomagnetic excursions can seemingly be tied into any date framework determined by other methods. Paleomagnetism, of course, can magically support either 3.3 Ma or ca. 2.2 Ma for the specimen.

Bruxelles et al. (2014) provided evidence indicating that the speleothems that were dated by Walker et al. (2006) and Pickering and Kramers (2010) and examined by Herries and Shaw (2011) significantly postdate the breccia that encases the skeleton, thus calling into question the previous age determinations that relied on interpretations of the flowstones and their purported penecontemporaneity with Stw 573. Indeed, Pickering and Kramers (2010: 84) had themselves observed that these "dated carbonates represent late fracture fills," but nevertheless concluded that the deposits, the fossil and the flowstones accumulated rapidly around 2.2 Ma.

Employing $^{26}Al/^{10}Be$ decay in quartz within the sediments that encase Stw 573, Granger et al. (2015) determined an age of 3.94 Ma for the skeleton. Kramers and Dirks (2017a), however, calculated a maximum age for Stw 572 of 2.8 Ma based on data published by Granger et al. (2015) that entails a two-stage burial scenario with re-deposition and mixing of sediment that had previously collected in and eroded from an upper chamber into the Stw 573 catchment. Kramers and Dirks (2017a, b) observed that their scenario provides an age that is not in conflict with the faunal estimate and U–Pb results that are concordant with an age equivalent to Member 4, and that this scenario might explain the inverse order of the two cosmogenic burial ages reported by Partridge et al. (2003).

Stratford et al. (2017), however, have argued that such a two-stage burial scenario in unsupported by any geological evidence. Moreover, it does not account for the largely concordant, independent cosmogenic age determinations of 4.17 Ma and 3.94 Ma obtained by Partridge et al. (2003) and Granger et al. (2015), and nor does it account for the largely concordant with the $^{26}Al/^{10}Be$ ages of 4.02–3.76 reported by Partridge et al. (2003) for the Member 2 deposits in Jacovec Cavern.

Partridge et al. (2003) obtained a cosmogenic nuclide ($^{26}Al/^{10}Be$) age of 4.02 ± 0.27 Ma for the "orange sandy" deposit from which Stw 578 and the other hominin fossils derived, and a somewhat younger estimate for a later, weakly calcified brown deposit of 3.76 ± 0.26 Ma.

Subsequent U–Pb dates and palaeomagnetic determinations for these same flowstones suggested a much younger age for the skeleton (Herries and Shaw, 2011; Pickering and Kramers, 2010; Walker et al., 2006). In particular, the U–Pb determinations suggested an age closer to 2.2 Ma for Stw 573 (Pickering and Kramers, 2010; Walker et al., 2006), which would make it contemporaneous with the specimens from Member 4. This date would correspond to the faunal age estimate provided by Berger et al. (2002). In concert with this date, Herries and Shaw (2011) reported a single short geomagnetic field event in a flowstone overlying the skeleton, which they suggested to represent the Réunion at 2.16 Ma; coupled with reversed polarity for the sediments below Stw 573, they determined that the fossil must postdate 2.58 Ma. Once again, supposed palaeomagnetic excursions can seemingly be tied into any date framework determined by other methods. Palaeomagnetism, of course, can magically support ages of either 3.3 Ma or ca. 2.2 Ma for the specimen. Indeed, this 'sequence' could be employed to support a date of ca. 1.0 Ma for Stw 573 if the reversed event is instead correlated with the Jaramillo!

Bruxelles et al. (2014) provided evidence indicating that the speleothems postdate the breccia that encases the skeleton, thus calling into question the previous age determinations that relied on interpretations of the flowstones and their purported penecontemporaneous association with the skeleton. Employing the radioactive decay of $^{26}Al/^{10}Be$ in quartz taken from the sediments that encase Stw 573, Granger et al. (2015) determined an age of 3.94 Ma for the skeleton.

Kramers and Dirks (2017a), however, calculated a maximum age for Stw 572 of 2.8 Ma based on data published by Granger et al. (2015) for chert samples recovered from the encasing breccia. This entails a two-stage burial scenario with re-deposition and mixing of sediment that had previously collected in and eroded from an upper chamber into the Stw 573 catchment. Kramers and Dirks (2017a) observed that this result does not conflict with the faunal and U–Pb studies. Stratford et al. (2017) have argued that the two-stage burial scenario is unsupported by geological evidence, but failed to present any evidence contradicting the chert data employed by Kramers and Dirks (2017a). In a response, Kramers and Dirks (2017b) provided rebuttals to the points raised by Stratford et al. (2017), and noted that the two-stage burial scenario might explain the inverse order of the three U–Pb burial ages reported earlier by Partridge et al. (2003).

Undoubtedly, the geochronological age of Stw 573 will continue to be a subject of debate, but as reported by Bruxelles et al. (2014) and Stratford et al. (2017), the stratigraphic details appear to support an age for the Stw 573-bearing sediments that is considerably older than Member 4, which is consistent with the cosmogenic burial isochron data of Granger et al. (2015). There is little to support the conclusion reached by Herries et al. (2013) that the

Silberberg Grotto (and the Jacovec Cavern) hominin fossils were deposited between 2.6 and 2.0 Ma.

Nevertheless, the outcome of these discussions about the geochronological age of the Stw 573 skeleton should not influence decisions pertaining to its species identity attribution.

What of the morphology of the skeleton? Unfortunately, this remains virtually unknown.

Despite the passing of nearly two decades since the discovery of Stw 573, its morphology is still largely undescribed. More attention has been paid to the cranium, although it, too, is largely undisclosed save for references in which Clarke (2008) attributed it to *Australopithecus prometheus*, drawing favorable comparisons to the Stw 252 and Stw 505 crania in terms of its robust zygomatic arch, lack of supraorbital thickening, and the presence of a small posteriorly restricted sagittal crest. Recently, Beaudet et al. (2019a) examined the endocast of Stw 573 and determined that it falls within the range of size and morphological variation displayed by other *A. africanus* specimens. Beaudet et al. (2019b) reported upon the structure of the bony labyrinth of this specimen but were unable to differentiate it from the variation exhibited by other *Australopithecus* specimens from Sterkfontein and Makapansgat.

Apart from a preprint that has been made available very recently by Heaton et al. (2018) in which the bones of the arm, forearm, thigh and leg are described, and their proportions (brachial, crural and intermembral indices) examined, the only elements to have been described and analyzed in any detail are the bones of the left foot and the right lateral cuneiform. The remainder of the postcranial skeleton has been afforded only brief mention by Harmon (2009b) and Clarke (2013). As noted above, Harmon (2009b) considered the Stw 99 proximal femur to be phenetically "very similar" to that of Stw 598 in possessing a longer neck in combination with a somewhat smaller head than other Sterkfontein homologues. Clarke (2013) offered the following observations on Stw 573: 1) the hand is proportioned as a modern human with a long thumb relative to the palm and fingers, 2) the manual phalanges show "strong" curvature, 3) the "arm" (presumably meaning upper limb rather than the humerus) is approximately of equal length to that of the "leg" (presumably meaning lower limb rather than the tibia) unlike relatively long-armed apes and relatively long-legged humans, and 4) the scapula has "some human-like and some ape-like features."

A highly mobile, medially divergent first metatarsal was inferred for the foot of Stw 573 by Clarke and Tobias (1995). However, the ape-like nature of this hallucial tarsometatarsal joint has been refuted by several studies, including those that have employed sophisticated morphometric analyses and substantially larger comparative hominoid samples (Harcourt-Smith and Aiello, 2004; Kidd and Oxnard, 2005; McHenry and Jones, 2006; Stern, 2000; R.L. Susman, pers. comm). Indeed, Proctor (2010) has shown that the base of the second metatarsal of Stw 573 is more human-like than that of Stw 89 from Member 4.

Heaton et al. (2018) detail a number of morphological features of the long bones of Stw 573, but do not undertake direct comparisons with homologous elements from Sterkfontein member 4. Thus, for example, they describe the tibia of Stw 573 as displaying several primitive morphological retentions, such as the absence of a clear soleal line, an ape-like interosseous border and a trapezoidal tibiotalar facet, but do not compare these features to the morphologies exhibited by other Sterkfontein tibiae. As such, do not address the issue of postcranial variation and the possibility of species differences among the *Australopithecus* fossils at the site.

While Stw 573 may show a mosaic of ape-like and derived human-like features or even a unique (intermediate) pattern of proportions, this is hardly unexpected for the postcranial skeleton of *Australopithecus africanus* (Green et al., 2007; McHenry, 1975; Toussaint et al., 2003). The purportedly abductable big-toe, which has been a cornerstone in differentiating Stw 573 from *A. africanus*, would seem to have been less decidedly divergent than originally proposed. What must be guarded against is the natural tendency to let the *possible* antiquity of Stw 573 color its perceived morphology vis-à-vis the australopith fossils from Member 4.

4.2. Postcranial remains from Jacovec Cavern

Another group of Sterkfontein fossils that is stratigraphically separated from the Type Site assemblage derives from the Jacovec Cavern.[2] An adult hominin cranium (Stw 578) was recovered in an "orange sandy breccia" that is preserved as a hanging remnant on the ceiling of the eastern end of the cave (Clarke, 2006, 2013; Partridge et al., 2003). Partridge (1978, 2000; Partridge and Watt, 1991) described this breccia as comprising part of Member 2. The eastern chamber of the cavern has recently been referred to as the "Thulasizwe Chamber" (Mavuso, 2017). Six additional cranial fossils and five postcranial specimens representing a minimum of six individuals – three adults and three juveniles – are currently known from this repository (Kibii, 2007; Partridge et al., 2003; Reynolds and Kibii, 2011).

All of the fossils seemingly derive from the an "orange sandy breccia" that is preserved as a hanging remnant on the ceiling of the cave. Partridge (1978, 2000; Partridge and Watt, 1991) described this breccia as comprising part of Member 2. Partridge et al. (2003) obtained a cosmogenic nuclide age of 4.02 ± 0.27 Ma for this deposit, which had been described by Partridge (1978, 2000; Partridge and Watt, 1991) as comprising part of Member 2.

There are other fossiliferous deposits in Jacovec Cavern, including a weakly calcified brown deposit. Although Partridge et al. (2003) regarded this as being somewhat younger than the "orange sandy breccia," Mavuso (2017) has argued that it is, in fact, older inasmuch as there are

[2] Spelling of this cavern's name varies. It was initially called the "Terror Chamber" or "Terror Cave" by M.J. Wilkinson, and although this name was used by him, he more formally referred to it as Jakovec Cavern (Wilkinson, 1973, 1985). This spelling has been adopted by some (Herries et al., 2010; Pickering and Kramers, 2010). Jacovec is the spelling employed by most others (e.g., Clarke, 2006; Kibii, 2007; Martini et al., 2003; Partridge and Watt, 1991; Partridge et al., 2003), including those who have been in charge of its excavation.

inclusions of the "brown breccia" deposits at the erosive base of the "orange breccia" deposit.

Partridge et al. (2003) published a somewhat younger estimate for this deposit of 3.76 ± 0.26 Ma, but there is considerable overlap in the cosmogenic nuclide dates for the two. Reynolds and Kibii (2011) have noted the presence of *Equus* fossils from this cave, which indicates the presence of even younger (< 2.4 Ma) deposits. While Herries et al. (2013) prefer to interpret the presence of *Equus* among the Jacovec Cavern fauna as indicating contemporaneity of the hominin fossils with Member 4, it is much more likely that Jacovec, like Milner Hall and other of the subterranean cavities at Sterkfontein record complexes of earlier and later infillings. *Equus* need not have been contemporary with the Stw 578 infill.

Partridge et al. (2003) drew a favorable comparison between frontal bones of the Jacovec Cavern partial cranium (Stw 578) and Stw 252, but observed that in its strongly sloping tympanic, Stw 578 "differs from all other *Australopithecus* temporals from Member 4." Beaudet et al. (2018) note that while Stw 578 has not been formally attributed to a particular species, it is similar to other Sterkfontein crania (e.g., Sts 5 and Sts 71) in exhibiting an absolutely and relatively thick cranial vault and a high proportion of diploë.

With regard to the five postcranial bones from Jacovec Cavern (Table 3), Partridge et al. (2003) discussed the morphologies of the proximal femur (Stw 598) and distal humerus (Stw 602) in relation to other Sterkfontein homologues, but were most impressed by the chimpanzee-like configuration of the clavicle (Stw 606) in relation to other Sterkfontein and Hadar elements.

Thus, Partridge et al. (2003) observed that the Jacovec proximal femur (Stw 598) has a much longer neck than one other Sterkfontein homologue with a similar-sized head (Stw 522), although they noted that at least one other specimen from Member 4 (Stw 99) possesses a neck of comparable relative length to Stw 598. They took this as suggesting that "two different forms of *Australopithecus* might be represented by the Sterkfontein femurs" (Partridge et al., 2003: 611). On the other hand, Harmon (2009b) found that the inclusion of Stw 598 does not increase the CV for the Sterkfontein sample with regard to the dimensions of either the head or neck. Indeed, her comparisons drew similarities between Stw 99 and Stw 573 from Silberberg Grotto rather than with the Jacovec Cavern specimen.

Partridge et al. (2003) noted that the Stw 602 distal humerus has some similarity to that of Stw 431 from Member 4, but with a "more flattened shaft." Variation in the anteroposterior flatness of the distal diaphysis was employed by Susman et al. (2001) to differentiate among humeri from the site of Swartkrans, and Lague (2014, 2015) has demonstrated that the shape of the distal diaphysis just proximal to the olecranon fossa has utility for taxonomic identification. The morphometric analyses undertaken by Lague (2014, 2015), in which coordinate landmarks were placed on 3D laser scans to quantify cross-sectional shape, have demonstrated differences between *Paranthropus* and *Homo*, and have served to question some of the attributions proposed by Susman et al. (2001). Perhaps most importantly, Lague (2015) has provided further documentation of a high degree of postcranial diversity in early *Homo*. Unfortunately, having been denied access to the Stw 602 humerus, the only specimen from Sterkfontein included by Lague (2015) is Stw 431.

Lague and Menter (2019), though still unable to gather cross-sectional data for the distal diaphysis of Stw 602, were able to record 2D landmark data from published photographs of the joint surfaces of this specimen. With respect to elbow joint morphology, Stw 602 is quite similar to Stw 431 (and both are similar to the elbow of MH 2). These specimens are rather distinct from other australopiths such as *A. afarensis* and *A. anamensis* (Lague and Menter, 2019). Thus, the two specimens from Sterkfontein Member 2 and Member 4 are similar to one another (and to *A. sediba*), but distinctive in the same way from the distal humeri of other *Australopithecus* species. Unfortunately, none of the other five distal humeri from Sterkfontein preserve articular morphology.

With reference to the Stw 606 clavicle, Partridge et al. (2003) were struck by its flange-like conoid tubercle (the attachment for the conoid ligament, which binds the clavicle to the coracoid process of the scapula), and its strongly angled shaft and curved superior surface. They saw these features contributing to its resemblance to the chimpanzee collar bone and its difference from human clavicles. They noted that a human-like morphology is evident in the three *Australopithecus* clavicles from Sterkfontein Member 4 (Stw 431, Stw 582 and Stw 616), as well as the two Hadar clavicles of *A. afarensis*. Since Clarke (2013) subsequently stated that Stw 606 is more ape-like than either *A. afarensis* or *A. africanus*, it would seem that he regards all three clavicles from Member 4 as belonging to the latter. It is not clear whether he attributes the Jacovec clavicle to *A. prometheus* or some other taxon. Harmon (2009), however, has cautioned that the small sample of chimpanzee clavicles (n = 7) employed by Partridge et al. (2003) in their description of Stw 606 precludes certainty in their assessment of its ape-like nature.

Most recently, Pickering et al. (2019) have described a proximal manual phalanx (Stw 605), an intermediate manual phalanx (Stw 620) and a metacarpal head (Stw 673) recovered from Jacovec Cavern. Their comparisons revealed no notable differences from other Sterkfontein (Member 4) homologues.

Most of the comparisons to date suggest that the Stw 578 cranium and dentition as well as the other Jacovec specimens are comparable with *A. africanus*. However, because none of these fossils has yet to be fully described and satisfactorily analyzed in the intervening 15 years since their announcement, it would be premature to ascribe them to this or any other hominin species. If they are, indeed, attributable to *A. africanus*, they would deepen its first appearance datum by a considerable margin.

5. Postcranial fossils and australopith diversity at Sterkfontein

Although the question of whether the hominin fossils from Sterkfontein Member 4, the Silberberg Grotto and Jacovec Cavern attest to the presence of more than

one australopith species has centered on the craniodental remains, postcranial bones have featured in these discussions. The potential existence of two partially or wholly contemporaneous and presumably sympatric species of *Australopithecus* in the Member 4 deposit is not wholly unreasonable given the apparent contemporaneity of australopiths in eastern Africa. Thus, *Paranthropus aethiopicus* and *Australopithecus garhi* are known from Ethiopia at ca 2.5 Ma (Asfaw et al., 1999), and it has been proposed recently that *Australopithecus afarensis* and *A. deyiremeda* were contemporaries in the Afar between 3.5–3.3 Ma (Haile-Selassie et al., 2015). In the present context, it is noteworthy that although craniodental morphology has been used to define *A. deyiremeda*, probably the best evidence for the existence of a second species that was contemporaneous with *A. afarensis* in the Afar takes the form of the foot from Burtele (Haile-Selassie et al., 2012). Similarly, the contemporaneity of early species of *Homo* in the Turkana Basin – for example, *Homo habilis* and *Homo rudolfensis* – is well-documented (Leakey et al., 2012; Spoor et al., 2015).

Thus, there is no reason to deny *a priori* the plausibility that two synchronous and sympatric hominin species are represented in the fossil assemblage from Sterkfontein, and several workers have suggested that there might be evidence for more than one form or taxon based on craniodental morphology (Grine, 2013). At the same time, however, there is a notable lack of agreement among them as to the sorting of these fossils (Grine, 2013). Of course, similar disagreements over hypodigm membership have also dogged interpretations of the early Pleistocene *Homo* fossils from Kenya and Tanzania, especially as pertaining to the relationships among specimens such as OH 7, OH 13, OH 16, OH 24, KNM-ER 1470, KNM-ER 1805, KNM-ER 1813 and KNM-ER 1802 (e.g., Chamberlain, 1987, 1989; Clarke, 2012; Groves, 1989; Leakey et al., 2012; Rightmire, 1993; Stringer, 1986, 1987; Tobias, 1991; Wood, 1991a,b, 1992). Nevertheless, much of the craniodental evidence that has been put forward in support of the taxonomic heterogeneity of the Sterkfontein australopith assemblage has been in the form of subjective, anecdotal observations related to specimens that are variably incomplete and/or distorted. It is perhaps particularly noteworthy that the existence of two australopith taxa at Sterkfontein has not gained support from quantitative studies of the dental remains where appropriate statistical analysis of variation have been employed (e.g., Calcagno et al., 1999; Fornai et al., 2015; Grine et al., 2013; Moggi-Cecchi, 2003; Moggi-Cecchi and Boccone, 2007).

The same critique would seem to apply to the postcranial evidence that has been cited in support of taxonomic heterogeneity. There may be hints of possible functional variance that are reflected in discrete morphological differences between some elements, such as the proximal tibia, the hallucial and second metatarsals, and the clavicle, but there has not been universal agreement about the morphological differences expressed by these bones. Studies that have incorporated multiple postcranial elements (e.g., the distal humerus and proximal femur) have seemingly failed to identify discrete morphological groups among them.

The question of taxonomic heterogeneity within the Sterkfontein hominin assemblage also involves the issue of the stratigraphic derivation of the bones. In some instance, it is open to question as to whether they are from Member 4 or from Member 5; the latter invokes the possibility that the fossils are attributable to *Homo* rather than *Australopithecus*. In other instances, the spatial dissociation of the fossils in repositories such as the Silberberg Grotto and Jacovec Cavern from those in the Type Site deposit have involved the issue of geochronological separation. Those few observations that have been made comparing elements among these repositories have been of a qualitative and subjective nature, and it is difficult to ascertain their validity in the absence of detailed morphological descriptions of the specimens from the Silberberg Grotto and Jacovec Cavern.

6. Conclusions

The possibility that the *Australopithecus africanus* hypodigm is taxonomically heterogeneous is significant for hominin paleontology because of the pivotal role that this species has played in discussions about human evolution.

Australopithecus africanus has been seen to occupy a variety of phylogenetic roles, and this uncertainty is likely owing to the fact that it is variable in a number of craniodental features. This variability has led to questions about the taxonomic homogeneity of the *A. africanus* hypodigm. The possibility that more than one australopith species is represented by the fossils from Sterkfontein Member 4 (and from Makapansgat) has been a topic of discussions, which have been dominated by the evidence afforded by the craniodental fossils. There are several instances in which the postcranial bones from these same deposits have been invoked. It has also been posited that postcranial remains from other repositories within the Sterkfontein cave system – the Silberberg Grotto and Jacovec Cavern – attest to a species of *Australopithecus* that differs from *A. africanus*.

There may be hints of possible functional differences that are reflected in discrete morphological differences between a few elements – these have been described for the proximal tibia, the hallucial and second metatarsals, and the clavicle. However, there has not been universal agreement about the morphological differences expressed by these bones. Moreover, the derivation of several – whether they are from Member 4 or from Member 5 is open to question. If they are from Member 5, this involves the possibility that they are attributable to *Homo* rather than *Australopithecus*.

Most of the comparative observations that have been made among the postcranial elements from Sterkfontein have been of a qualitative and subjective nature. In this, the postcranial evidence that has been cited in potential support of taxonomic heterogeneity reflects the craniodental observations for such disparateness. Analyses that have employed quantitative assessments of variability have not yielded results that are necessarily consistent with the hypothesis of australopith taxonomic heterogeneity at Sterkfontein.

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