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The *Australopithecus* assemblage from Sterkfontein Member 4 (South Africa) and the concept of variation in palaeontology

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Abstract

Interpreting morphological variation within the early hominin fossil record is particularly challenging. Apart from the fact that there is no absolute threshold for defining species boundaries in palaeontology, the degree of variation related to sexual dimorphism, temporal depth, geographic variation or ontogeny is difficult to appreciate in a fossil taxon mainly represented by fragmentary specimens, and such variation could easily be conflated with taxonomic diversity. One of the most emblematic examples in paleoanthropology is the *Australopithecus* assemblage from the Sterkfontein Caves in South Africa. Whereas some studies support the presence of multiple *Australopithecus* species at Sterkfontein, others explore alternative hypotheses to explain the morphological variation within the hominin assemblage. In this review, I briefly summarize the ongoing debates surrounding the interpretation of morphological variation at Sterkfontein Member 4 before exploring two promising avenues that would deserve specific attention in the future, that is, temporal depth and nonhuman primate diversity.

KEYWORDS

anagenesis, Cradle of Humankind, early hominins, morphological variation, Plio-Pleistocene

1 | SOUTH AFRICA, THE HISTORICAL BIRTHPLACE OF THE GENUS AUSTRALOPITHECUS

Southern Africa has played a crucial role in the search for human origins. The discovery of the Taung child in 1924 by Raymond Dart¹ was the first evidence of early hominin evolution on the continent that supported Darwin's prediction that Africa was where humans originated.² Dart erected a new genus and species, *Australopithecus africanus*, to accommodate the new fossil specimen, which preserves the face, mandible, and natural endocast (i.e., the replica of the inner surface of the braincase¹). Since then, over a thousand fossil hominin remains have been discovered in southern Africa and attributed to *Australopithecus*. Among all the southern African hominin-bearing localities, the Sterkfontein Caves, situated in the "Cradle of

Humankind," UNESCO World Heritage Site, is the most prolific site with more than 800 *Australopithecus* remains unearthed since the initial discovery by Robert Broom in 1936.^{3,4} The Sterkfontein hominin fossil record includes exceptionally well-preserved *Australopithecus* specimens, such as the nearly complete cranium "Mrs. Ples" (Sts* 5; Figure 1) or "Little Foot" (StW** 573), the most complete *Australopithecus* skeleton yet found. The high density of the *Australopithecus* specimens at the Sterkfontein Caves, and more broadly in southern Africa, can be explained by the geological and depositional context. In southern Africa, nearly all early hominin specimens derive from underground deposits accumulated within deep dolomitic caves via avens that connect the caves to the land

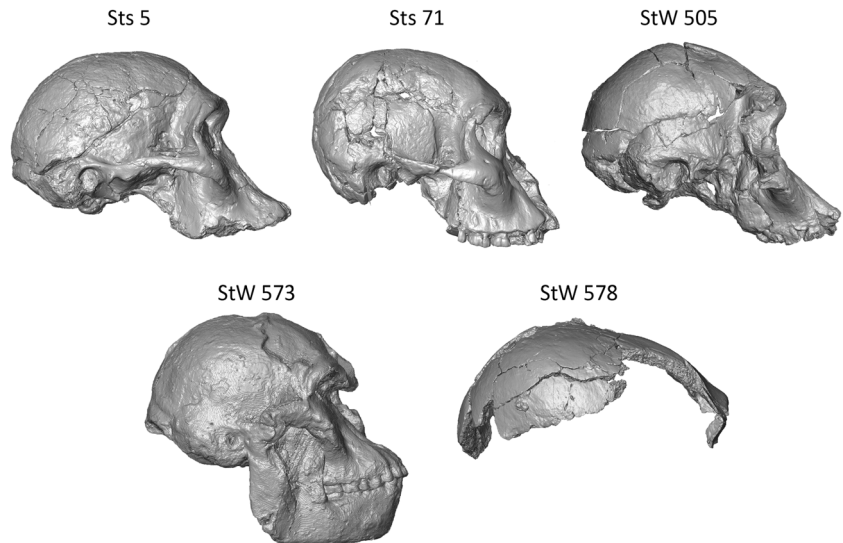
*Sts stands for "Sterkfontein" and refers to specimens found in the Type Site.

**StW stands for "Sterkfontein Wits" and refers to specimens found after 1966⁴

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FIGURE 1 Virtual renderings of the *Australopithecus* specimens Sts 5, Sts 71, and StW 505 (Member 4), StW 573 (Member 2), and StW 578 (Jacovec Cavern). StW 505 has been mirrored



surface (rev. in⁵⁻⁷). Large carnivores, death trap, and slope wash were likely key factors in the accumulation of the hominin assemblages.⁸⁻¹⁰ Once underground, specimens were buried in talus deposits cemented with calcite into hard breccias and largely protected from the exposure and erosion taking place on the surface.

Besides the relatively high density and sometimes excellent preservation of the fossil remains, the fossiliferous deposits of the Sterkfontein Caves document a substantial period of time (¹¹⁻¹⁷; rev. in¹⁸). The Sterkfontein Formation¹² is composed of six stratigraphic units identified as Members (rev. in¹⁹). Among the six Members, Members 2, 4, and 5 have provided hominin remains. Member 4 has been exposed on the land surface following erosion of the cave roof. This Member was excavated by Robert Broom and John Robinson in the late 1940s and then Philip Tobias and Alun Hughes beginning in 1966²⁰ (rev. in⁴). It has yielded most of the hominins from the site, all attributed to *Australopithecus* (¹⁹; but see also^{21,22}). A few hominin remains, assigned to *Homo* and *Paranthropus*, come from the more recent deposits of Member 5.²² In addition to the Sterkfontein Formation, there are two additional deeper localities—the Jacovec Cavern and Milner Hall—that have provided, respectively, *Australopithecus* and *Homo* remains.^{14,23-25} Deposits from Milner Hall consist of a mixture of sediments from Member 2 and Member 5 of the Sterkfontein Formation.²⁵

Cosmogenic radionuclide dating corresponding to the burial age based on the radioactive decay of the aluminium-26 and beryllium-10, provided an age of ca. 3.67 Ma for “Little Foot” and of 3.61 Ma for the fossiliferous deposits in the Jacovec Cavern.^{11,14,26} Absolute (i.e., U-Pb and U-Th) and relative (i.e., faunal correlations and ESR) datings applied to the fossiliferous deposits of Member 4 converge towards an age in between 2 and 2.6 Ma for the fossil assemblage^{15,27-32} while cosmogenic radionuclide datings indicate an age of 3.49-3.41 Ma for Member 4 and of 2.18 Ma for Member 5.²⁶ According to this chronological setting, Member 4, the most extensive Member of the Sterkfontein Formation, may have taken up to 600,000 years or more to accumulate.^{15,18} As such, this stratigraphic unit has been the focus of much attention during the last decades of research in palaeoanthropology and contributed to the

long-standing debate about one or more species at Sterkfontein. This review will thus focus primarily on Sterkfontein Member 4.

2 | VARIATION IN THE AUSTRALOPITHECUS ASSEMBLAGE OF STERKFORTEIN

2.1 | Historical comments and interpretations

The first adult *Australopithecus* specimen, TM*** 1511 was found in Member 4 (originally referred to as the “Type Site deposits”) and was initially assigned to a new species named *Australopithecus transvaalensis* (³; see Table 1 for a summary). However, upon further examination, Broom³³ considered the species distinct enough from the *A. africanus* type specimen (i.e., the Taung child) that he erected a new genus, *Plesianthropus*, for his Sterkfontein discoveries. The most famous specimen from these deposits, a complete cranium catalogued as Sts 5, was nicknamed “Mrs. Ples” on the basis of this generic distinction. Similarly, Dart³⁴ identified another species from the fossiliferous deposits of Makapansgat in South Africa, *Australopithecus prometheus*, based on MLD 1. However, later, scholars “lumped” the southern African *Australopithecus* specimens into the type species *A. africanus*.^{35,36}

Despite the consensus on the conspecificity of the *Australopithecus* specimens from Taung, Sterkfontein and Makapansgat, the growing *Australopithecus* sample from Sterkfontein Member 4 added to our understanding of variation within *A. africanus* (rev. in⁴), with scholars reporting a remarkably high degree of polymorphism within the enlarged *Australopithecus* Sterkfontein assemblage. How then to interpret this variability? Assessing the amount of variation in a fossil sample is essential for deciding if the specimens could be subsumed within a single species or if several species must be recognized. In the former case the degree of variation should be compatible with the interindividual pattern of

***TM stands for “Transvaal Museum” which is now the Ditsong National Museum of Natural History.

TABLE 1 Milestones in interpreting morphological variation within the southern African *Australopithecus* hypodigm

Key dates	Key specimens/material	Interpretations	Key references
1925	Taung child	Type specimen of <i>Australopithecus africanus</i>	Dart ¹
1936	TM 1511	First adult <i>Australopithecus</i> specimen; attributed to <i>Australopithecus transvaalensis</i>	Broom ³
1947	Sts 5 (Mrs Ples)	Attributed to <i>Plesianthropus transvaalensis</i>	Broom ³⁷
1948	MLD1	Type specimen of <i>Australopithecus prometheus</i>	Dart ³³
From 1954	Analyses of the southern African <i>Australopithecus</i> hypodigm	Lumped into <i>A. africanus</i>	Robinson ³⁴
1980s-present	Analyses of the <i>A. africanus</i> hypodigm	Polymorphism	Kimbel and White ³⁸ ; Ahern ³⁹ ; Lockwood and Tobias ⁴⁰ ; Haeusler ⁴¹ ; Toussaint et al. ⁴² ; Schwartz and Tattersall ⁴³ ; Moggi-Cecchi et al. ⁵ ; Ward and Zipfel ⁶
	StW 573 (Little Foot) and <i>Australopithecus</i> specimens from Sterkfontein Member 4	Presence of two <i>Australopithecus</i> species at Sterkfontein	Clarke ^{7,21,44,45,46,54} ; Clarke and Kuman ⁴⁷ ; Fornai et al. ⁴⁸

variation observed within extant species, while in the latter the degree of variation should exceed the interindividual variation observed within extant species. The Sterkfontein Member 4 fossil assemblage has thus been the focus of sometimes intense debate between scholars defending either the single- or multiple-species hypotheses.

If we consider the past and ongoing debates on the fossils recovered from Sterkfontein Member 4 [Grine^{49,50} thoroughly reviewed craniodental and postcranial evidence from the southern African paleontological sites that would support the presence of one or more species in the *A. africanus* hypodigm] it is noteworthy that most of the studies acknowledged substantial morphological variation. For example, Kimbel and White³⁸ noticed a high degree of dental (i.e., bimodal distribution of the buccolingual diameter of the upper second molars) and craniofacial (i.e., identification of gracile and robust individuals) variability in *A. africanus* and mentioned the possibility of a temporally mixed sample. Later on, Lockwood and Tobias⁴⁰ observed a high degree of polymorphism in the assemblage and noticed a mosaic of cranial characters, with some features (e.g., incipient maxillary trigon, rounded lateral portion of the inferior orbital margin, orientation of the posterior petrosal surface) showing strong affinities with “robust” early hominin taxa (i.e., *Paranthropus* species) from eastern and southern Africa, and others that were human-like. They recognized “the possibility that more than one hominin species may be present in the sample of fossils from Member 4 of Sterkfontein, that some of the specimens described may not represent *A. africanus*.”^{40,pp.444–445} Schwartz and Tattersall⁴³ subdivided the *Australopithecus* sample based on the degree of expression of the upper molar cingulum into up to 10 “morphs.” Yet, when Moggi-Cecchi et al.⁵ studied the variation of the dimensions of the permanent teeth of the fossil specimens from Member 4, they concluded that the degree of variation did not suggest the presence of a second species. Similarly, Ahern³⁹ argued that differences reported between species and used as an argument for an exceptionally high degree of morphological variation at

Sterkfontein, more particularly basicranial characters (e.g., inclination of the tympanic plate relative to the occlusal plane, absence/presence of a petrous crest, orientation of petrous relative to the sagittal plane, see Table 2 in³⁹ for a complete list of characters) did not exceed what is seen in extant chimpanzees.

On the other hand, some authors acknowledge the presence of a second *Australopithecus* species at Sterkfontein. Based on his study of the fossil specimens from Member 4 (in particular StW 252) and of the nearly complete *Australopithecus* skeleton from Member 2 (“Little Foot,” StW 573), Ron Clarke suggested that the fossil assemblage at Sterkfontein contains a “*Paranthropus*-like species of *Australopithecus*” (45,p.448) distinguished from *A. africanus* by a series of craniodental characters, including low bulbous cheek teeth, converging temporal lines that often join the sagittal crest, robust zygomatic arch, no metopic ridge and broad interorbital distance (see⁴⁷ for a more comprehensive list of diagnostic characters). A certain number of fossils from Member 4 (e.g., StW 252, Sts 71, StW 505), as well as StW 573 (Figure 1), were then allocated by Clarke to this second species identified as *A. prometheus*.^{7,21,44,45,47,54} Interestingly, the presence of *Paranthropus*-like cranial features were previously documented in the hominin assemblage from Makapansgat by Aguirre⁵⁵, who also came to the conclusion that a second *Australopithecus* species should have existed at the same time as *A. africanus* based on his observations of craniodental features (e.g., mandibular profile, size, and shape of the lower premolars and molars).

Postcranial remains have also been prominent in discussion of how to interpret variation in the Sterkfontein Member 4 hominins (rev. in⁵⁰; see also⁵⁶). Many authors see a mosaic of more ape-like and more modern human-like features of the postcranial elements (e.g., ape-like morphology of the tibia StW 514^{57,58}; human-like characters in the tibia StW 396⁴⁶; human-like and ape-like characters in the metatarsals StW 562 and StW 595, respectively;⁵⁹ differences reported in the second metatarsals StW 89 and StW 377⁶⁰; human-like and ape-like

features in the radii and ulnae of Member 4;⁶¹ identification of a human-like morph based on the humeri StW 150 and StW 182 and of a *Australopithecus-Paranthropus* morph that includes the humerus of StW 431,⁶²). Some interpret this as evidence for multiple (e.g.,⁴⁶) or single species,⁶ whereas others see it as inconclusive in that regard.^{60,62} Interpretations of the differences between the two partial skeletons, Sts 14 and StW 431, mainly focusing on the reconstruction of the pelvis, also differ, with some suggesting that the differences are consistent with variation within a single species,^{41,42} whereas others interpret the differences as evidence for multiple species in Member 4.⁴⁸

2.2 | Insights from the inside

With the gradual incorporation of high-resolution imaging techniques in paleoanthropological studies, new diagnostic features have become accessible that can noninvasively explore the fossil record of the Sterkfontein Caves. For instance, Fornai et al.⁶³ investigated the topography of the occlusal (OES) and enamel-dentine (EDJ) surfaces in the second lower molars of Member 4 using noninvasive 3D methods. Besides being the focus of many studies because of their abundance in the fossil record, teeth provide valuable taxonomic signals, in particular the surface in between the enamel and dentine (e.g.,⁶⁴). While the morphometric analysis of the OES and EDJ failed in discriminating *Australopithecus* from *Paranthropus*, thus being unable to falsify the hypothesis of a second *Paranthropus*-like *Australopithecus* species,⁴⁵ this study demonstrated the presence of a “morphological gradient” in terms of relative buccolingual and mesiodistal proportions of the marginal and occlusal ridges and the relative height of the dentine horns and cusps of the EDJs and OESs within the Sterkfontein *Australopithecus* assemblage.

More recently, Beaudet et al.^{23,65,66} developed a computer-assisted revision of the *Australopithecus* hypodigm of Sterkfontein Member 4 to report subtle variations in taxonomically and/or functionally informative cranial and postcranial features. The first series of papers aimed at noninvasively quantifying potential variation in the braincase, more particularly focusing on the close geometrical and biological relationships between the brain and the braincase.^{23,65,67,68} Indeed, diagnostic information could be retrieved from the cranial vault thickness, which has been widely used in the identification of fossil hominins, and in particular *Homo erectus* (e.g.,⁶⁹). These studies revealed a pattern of cranial vault inner organization and thickness (i.e., highly developed diploic bone combined with thick frontal bones and posterosuperior regions of the parietal bone) that was shared by the hominins from Member 4.⁶⁵ More specifically, the diploic bone in the cranial vault of the specimens Sts 5 and Sts 71 from Member 4 represent more than 80% of the total thickness. The cranial vault thickness ranges from 5.4 to 20 mm along a parasagittal cross-section when Sts 5, Sts 71, and StW 505 are considered, and from 4.4 to 8.5 along a coronal cross-section when Sts 5 and StW 505 are considered. This degree of variation is consistent with what is observed in extant humans and chimpanzees (Figure 2a–b). Moreover,

the brain endocast (i.e., replica of the inner surface of the braincase) was included in the past in the description of new hominin species (e.g.,¹). The shape and organization of the brain was demonstrated to be consistent across the Member 4 specimens, showing an overall ape-like condition, that includes a supero-inferiorly low and rostro-caudally elongated endocast and the presence of a fronto-orbital sulcus in the inferior part of the frontal lobes.^{66,68} Concerning the endocranial vascular system, while the middle meningeal vessel pattern reveals a certain degree of variability within the *Australopithecus* sample (but likely compatible with intraspecific variation if compared with later hominin groups,^{70,71}), the measurements of the carotid canal in the basicrania of specimens from Member 4 range from 8.1 to 19.0 mm² (if StW 53 is considered as coming from Member 4) and fit within the variation observed in extant chimpanzees (i.e., from 6.9 to 20.8 mm², see Figure 2c).^{67,68}

The second series of papers dealt with cranial and postcranial elements that have the potential to deliver locomotor-related signals, that is, the inner ear (the organ of balance) and the first cervical vertebra (or atlas).^{67,72} Locomotor behaviors as inferred from bony elements is of particular interest to describe the habitat and ecology of fossil primates, and, in some extent, niche partition.⁷³ The inner ear provided statistical evidence of significant variation within the *Australopithecus* sample (Figure 3a).⁷² This study suggested a high degree of polymorphism with a mosaic of *Paranthropus*-like (e.g., mediolaterally large and twisted posterior semicircular canal with loose turn in the apical portion of the cochlear), early *Homo*-like (e.g., mediolaterally small and straight lateral semicircular canal with an anteroposteriorly large posterior semicircular canal, and an extremely tight apical turn in the cochlea), ape-like (e.g., mediolaterally large, twisted lateral semicircular canal associated with a tight apical turn in the cochlea) and human-like (e.g., mediolaterally small and straight lateral semicircular canal with a long cochlear with a lower number of turns) characters, compatible with previous observations from postcranial elements (see Section 2.1). In this respect, extant human- and ape-like features found in the semicircular canal of the *Australopithecus* specimens (particularly the lateral one) would indicate a highly variable demand placed on head position and a potentially high degree of locomotor diversity within the hypodigm. Indeed, the lateral canal is known to be related to head movements in the transverse plane and morphological differences within the sample may indicate variation in terms of agility.⁷⁴ In addition to the inner ear, an incomplete atlas of a specimen from Member 4 could be compared to one *Australopithecus afarensis* atlas from Hadar, in Ethiopia, and the atlas of StW 573 (Figure 3b).⁶⁷ This study demonstrated potential diachronic variation, with the morphology of the partial atlas from Member 4 (Figure 3b) being more human-like (i.e., less vertically oriented articular facets) than the one of “Little Foot” that shared more similarities with the extant apes (i.e., overall dimensions, more vertically oriented articular facets, posteriorly oriented transverse processes, prominent anterior tubercle) and the specimen from Hadar.

In summary, studies of the external morphology and internal aspects of the fossil hominin remains at Sterkfontein were able to detect subtle but quantifiable variation. The fact that this variation is perceptible in

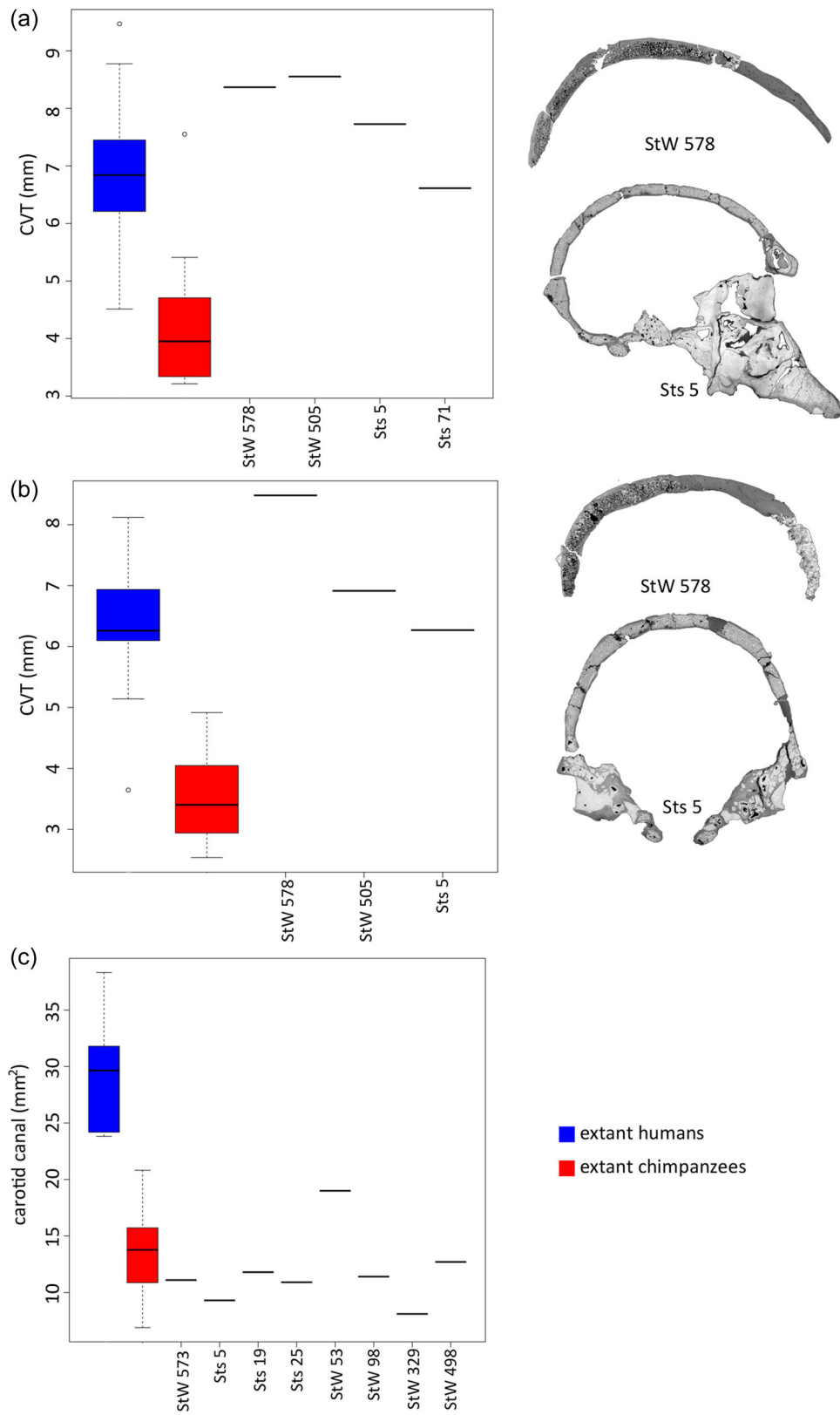


FIGURE 2 Boxplots of cranial vault thickness (CVT) in parasagittal (a) and coronal (b) sections and of cross-sectional areas of the carotid canals (c) in *Australopithecus* specimens from Sterkfontein in comparison to extant humans and chimpanzees. All of the *Australopithecus* specimens included in these studies come from Sterkfontein Member 4 except StW 573 (Member 2) and StW 578 (Jacovec Cavern). Modified from Beaudet et al. ^{65,67}

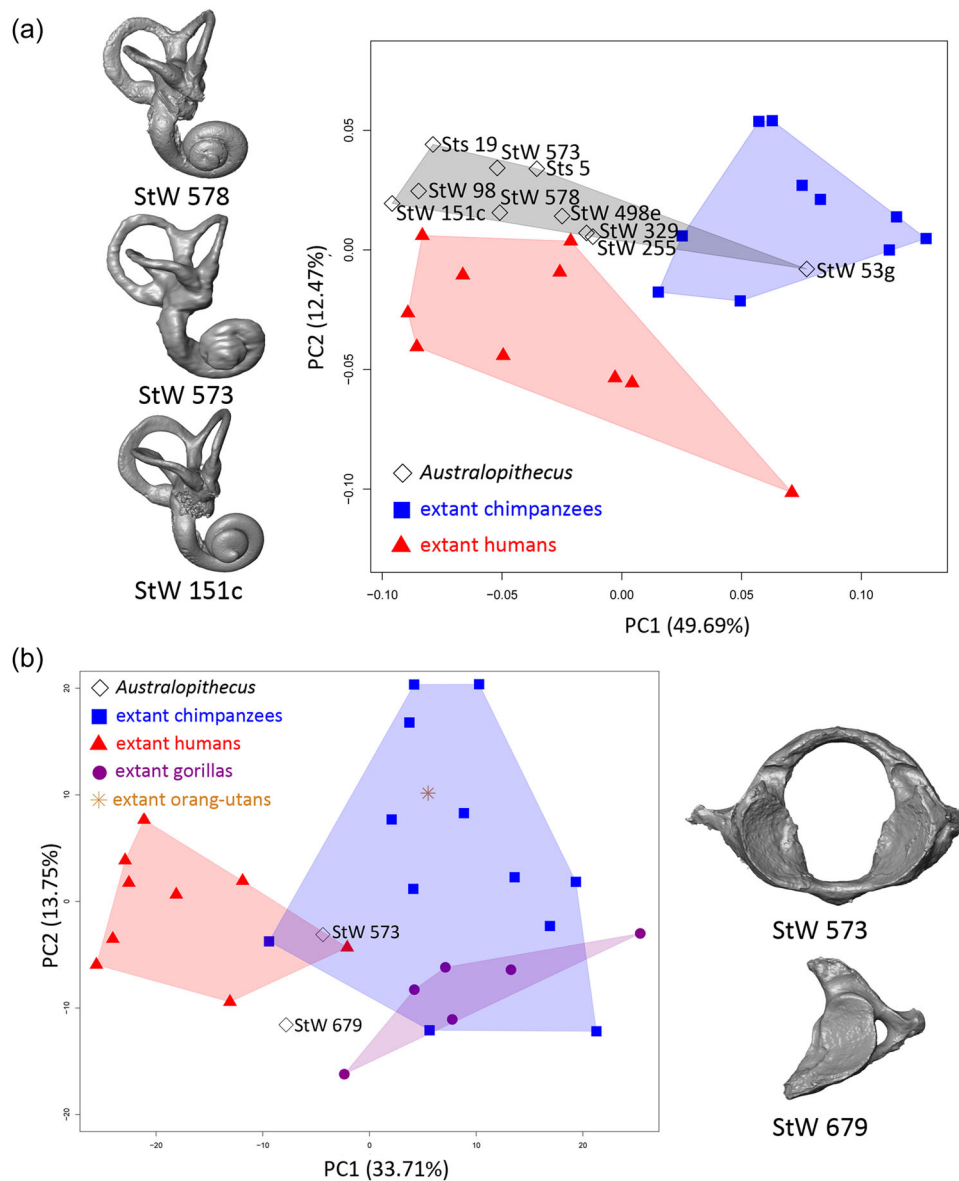


FIGURE 3 Multivariate analyses of the shape variation of the bony labyrinth (a) and atlas (b) of *Australopithecus* specimens from Sterkfontein in comparison to extant humans, chimpanzees, gorillas, and orang-utans. All of the *Australopithecus* specimens included in these studies come from Sterkfontein Member 4 to the exception of StW 573 (Member 2) and StW 578 (Jacovec Cavern). Modified from Beaudet et al.^{67,72}

various parts of the skeleton, some that are known as being influenced by sexual dimorphism (e.g., pelvis), others with functional implications (e.g., inner ear), raises crucial questions on the potential factors that may be responsible for this morphological disparity.

3 | THE CONCEPT OF VARIATION IN PALAEOLOGY AND HOW IT APPLIES TO THE STERKFONTAIN ASSEMBLAGE

Morphological heterogeneity observed in the *Australopithecus* hypodigm of Sterkfontein, particularly amplified within the Member 4 assemblage, and the related debates among scholars on its

significance and signification, exemplifies one of the most intractable questions in palaeontology, that is, how to interpret variation in the fossil record?

Interpreting variation in the fossil record as a taxonomical signal requires an agreement on which species concept would be the most appropriate.⁷⁵ Species concepts in palaeontology have to integrate a number of limitations, starting with the nature of the fossil record that mainly consists in dentognathic material. As such, the biological species concept introduced by Mayr⁷⁶ that defines a species as a group of organisms capable of interbreeding with one another in nature and produce fertile offspring, is difficult (if not impossible) to apply to the fossil record. On the contrary, the phylogenetic species concept, which relies on the identification of a unique combination of

character states that represent a species,⁷⁷ is particularly useful in the context of fossil remains. Similarly, the evolutionary species concept has been the focus of much interest in palaeontology. According to this definition, a species is considered as a lineage that evolves separately from other lineages, and thus has its own evolution history.⁷⁸ Nonetheless, there is no consensus on which definition and criteria should guide our assessment of past taxonomic diversity, even if the phylogenetic species concept has been largely favored.

While describing new specimens from Sterkfontein Member 4 and adding further evidence of the unusual degree of polymorphism in this fossil assemblage, Lockwood and Tobias⁴⁰ evaluated the main plausible sources of variation as follows (p. 447): “[...] among the principal sources of intraspecific variation, neither geographic variation (by definition) nor sexual dimorphism offers a convincing explanation for some patterns of variation in the Sterkfontein Member 4 sample. The influence of temporal variation at the site is unknown, though it represents a potentially important factor. Variation due to ontogenetic differences is poorly understood, but it is among the most productive future directions of study, given the availability of specimens such as Stw 183 and Stw 329.” This synthesis highlights important confounding factors when examining a fossil assemblage, that is, geographical variation, sexual dimorphism, ontogenetic immaturity, and temporal depth (see also Plavcan and Cope⁷⁹ for a review and Albrecht and Miller⁸⁰ for further discussion about geographic variation).

Geographical variation may account for the presence of regional variants of a taxon, but also contributes to the definition of chronospecies (i.e., chronological segmentation of a single evolving lineage) when these variants come from distinct chronological contexts. In the context of the *Australopithecus* hypodigm from Sterkfontein, because all the specimens come from the same site, geographical variation is not a source of variation. However, it might be considered as a factor in the case of migration. Early hominin biogeography and dispersals remain poorly known. The ancestors of *A. africanus* have been suggested to have migrated from eastern to southern Africa.⁸¹ The possibility of later dispersals that would have contributed to the *Australopithecus* population in South Africa would need to be further explored.

Our lack of knowledge on the degree of sexual dimorphism (i.e., sexually based variation) in past populations represents a significant limitation when sexually allocating fossil hominins that are often incomplete. Fossil hominin specimens are traditionally sexually diagnosed based on osteological markers (e.g., size of the canine, the morphology of the pelvis, or the overall skeletal robusticity) and the comparative study of patterns of skeletal dimorphism in modern analogues (e.g.,^{38,82}). However, these criteria, and the modern standards used, may not be appropriate in the case of fossil species (rev. in⁷⁹). Consequently, there were crucial historical uncertainties on the sex of *Australopithecus* specimens (rev. in⁴⁹). For example, “Mrs. Ples,” which is probably the best cranial representative of the adult *A. africanus* (and, as such, often figured in paleoanthropological studies establishing the diagnosis of newly described specimens), has been attributed to a female (e.g.,⁸³) or a male (e.g.,⁸⁴) specimen.

The presence of immature specimens in a fossil assemblage may interfere with the interpretation of fossil hominin diversity. Indeed, the absence of fully mature features traditionally used to assign fossil remains taxonomically may complicate the diagnosis of the concerned specimens and inflate our appreciation of the diversity. Developmental stages are traditionally assessed by the study of the dentition (e.g., presence/absence of decidual/permanent teeth, incremental lines recorded in dental tissues⁸⁵) as well as cranial (e.g., closing of the sutures, degree of obliteration of the subarcuate fossa, histological activities^{86,87}) and postcranial (e.g., fusion of bone epiphyses, e.g.,⁸⁸) evidence. Unfortunately, partial specimens may not preserve appropriate developmental markers, leaving room for speculations about their developmental age. Interestingly, several of the specimens that Lockwood and Tobias⁴⁰ noted as being different from *A. africanus* at Sterkfontein Member 4 are immature (e.g., StW 329, StW 183). Moreover, the fact that the holotype of *A. africanus*, that is, the “Taung child” is an immature specimen,¹ complicates species diagnoses and taxonomic identifications of subsequent fossil specimens at different developmental stages. Even if not from Sterkfontein, it is noteworthy to mention that similar debates emerged following the description of the species *Australopithecus sediba* at Malapa (South Africa) based on the immature specimen MH 1.⁸⁹ Authors questioned the validity of the diagnosis given that craniofacial traits used would be subject to ontogenetic changes.⁹⁰

One last factor deserves further attention. Concerns on how the temporal depth of a fossil assemblage may be conflated with taxic diversity are synthesized by the concept of “time-averaging,” which is defined by Kowalewski⁹¹ as “the process by which events that happened at different times appear to be synchronous in the geological record.” Kowalewski and Bambach⁹² further refer to a “subtle temporal mixing” with “fossils mixed over time intervals notably exceeding the life span of organisms.” While geographical variation, sexual dimorphism, and ontogenetic immaturity have been discussed as a potential source of variation that may affect our appreciation of hominin taxic diversity, temporal depth as a factor has been less explored. Indeed, time-averaging has been demonstrated to increase variance of fossil samples but also, at the same time, to act as a filter for eliminating short-term variations.^{93,95} As such, rather than being seen as a drawback, time-averaging could be used to identify and interpret evolutionary processes and rate within fossil taxa, as for example in ostracodes⁹⁵ or primates.⁹⁵ Could this effect be observed at Sterkfontein Member 4, and therefore be considered as a plausible explanation for such a high degree of variation?

4 | HOW TEMPORAL DEPTH MIGHT AFFECT OUR ATTEMPTS TO UNDERSTAND VARIATION AT STERKFONTAIN

If we consider the deposits of Sterkfontein Member 4 span more than 600,000 years, temporal depth might potentially bias our estimation of morphological diversity within the Sterkfontein

TABLE 2 A synthesis of the plausible scenarios and ways forward

Hypotheses/theoretical framework	Assumptions	Implications	How to test these hypotheses
Multiple <i>Australopithecus</i> species at Sterkfontein	High degree of morphological variation within the <i>Australopithecus</i> assemblage of Member 4 (e.g., ⁴⁰); similarities between specimens from Member 4 and Member 2 (e.g., ⁴⁵)	Coexistence of <i>Australopithecus africanus</i> and a second species identified in Member 2	Morphological variation should exceed intraspecific variation quantified in extant and fossil comparative groups
Temporal depth responsible of morphological variation within Sterkfontein Member 4	Deposits of Sterkfontein Member 4 span about 600,000 years or more ^{15,26} ; possible anagenetically evolving lineage in eastern African <i>Australopithecus</i> ⁵¹	Anagenetic evolution within the same <i>Australopithecus</i> lineage	Morphological variation should be explained by different stratigraphic positions of specimens and diachronic changes
Cercopithecoids as an analogue	Taxic diversity within <i>Parapapio</i> in Sterkfontein Member 4 (e.g., ⁵²)	Taxic diversity within <i>Australopithecus</i> in Sterkfontein Member 4	Environmental changes and adaptive radiation in primates should be identified; locomotor and dietary diversity within primates should support the hypothesis of niche partitioning
	Overestimated taxic diversity within <i>Parapapio</i> in Sterkfontein Member 4 (e.g., ⁵³)	Overestimated taxic diversity within <i>Australopithecus</i> in Sterkfontein Member 4	Concerted revision of the papionin and hominin craniodental material in a taxonomic and evolutionary perspective using internal structures

Australopithecus hypodigm. In this case, there are two potential scenarios (Table 2). If we first consider the multiple species hypothesis,^{45,47} there would have been a sudden speciation event during Member 4 responsible for the emergence of a new species (i.e., *A. africanus*) that would have lived along with the ancestor (i.e., budding cladogenesis). To falsify this hypothesis, the presence of the two species should be verified by investigating the variation in Member 4 and demonstrating that it exceeds intraspecific variation attributed to the factors detailed above, using extant and fossil comparative groups (see below). Additionally, the ancestral population should also be identified in older deposits, such as Member 2. In the second scenario, variation may correspond to diachronic changes through time within the same lineage, which may indicate a gradual evolution of an ancestral species into a descendant species (i.e., anagenesis) within Member 4. If we consider the second option, the variation observed at Sterkfontein could be thus explained by anagenetic evolution of a lineage. In this case, variation quantified within Member 4 should reflect diachronic changes, and thus morphotypes identified are expected to be related to different stratigraphic positions indicating older and more recent remains.

Several studies have questioned the evolutionary pattern in early hominins, testing more specifically the hypothesis of stasis⁹⁶ and anagenesis^{51,97} in *Australopithecus* and *Paranthropus*.⁹⁸ If we apply the proposal by Wood^{82,99} of using paleontological models for evaluating species diversity in the fossil record (which could be done in conjunction with extant models), we may compare the Sterkfontein assemblage to the *Australopithecus* sample from East Africa. More specifically, Allia Bay, Kanapoi, Laetoli, and Hadar represent four site-samples ordered in time documenting diachronic changes in the

hypodigm of *Australopithecus anamensis* and *Australopithecus afarensis* that would be compatible with an anagenetically evolving lineage⁵¹; however, it should be noted that the recent discovery of the 3.8 million-year-old cranium of *A. anamensis* from Woranso-Mille, Ethiopia, questions the hypothesis of anagenesis in the *A. anamensis-afarensis* lineage as the two species overlap for 100,000 years, see⁹⁷. Du et al.¹⁰⁰ estimated the first and last appearance datum of the *A. anamensis-afarensis* lineage of 4.15 and 3.00 Ma (age midpoints). Interestingly, a mixture of primitive and derived characters in the C/P3 complex was captured in the Hadar record of *A. afarensis*,^{51,96} thus resembling the mosaic nature of the characters seen in Member 4 (as described in Sections 2 and 3). Moggi-Cecchi et al.⁵ further noticed that *Australopithecus* from Sterkfontein Member 4 "has generally similar levels of variability when compared to *A. afarensis*, a species that shows the influence of temporal variation in some aspects of its dentition."^{40,p.5} In this comparative framework, we may hypothesize that the pattern of variation observed at Sterkfontein is consistent with an anagenetically evolutionary species. However, anagenetic and cladogenetic processes are not mutually exclusive. Thus, anagenesis may have occurred in *Australopithecus* through Members 2 and 4 with a speciation event occurring between Members 4 and 5 (before 2.2 Ma) leading to the appearance of *Homo* and *Paranthropus*. This scenario would be consistent with the first appearance date of *Homo* and *Paranthropus* (2.2 or 2.0 Ma at Swartkrans and Drimolen^{101,102}) in southern Africa. However, one should be cautious with first appearance dating, as it may not coincide with the actual emergence of a taxon. The next question to be addressed will be the potential role of the *Australopithecus* population sampled in Member 4 in this evolutionary history, and its

implication as putative ancestors to *Homo* and *Paranthropus*. Indeed, previous studies have suggested, for example, that part of the *Australopithecus* assemblage from Sterkfontein could be phylogenetically related with *Paranthropus*⁴⁵ while others view *A. africanus* as a sister group of *Homo* + *Paranthropus*⁽¹⁰³⁾; it is interesting to note that, in this paper, the placement of *A. africanus* is noted as being particularly variable as compared to other early hominin taxa, which emphasises the critical need for a better understanding the nature of the morphological variation within the hypodigm).

High-resolution geospatial analysis of the distribution of the fossil remains within Member 4 will be essential to falsify the hypothesis of an anagenetic evolutionary species.⁴ Additionally, stratigraphically sensitive cosmogenic nuclide dating would help in refining the extent of mixing of Member 4. Indeed, Clarke⁵⁴ and Clarke and Kuman⁴⁷ negated the hypothesis of temporal variation noting the fact that “small and large-toothed morphotypes are found together at both high and low levels in the talus cone, suggesting that one was not ancestral to the other.”^{46,p.45} However, the stratigraphic provenance of some of the hominins, including those that have featured in the discussion of the multiple-species hypotheses remains debated. More particularly, craniodental and postcranial specimens showing *Homo*-like features have been associated alternatively with deposits of Members 4 or 5. For instance, StW 151, recovered from partly decalcified in-situ breccia in a single solution pocket in the southern area of the surface-exposed deposits, has been suggested to derive from vertical contamination from Member 5 or a southern, more widely distributed infill (containing StW 53) related to Member 4.^{22,104,105} Similarly, the stratigraphic origin of Sts 19, found in a mining dump, is uncertain and, even if usually considered as coming from Member 4, this specimen might potentially come from a small portion of Member 5 overlying Member 4 at the western end of the exposed sediments.^{7,20,106} Finally, the postcranial remains StW 89, StW 150, and StW 182 have been suggested to come from either Member 4^{9,21,22} or Member 5^(107,108; rev.50). Thus, differences in the initial stratigraphic positions of these specimens might be consistent with the hypothesis of time-related changes. Within this context, the way forward should be a careful study of key-features in the fossil hominin skeleton coupled with a meticulous revision of the stratigraphic provenance of the fossils and new dating. The first step would be the development of a matrix of characters that are proved to be informative from a diagnostic point of view. As discussed above, the use of imaging techniques opened up new opportunities for the identification of characters that carry valuable information in terms of taxonomy and phylogeny (e.g., EDJs,⁶⁴) and that should be quantifiable (i.e., excluding character states such as absence/presence, which can be coded but may be subject to inter-observer error). The study of these features in extant primates would be a prerequisite, and more particularly the assessment of their degree of interspecific and intraspecific variation in a sample that meets the statistical requirement to be considered as representative of the living population. The

impact of factors such as sex, age, and geographic distribution onto the pattern of intraspecific variation (including metric and morphometric variation) should be duly quantified. Only within these conditions the assemblage from Sterkfontein could be interpreted in a taxonomic perspective. Simultaneously, providing new dates for Member 4, with a sampling strategy guided by the coordinates of key-specimens that feature in the discussion about taxonomic diversity (e.g., Sts 5, Sts 71, StW 505) in addition of the geomorphological context, would help controlling for temporal depth and lead future evolutionary interpretations.

5 | AN ECOLOGICAL PERSPECTIVE: PRIMATE DIVERSITY

As discussed in the previous section, craniodental and postcranial evidence provided contrasted results regarding the presence of a second species in Sterkfontein Member 4. We might thus have to look beyond the hominin assemblage to understand the nature of morphological variation. As stated by White,¹⁰⁹ (p. 31) “phylogenetically and ecologically related extant species lineages provide guidance in circumscribing the amount of variance expected for earlier species sampled as fossils.” In this respect, fossil monkeys (cercopithecoids) could be considered as a relevant “control-group” for the understanding of evolutionary trends and adaptations of early hominins (sensu^{110–113}). Indeed, cercopithecoids are particularly abundant in the Plio-Pleistocene African fossil record,^{113,114} and they are frequently found in stratigraphic association with hominin remains in most of the southern African paleontological deposits.^{27,116} Besides being part of the same ecological community as early hominins, they have also been used as an ecological analogue to fossil hominins for testing taxonomic hypotheses (e.g.,¹¹⁷). Finally, in the absence of great apes in the Plio-Pleistocene fossil record cercopithecoids represent the closest relatives to hominins and, thus, the most appropriate comparative group for early hominins.

The fact that hominins and cercopithecoids were coeval and lived in the same environment is of particular interest for addressing the issue of taxonomic diversity. Indeed, their evolution was shaped by the same environmental fluctuations that have influenced hominin evolution (rev.¹¹⁰). Speciation (i.e., the split of a lineage to form new species) involves reproductive isolation, and may happen within allopatric or sympatric populations. The role of the physical environment in the speciation process has been emphasized in two popular models, which are the Court Jester hypothesis (i.e., random perturbations to the physical environment are the main drivers of evolutionary changes¹¹⁸) and the Turnover Pulse hypothesis (i.e., changes in the physical environment are the main drivers of species turnover within the African mammal community¹¹⁹). Within this context, the role of climatic changes in hominin evolution has been widely explored in the literature, and suggested to correlate with the emergence of derived traits (morphological and behavioral) or even new species (e.g.,^{120,121} but see¹²² about the limitations of such inferences). Interestingly, cercopithecoids are often included in the

studies that look for evidence of shifts through time in the ecological dominance of mammal taxa (e.g.,¹²⁰). Cercopithecoids are thus a relevant comparative group in the study of primate diversity.

Sterkfontein Member 4 has yielded the largest fossil cercopithecoid assemblage in South Africa.^{52,123} This fossil material documents the presence of two papionin genera, *Parapapio* and *Papio*, as well as one colobine genus, *Cercopithecoides*.^{27,53,115,116,123–125} Similar to the hominins, the fossil monkey assemblage has been the focus of intense discussion about the pattern of variation and the existence of multiple species, especially concerning the presence of one or more *Parapapio* species. Based on molar size, Broom⁵² initially recognized three species of *Parapapio* at Sterkfontein, that is, *Parapapio broomi*, *Parapapio jonesi*, and *Parapapio whitei*. Since then, a number of studies questioned the validity of Broom's trimodal system.^{53,123,126–130} For instance, Heaton⁵³ suggested that specimens of *P. whitei* should be reassigned to either *P. broomi* or *Papio izodi*. Moreover, Thackeray and Myer¹²⁸ demonstrated that the pattern of tooth size variation in *P. broomi* and *P. jonesi* overlapped and that the two species may represent males and females of the same, highly sexually-dimorphic, species. More recently, the analysis of cercopithecoid craniodental inner structures (i.e., enamel-dentine junction, bony labyrinth) from South Africa tentatively supported the hypothesis of overestimated taxic diversity within *Parapapio*.^{129,131,132} Interestingly, in his monograph, even Brain⁸ noted that the coexistence of three related species varying mainly in size in the same locality would be “remarkable” (p. 152). As such, as for hominins, the taxonomic context of the fossil papionins remains controversial. The fact that we are facing similar challenge in understanding the diversity of the two primate taxa that co-existed at Sterkfontein may reveal more profound problems with the concept of species in palaeontology. Within this context, looking more closely at the evolutionary mechanisms underlying such taxonomic diversity with both taxa might shed new light on the speciation processes involved. More specifically, because the fossil papionins are so abundant, their assemblage has the potential to clarify the polarity of the morphological variation observed and their evolutionary context.

Since they were part of the same ecological community, we might expect a similar response to rapidly changing environments. If the number of papionin species is lower than what is currently acknowledged, it might then fit the pattern seen in *Australopithecus* (i.e., one or two species). If there are multiple species in the two groups, their split might have coincided with a speciation event that occurred prior to the Plio-Pleistocene transition. Global climate change during this period has been suggested to be related to significant faunal turnover and the emergence of the genus *Homo*.^{133–135} To evaluate the impact of these changes, we need to consider the diversity of *Parapapio* and *Australopithecus* before the time of Sterkfontein Member 4. So far, only one *Australopithecus* specimen is unambiguously associated to Pliocene deposits (i.e., StW 573,^{11,136} with potential *Australopithecus*-bearing older deposits in the Jacovec Cavern,¹⁴; but see 26 Figure 1). There is evidence of *P. broomi* and *P. jonesi* from Sterkfontein Member 2⁵² and few *Parapapio* sp. cranial and postcranial remains from the 4-million-years-old site

of Bolt's Farm.^{137,138} If we consider the multi-species hypothesis for both taxa in Member 4 with two *Australopithecus* species and three *Parapapio* species, then indeed environmental changes between Member 2 and Member 4 might have been responsible for an adaptive radiation in primates. But is this hypothesis tenable when looking at ecological factors?

Craniodental evidence and postcranial record are also valuable for testing the possibility of multiple papionin and hominin species at Sterkfontein occupying several ecological niches. In her taxon-free ecomorphic study, Elton¹³⁹ suggested that *P. broomi* was probably an arboreal monkey exploiting a “forest arboreal” habitat, while the locomotor strategy in *P. jonesi* was more terrestrial and would indicate an “open terrestrial” habitat. The presence of arboreal primates during the time of Member 4 is also supported by paleoenvironmental reconstructions (e.g.,¹⁴⁰) and the presence of fossil hominins retaining arboreal capabilities (e.g.,^{61,141–145}). In this case, *Parapapio* species from Sterkfontein Member 4 may have differed in terms of ecology. Concerning the dietary patterns, microwear analysis did not find significant differences in the diet of the sympatric species *P. broomi* and *P. jonesi*.¹⁴⁶ Moreover, biogeochemical analyses coupled with craniometric studies did not support niche separation between the *Parapapio* species at Makapansgat but rather reveal that these monkeys were adaptable generalists, a conclusion that could probably apply to Sterkfontein.^{126,147} Carbon isotope ratios of *Australopithecus* tooth enamel from Member 4 revealed high dietary variation in the consumption of C4-based food that would indicate opportunistic and adaptable dietary behaviors and could either support the hypothesis of the coexistence of two species with “equally unusual diets” (p. 593), or one species with a dietary behavior that is particularly variable.¹⁴⁸ Examples in other living lineages have demonstrated that ecological polymorphism may be possible within the same species (see the example of cichlid fishes,¹⁴⁹).

In conclusion, when considering the ecological factors that may have played a role in the evolution of the hominins and papionins, there is no clear evidence supporting niche partitioning and thus taxic diversity within these two groups. As such, the nonhominin primate assemblage may help better understanding the taxonomic situation at Sterkfontein in the future if the following steps are undertaken: (i) a concerted revision of the papionin and hominin craniodental material in a taxonomic and evolutionary perspective, (ii) a comprehensive study of the papionin and hominin postcranial material in parallel of isotopic studies in an ecological perspective, and (iii) a synthesis on the pattern of morphological and ecological variation within the primate assemblage of Sterkfontein. The first step will consist in the analysis of the same set of characters within the papionin and hominin samples that were proved to be useful in the context of taxonomic discussion (e.g., EDJ, inner ear, endocasts^{65,66,68,131,132}). This data set will be crucial to falsify the hypothesis of a potential primate radiation during the time of Sterkfontein Member 4. Moreover, information about their ecological behavior, throughout the study of locomotor-related markers within the skeleton indicative of specific niche⁷³ and of isotopic data that have the potential to

track dietary changes (e.g.,^{126,147,148}), would be essential to reconstruct the niches occupied by these taxa, and infer niche occupations and ecological strategies that could explain such a diversity. These analyses will ultimately contribute to test the scenarios mentioned above, that is, that we do (or we do not) identify a signal in the fossil record that supports the multispecies hypothesis in any of the primate taxa present during that time.

6 | SYNTHESIS AND CONCLUDING REMARKS

The Sterkfontein *Australopithecus* hypodigm offers the opportunity to investigate early hominin variation in the same locality, thus excluding potential bias represented by geographical variation. Moreover, the fossil record at Sterkfontein is exceptional by its relatively good degree of preservation (e.g., the nearly complete skeleton of “Little Foot”), the density of the fossil remains (i.e., more than 800 hominin remains found), and the extensive stratigraphic sequence documenting hominin evolution. Studies of the craniodental and postcranial elements of early hominins from Sterkfontein Member 4 revealed a significant degree of variation and a mosaic of *Australopithecus*-, *Paranthropus*-, ape-, and human-like characters. The pattern of variation described in this record opens critical questions about the biological, taxonomic, and evolutionary implications of such polymorphism. Could this variation be explained by sexual dimorphism? Does this record sample specimens of different ages? Could two *Australopithecus* species coexist in the vicinity of the Sterkfontein Caves during the Plio-Pleistocene period? Would temporal depth be a source of variation?

The lack of clear morphological evidence for distinguishing females from males blurs our appreciation of the sex-related variation. The presence of immature specimens, especially among the holotypes (e.g., Taung child¹), represents an additional confounding factor. On the other hand, the substantial degree of morphological heterogeneity may reflect the presence of two *Australopithecus* species in the Sterkfontein fossil record. While some authors mention this possibility without naming this second species or reassigning specimens (e.g.,^{38,40}), others propose to allocate some specimens to *A. prometheus* species and reattribute the fossil remains from Sterkfontein to either *A. africanus* or to this second *Paranthropus*-like *Australopithecus* species (e.g.,^{45,47}). The study of craniodental and postcranial remains from Sterkfontein yields interesting conflicting signals. On the one hand studies of postcranial remains or inner cranial structure with functional implications for locomotion, as the inner ear, suggest variable locomotor behavior consistent with the presence of two species. On the other hand, studies of craniodental material suggest a polymorphic single species. The comparative study of the fossil papionins from Sterkfontein contemporaneous to *Australopithecus* reaches similar conclusions. The last factor to be closely considered, and which is likely the main one operating at Sterkfontein, is temporal depth. Deposits at Member 4 yielded most of the fossil hominins at Sterkfontein and accumulated over

potentially more than 600,000 years. If we consider the possibility of diachronic variation, the degree of polymorphism at Sterkfontein may be compatible with an anagenetically evolving lineage that could be similarly observed in the *A. anamensis-afarensis* sample in eastern Africa. As a whole, the primate assemblage from Sterkfontein might thus reflect diachronic changes in adaptable evolutionary species.

In conclusion, the Sterkfontein fossil record has probably more to offer than a Manichean view centered on whether there are two species or not. The degree of variation reported in the assemblage from Member 4 raises interesting questions on our definition of species in palaeoanthropology and might justify reviving the concept of evolutionary species first introduced by Simpson.⁷⁸ This assemblage does not only offer a glimpse of morphological variation within a taxon that is probably ancestral to our own genus, but also demonstrates how time has shaped the history of our lineage. In that sense, with appropriate geospatial data, the study of this variation could tell us more about the evolutionary processes and rates at a time in which hominins were facing important changes in their environment. Hominins were not the only primate taxa wandering around Sterkfontein at that time, and just like *Homo sapiens* is “another unique species,”¹⁵⁰ *Australopithecus* had to overcome challenges that papionins were also dealing with. In that respect, the palaeobiology of *Australopithecus* cannot be fully understood without considering the ecological system in which they were living and the fundamental concepts of ecological niches and speciation, as echoed by.¹⁵¹

GLOSSARY

<i>Anagenesis</i>	evolutionary process with an ancestral species gradually evolving into a descendant species.
<i>Chronospecies</i>	chronological segmentation of a single evolving lineage.
<i>Cladogenesis</i>	evolutionary process in which an ancestral species split into two descendant species.
<i>Conspecificity</i>	from the same species.
<i>Degree</i>	magnitude.
<i>Diversity</i>	number of taxonomical/morphological entities (e.g., taxa, morphogroups) within a sample.
<i>Evolutionary species</i>	temporally extended species including both ancestors and descendants forming an evolving lineage.
<i>Holotypes</i>	type specimens after which a taxon is defined.
<i>Morphogroup</i>	a group defined by a dominant morphology.
<i>Pattern</i>	mode.
<i>Phenotype</i>	observable features of one individual.
<i>Polymorphism</i>	presence of multiple morphogroups within a sample.
<i>Single-species hypothesis</i>	according to this hypothesis, only one species might be present in a specific chronological and ecological context.

<i>Stasis</i>	evolutionary pattern with no noticeable changes in the phenotype of the specimens considered though time.
<i>Sympatry</i>	species that live in the same geographical area within the same time interval.
<i>Time-averaging</i>	fossil specimens from different time periods that are preserved in the same stratigraphical unit and thus interpreted as penecontemporaneous.
<i>Variation</i>	observable differences in the phenotype of the specimens included in the same taxonomical, chronological, geographical or morphological unit.
<i>Variability</i>	variation within a sample.

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