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Dental data challenge the ubiquitous presence of *Homo* in the Cradle of Humankind

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The origins of *Homo*, as well as the diversity and biogeographic distribution of early *Homo* species, remain critical outstanding issues in paleoanthropology. Debates about the recognition of early *Homo*, first appearance dates, and taxonomic diversity within *Homo* are particularly important for determining the role that southern African taxa may have played in the origins of the genus. The correct identification of *Homo* remains also has implications for reconstructing phylogenetic relationships between species of *Australopithecus* and *Paranthropus*, and the links between early *Homo* species and *Homo erectus*. We use microcomputed tomography and landmark-free deformation-based three-dimensional geometric morphometrics to extract taxonomically informative data from the internal structure of postcanine teeth attributed to Early Pleistocene *Homo* in the southern African hominin-bearing sites of Sterkfontein, Swartkrans, Drimolen, and Kromdraai B. Our results indicate that, from our sample of 23 specimens, only 4 are unambiguously attributed to *Homo*, 3 of them coming from Swartkrans member 1 (SK 27, SK 847, and SKX 21204) and 1 from Sterkfontein (Sts 9). Three other specimens from Sterkfontein (StW 80 and 81, SE 1508, and StW 669) approximate the *Homo* condition in terms of overall enamel–denture junction shape, but retain *Australopithecus*-like dental traits, and their generic status remains unclear. The other specimens, including SK 15, present a dominant australopith dental signature. In light of these results, previous dietary and ecological interpretations can be reevaluated, showing that the geochemical signal of one tooth from Kromdraai (KB 5223) and two from Swartkrans (SK 96 and SKX 268) is consistent with that of australopiths.

early *Homo* | taxonomic assessment | dental structure | geometric morphometrics

The South African cave sites of the Cradle of Humankind (Gauteng Province), declared a World Heritage area by the United Nations Educational, Scientific, and Cultural Organization, have yielded hundreds of Pliocene–Pleistocene (Gelasian–Calabrian, <https://stratigraphy.org>) hominin remains assigned to the genera *Australopithecus*, *Paranthropus*, and *Homo*. At Sterkfontein, specimens variously assigned to *Australopithecus*, *Paranthropus robustus*, and early *Homo* have been found in western breccias equivalent in age to post–member 4 infills (member 5 and the StW 53 infill) (1, 2). Currently available dates for the StW 53 infill and member 5 deposits suggest that the genera associated with these units existed in close temporal proximity on the southern African landscape during the Late Pliocene to Early Pleistocene (3), even if a better chronological framework is needed to accurately compare specimens from the various sites. Additionally, the identification of specimens belonging to early *Homo* that are penecontemporaneous with *Australopithecus* and/or *Paranthropus* at sites such as Kromdraai B, Drimolen, and Swartkrans has led to interpretations of a widespread presence of early *Homo* throughout the Cradle of Humankind since ~2.5 Ma (see debates about the geochronology of southern African hominin sites in refs. 4–7). However, the attribution of a number of these specimens to *Homo* has been questioned. In this study, we analyze the dentine shape of postcanine tooth crowns, which has demonstrated a strong taxonomic signal at the generic level. We reexamine the taxonomic attribution of the majority of specimens previously considered to represent early *Homo*, and test the hypothesis of a ubiquitous presence of early *Homo* in the Early Pleistocene sites of southern Africa.

The first species described for *Australopithecus*, *Australopithecus africanus*, was erected based on the Late Pliocene juvenile skull Taung 1 from the eponymous site (8), and the hypodigm was later supplemented by specimens from Sterkfontein, Makapansgat, and Gladysvale (9). *Australopithecus prometheus* was first described on the basis of the

Significance

Identifying the earliest members of the genus *Homo* is crucial for understanding when and where selective pressures resulted in its emergence from a Pliocene–Pleistocene hominin taxon. Our revision of a large part of the dental fossil record from southern Africa provides evidence suggesting a paucity of *Homo* remains and indicates increased levels of dental variation in australopith taxa. Results of the Ba/Ca, Sr/Ca, and elemental mapping of enamel and dentine also indicate that some of the purported *Homo* specimens show a paleoecological signal similar to that of the australopiths.

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The authors declare no competing interest.

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parietooccipital portion of braincase MLD 1 from Makapansgat (10). It was also recognized in the Late Pliocene deposits of Sterkfontein (11). The Early Pleistocene species *Australopithecus sediba* was identified at Malapa and described as showing *Homo*-like features even if the postcanine teeth exhibit an *Australopithecus* morphology, including birooted lower third premolars and the presence of a marked protostylid on the lower molars (12). The type species of *Paranthropus*, *P. robustus*, was described on the basis of the Early Pleistocene partial skull TM 1517 from Kromdraai (13) and was recognized at several other sites such as Drimolen, Cooper's Cave, Gondolin, Sterkfontein, and Swartkrans (9).

While less plentiful, remains attributed to early *Homo* have been described in four sites of the Cradle of Humankind: Swartkrans, Kromdraai B, Sterkfontein, and Drimolen. The first fossil from southern Africa attributed to early *Homo* was the Early Pleistocene mandible SK 15 from Swartkrans member 2, dated to ~1.4 Ma (14). It was originally attributed to *Telanthropus capensis* (15) and was later assigned to *Homo erectus*/*Homo ergaster* (16), but it was recently suggested to belong to *Australopithecus* (17). Additional specimens, including SK 27, SK 847, and SKX 21204 from the 2.2 Ma to 1.8 Ma Swartkrans member 1 (7), and the isolated teeth SKX 257 and 258 and SKX 267 through 269 from the chronologically younger member 2, are generally recognized as early *Homo* (18–20). Several specimens from this site, including SK 47, SK 843, SK 846, and SKX 4446, were previously attributed to *Homo* (21, 22), but further analyses suggested that they belong to the *P. robustus* hypodigm (23, 24).

The associated dentition of KB 5223 from Kromdraai B, chronologically assessed to the beginning of the Early Pleistocene (25), was attributed to *Homo*, due, in part, to the small tooth crown dimensions (26), but was also regarded as morphologically compatible with *P. robustus* (27). More than a dozen specimens from Sterkfontein member 4 (~2.8 Ma to 2.2 Ma) and member 5 (2.2 Ma to 2.0 Ma) (4), have been attributed to *Homo* (SE 255, SE 1508, SE 1579, SE 1937, SE 2396, Sts 19, StW 19b, StW 42, StW 53, StW 75, StW 80 and 81, StW 84, StW 87, and StW 151) (1, 2, 16, 27), although some specimens, including StW 53, were also regarded as representative of *A. africanus* (28, 29). In addition to the recently described calvaria (6), 10 isolated teeth from Drimolen (DNH 24, DNH 35, DNH 39, DNH 42, DNH 45, DNH 62, DNH 67, DNH 70, DNH 71, and DNH 80) were also suggested to represent early *Homo* (30, 31).

Collectively, this southern African sample of the early *Homo* hypodigm exhibits a high degree of dentognathic dimensional and morphological variation, and the attribution to *Homo* of some specimens remains a matter of contention (e.g., refs. 1, 2, 6, 19, 20, 22, 24, 27, and 32–40). Indeed, this assemblage has been referred to as *Homo* sp., *Homo habilis*, and *H. erectus*/*H. ergaster*, but many of the specimens differ in dental morphology from the eastern African remains allocated to the latter two species (27). This casts doubts on the nature and identity of the southern African Early Pleistocene material regarded as *Homo*. In addition, a new species *Homo gautengensis* (40) was erected to accommodate most of the Early Pleistocene southern African *Homo*-like specimens. StW 53 was defined as the holotype, along with a number of paratypes (SE 255, SE 1508, StW 19b/33, StW 75–79, StW 80, StW 84, StW 151, SK 15, SK 27, SK 45, SK 847, SKX 257/258, SKX 267/268, SKX 339, SKX 610, SKW 3114, and DNH 70). However, the type specimen of *H. gautengensis*, StW 53, has been generally regarded as representing *H. habilis* (27), and has also been shown to be morphologically indistinguishable from *A.*

africanus (28, 29). For this reason, the validity of this endemic taxon has not been generally accepted, and the attribution of the specimens remains controversial (41). Disagreements partly arose because previous studies were restricted to the analysis of a few incomplete mandibles and cranial remains chronologically spanning 700 ka to 500 ka (27). However, the majority of the southern African *Homo* record is represented by dental remains, and the analysis of the internal structure of these teeth has the potential to shed light on their taxonomic affiliation, augmenting debate around the origins and distribution of early *Homo* in the Cradle of Humankind.

To reassess the taxonomic attribution of the southern African early *Homo* dentognathic assemblage, we focus on the morphology of the enamel–dentine junction (EDJ). This interface is preserved in fully formed tooth crowns between enamel and dentine and captures the morphology of the membrana praeformativa, a basement membrane serving as the template for the majority of the taxonomically relevant aspects of crown morphology (42, 43). Unlike the outer enamel surface, which is often affected by occlusal wear, the EDJ is generally well preserved and recognized as a reliable taxonomic proxy to distinguish between hominid taxa, even at the subspecies level (44–48). Three-dimensional geometric morphometric (3D GM) analyses using landmarks and semilandmarks show that dentine horn height, crown height, and cervix shape can distinguish the postcanine teeth of *Australopithecus*, *P. robustus*, and Late Pleistocene to Holocene *Homo* (47, 49, 50). The recently developed diffeomorphic surface matching (DSM) method (51), which models the deformation between shapes, captures the geometric details of an anatomical structure and is now used as an advanced analytical tool in morphometrics (51–54). Indeed, DSM analyses can capture the taxonomically relevant aspects of the EDJ morphology, including both prominent features (such as the dentine horns and marginal crests) and more subtle features (like the protostylid and occlusal basin morphology), and might thus improve on traditional GM analyses that focus only on the shape of the cervix and marginal ridge (53, 55, 56).

We use the DSM approach to investigate the EDJ shape of an assemblage of permanent premolars and molars from Drimolen (DNH 39, DNH 62, DNH 67, and DNH 70), Kromdraai (KB 5223), Sterkfontein (SE 255, SE 1508, Sts 9, StW 19b, StW 53, StW 80, StW 81, StW 87, StW 151, and StW 669), and Swartkrans (SK 15, SK 18a, SK 27, SK 96, SK 847, SKX 257, SKX 268, and SKX 21204) attributed to, or suggested to represent, *Homo* (*SI Appendix, Supplementary Note 1 and Table S1*). We test whether their EDJ morphology more closely approximates the condition of Early–Middle Pleistocene *Homo* from eastern Africa ($n = 22/65$) and Asia ($n = 43/65$) or the australopithecine (*Australopithecus* and *Paranthropus* from southern Africa) pattern (for the list of the comparative material, see *SI Appendix, Table S2*). The reference *Homo* sample includes specimens attributed to *H. erectus*/*H. ergaster* or early *Homo* and that are widely accepted to unambiguously belong to our genus during the early period of its evolution.

Results

As illustrated in the assemblage from Swartkrans (Fig. 1), for all tooth positions, there are aspects of EDJ morphology of the southern African purported *Homo* specimens that are more typical of *Australopithecus* and *Paranthropus* (*SI Appendix, Figs. S1–S8*). To quantitatively assess EDJ shape variation and reassess taxonomic attribution of the purported *Homo* teeth, we conducted DSM GM analyses of the EDJ using specimens of *Australopithecus*, *Paranthropus*, and *Homo* whose taxonomic

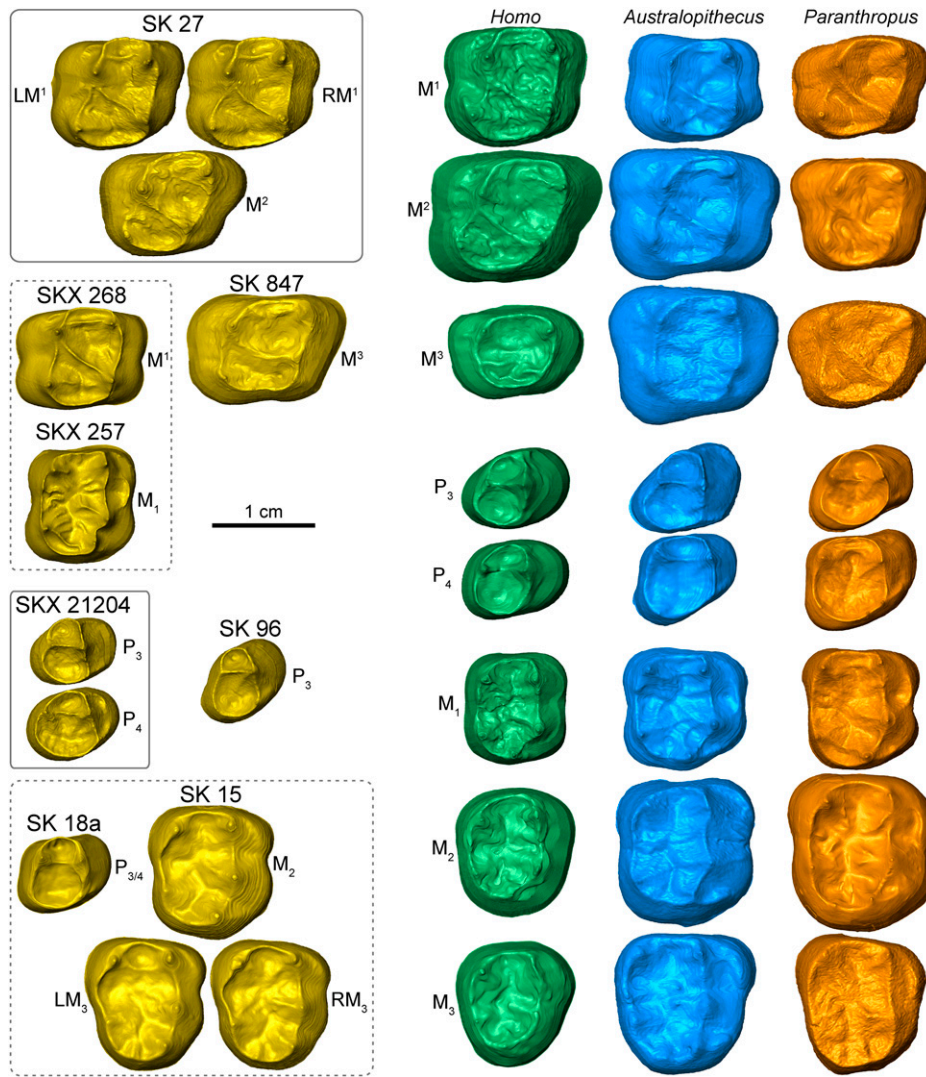


Fig. 1. The EDJ of the postcanine teeth of the purported *Homo* specimens from Swartkrans compared with those of Early Pleistocene *Homo* (KNM-ER 1590 M¹ and M², Sangiran 4 M³, and KNM-ER 992 lower postcanine teeth), *Australopithecus* (Taung M¹ and M₁, StW 183 M², StW 128 M³, StW 498 P₃, StW 104 P₄, StW 133 M₂, and StW 312 M₃), and *Paranthropus* (TM 1517 upper molars and P₃, P₄, M₁, and M₃, and SK 1 M₂). Specimens belonging to the same individual are enclosed by a plain line, and specimens that likely belong to the same individual are enclosed by a dotted line.

identity at genus level is well established and undisputed as reference samples. In all between-group principal component analyses (bgPCA) based on the deformation fields computed by DSM, the three hominin genera are well discriminated, despite a slight overlap between *Australopithecus* and *Paranthropus* for the M³ and P₄ (Figs. 2 and 3). The cross-validated bgPCA (cv-bgPCA) confirm the general distinction of the three groups. In this case, while the australopithecids overlap for the premolars and third molars, *Homo* is largely well distinguished (*SI Appendix*, Figs. S9 and S10). Additionally, we conducted canonical variate analyses (CVA) on subsets of the principal components, and results are consistent with those of the bgPCA and cv-bgPCA (*SI Appendix*, Figs. S11 and S12). As shown by the statistical analyses, all cv-bgPCA and CVA of PC scores exhibit high degrees of classification accuracy for the comparative specimens (*SI Appendix*, Tables S3 and S4), and group differences are not purely allometric, as they remain large and significant after controlling for allometry (*SI Appendix*, Table S5). With respect to the australopithecids, *Homo* generally shows a taller EDJ crown with a smaller EDJ central basin in the premolars, and a proportionally larger basin with respect to the crown base (except in the third molars) and a rounder or

more regular cervical outline in the molars. *Australopithecus* is distinguished from *Paranthropus* by a more developed lingual than buccal aspect in upper molars, a less distally positioned protoconid in the P₃, a shorter P₄ EDJ crown, and a more expanded buccal shelf in the lower molars.

The purported *Homo* specimens were projected into the bgPCA and CVA, and the typicality probabilities were computed (Table 1). With a few exceptions, the results of the bgPCA and CVA are consistent. Specimens from Drimolen (DNH 39, DNH 62, DNH 67, and DNH 70) and Kromdraai B (KB 5223) are statistically attributed to *Paranthropus*, sharing with the teeth of this genus a more mesiodistally compressed lingual aspect of the EDJ than the buccal one in the upper molars (Fig. 2) and a developed lower molar protostylid (Fig. 3). The specimen SK 15 also shows strong affinities with *Paranthropus* (of the three lower molars analyzed, the M₂ and left M₃ fall within *Paranthropus*, while the right M₃ is intermediate between *Paranthropus* and *Australopithecus*). The P_{3/4} SK 18a, that was suggested to belong to the SK 15 mandible, also displays an intermediate signal, and is closer to *Australopithecus* if it is a P₄ (Figs. 1 and 3). The specimens SE 255, StW 19b, StW 87, and StW 151 from Sterkfontein and SKX 257 and

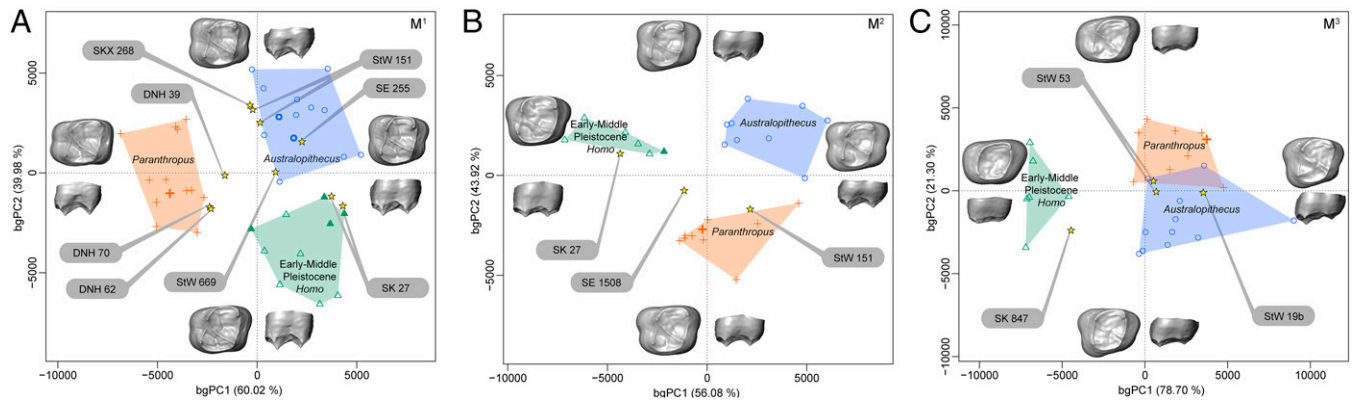


Fig. 2. Bivariate plot of the bgPCA scores based on the DSM deformation fields for the M¹ (A), M² (B), and M³ (C). The totality of the variance refers to between-group variation. Symbols highlighted in bold represent the holotype specimens of *Australopithecus* (Taung) and *Paranthropus* (TM 1517). Filled triangles indicate African *Homo*, while open triangles represent Asian *Homo*.

SKX 268 from Swartkrans are distinctly classified within *Australopithecus* (even if the M² of StW 151 is closer to the *Paranthropus* morphology). The M³s of StW 53 exhibit a mosaic of *Paranthropus* and *Australopithecus* morphology, while the M₃ shape is compatible with the *Australopithecus* variation.

Conversely, the specimens SK 27 and SKX 21204 from Swartkrans, as well as Sts 9 from Sterkfontein, fall well within *Homo*, showing a taller EDJ crown than in the australopiths (Figs. 2 and 3). The M³ of SK 847 has a mesiodistally compressed shape that is similar to that of *Homo*, but also a trapezoidal outline reminiscent of the *Australopithecus* condition. The classification of the specimens StW 80 and 81 from Sterkfontein varies depending on tooth position. The P₃ and M₃ EDJ are comparable to *Homo* but outside the variation range displayed by the comparative sample used in this study, while the P₄ exhibits an australopith morphology, and the M₂ is intermediate between *Homo* and *Australopithecus*. The specimens SK 96 from Swartkrans, as well as SE 1508 and StW 669 from Sterkfontein, are less definitive, as their EDJ shape is intermediate between all three genera (Figs. 2 and 3 and *SI Appendix*, Figs. S11 and S12).

We also scored nonmetric morphological features of the EDJ in the purported early *Homo* and comparative samples, showing that there is an overlap in the presence/absence and degree of expression of most nonmetric dental features recorded at the EDJ of the three hominin genera. None of these traits in isolation can be considered diagnostic of *Homo* (*SI Appendix*, *Supplementary Note 2* and Table S6).

Finally, we investigated whether tooth size (assessed here using the EDJ surface area as a proxy) is a diagnostic feature to distinguish early *Homo* from the australopiths. With the exceptions of SK 15, StW 19b, StW 81, and StW 53 that have relatively large EDJ areas (in the upper range of *Australopithecus* and *Paranthropus*), the size of most of the purported early *Homo* specimens is in the lower range of the australopiths and within the range of Early to Middle Pleistocene *Homo* (*SI Appendix*, Fig. S13). In addition, even if Early to Middle Pleistocene *Homo* tends to have smaller tooth dimensions than the australopiths, there is overlap with *Australopithecus* for most tooth positions. A summary of the results for the metric, nonmetric, and size analyses is presented in *SI Appendix*, Tables S6–S8 along with an overall assessment of the taxonomic affiliation of each of the purported *Homo* specimens.

Discussion

The definition of the genus *Homo* on paleontological grounds remains a conundrum (57, 58). When the species *H. habilis*

was erected, Leakey et al. (59) proposed several morphological dental features distinguishing *Homo* from *Australopithecus*, including a bicuspid P₃, smaller postcanine teeth (in particular the M³, generally smaller than the M² or M¹), anterior teeth proportionally less reduced than the postcanine elements, and less buccolingually expanded premolars and molars (essentially due to the reduction or absence of the protostylid in *Homo*). However, these features are also variably found in australopith specimens, sometimes in combination (for example, the *Australopithecus* specimen Sts 52 has a smaller M³ relative to the M² and a bicuspid P₃), whereas some specimens attributed to *Homo* (e.g., the *H. habilis* specimen OH 16) show a larger M³ than M² and a mesiodistally elongated P₃ (36, 59). Wood and Collard (57) suggested that fossil specimens/species should be included in *Homo* only if their teeth are more similar in morphology and relative proportions to the modern human condition than they are to the australopiths. However, modern human tooth morphology differs from most of the earlier species of *Homo*: The P₃ and P₄ have a small to absent metaconid and have a high crown, the M² and M³ variably display only three cusps (lacking a hypocone), and the M₂ and M₃ often have only four cusps (*SI Appendix*, *Supplementary Note 2*). This is largely due to the trend for reduction of the size and prognathism of the face, the jaw, and tooth dimensions that occurred through the Late Pleistocene (60). Conversely, Early to Middle Pleistocene *Homo* species have more-complex lower premolars (with a large metaconid and an extended talonid), four-cusped upper molars, and five-cusped lower molars, making them more suitable for comparison with the Late Pliocene to Early Pleistocene record and the identification of early *Homo*.

In the bgPCA, cv-bgPCA, and CVA of PC scores conducted here, fossil *Homo*, *Australopithecus*, and *Paranthropus* are generally well discriminated, further demonstrating the relevance of the EDJ for taxonomic diagnosis (44, 45, 48, 53). The Early to Middle Pleistocene reference sample includes both African and Asian specimens that group closely and are mixed together in the plots despite their wide chronogeographic distribution. Due to the inherent nature of the fossil record, hominin taxa (including early *Homo* species) are represented by a limited number of specimens, which complicates assessment of intrataxonomic and intertaxonomic variation, and, ultimately, taxonomic attribution (27, 57). However, in the absence of molecular data for early hominins, studying morphology remains the only way to diagnose extinct taxa. Among the 23 southern African specimens previously suggested to belong to *Homo* examined in this study (Table 2), only three are unequivocally attributed to *Homo* (SK 27, SKX 21204,

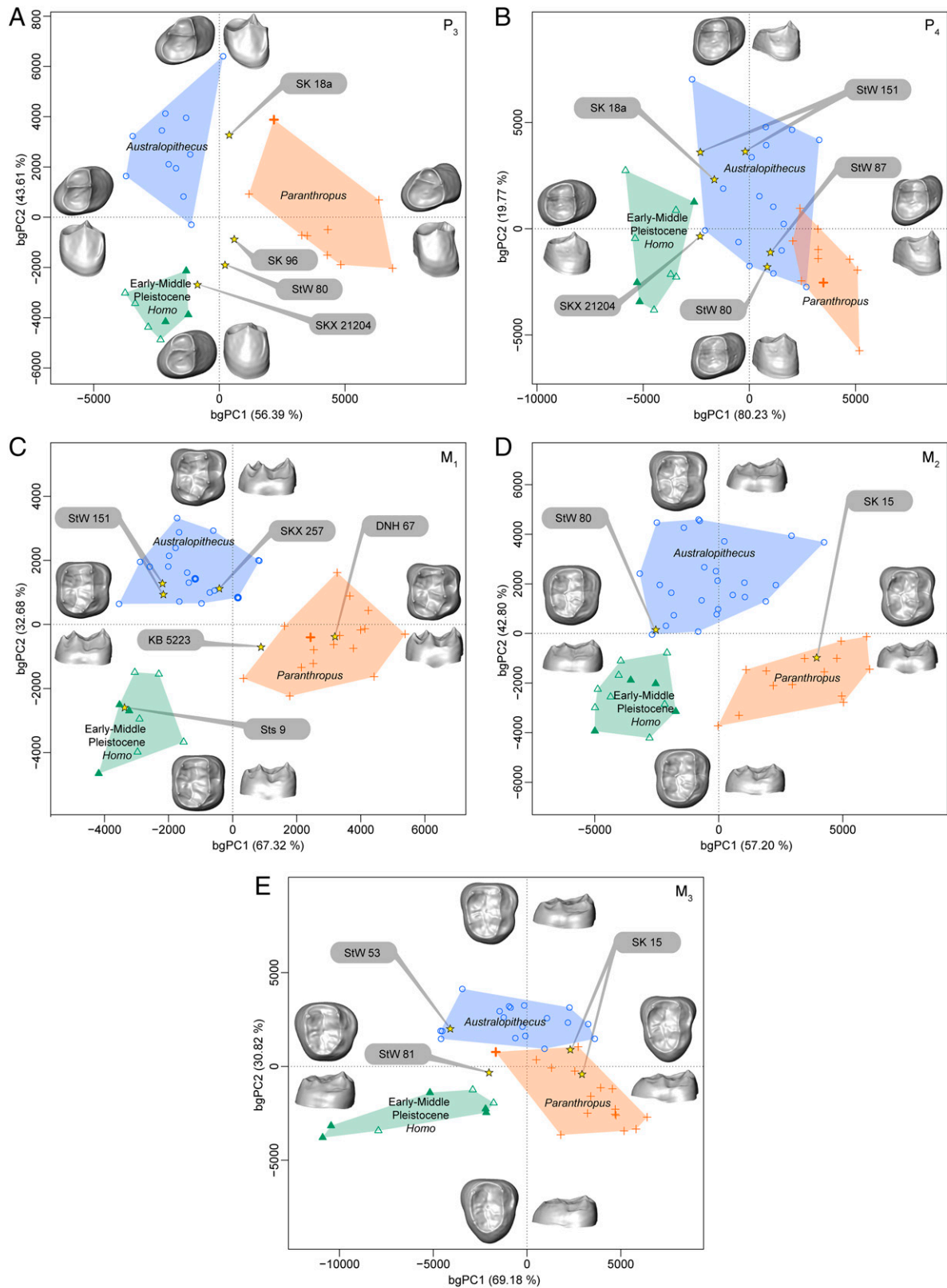


Fig. 3. Bivariate plot of the between-group principal component analysis (bgPCA) scores based on the DSM deformation fields for the P₃ (A), P₄ (B), M₁ (C), M₂ (D), and M₃ (E). The totality of the variance refers to between-group variation. Symbols highlighted in bold represent the holotype specimens of *Australopithecus* (Taung) and *Paranthropus* (TM 1517). Filled triangles indicate African *Homo*, while open triangles represent Asian *Homo*.

and Sts 9). SK 847 morphology is closer to *Homo*, even if the overall EDJ configuration retains *Australopithecus* features (Fig. 2 and *SI Appendix*, Fig. S3) and can also be confidently attributed to the former genus. This is compatible with the analysis of the morphology of the face and partial cranium of this specimen

showing that it shares synapomorphies of the *Homo* clade but probably represents a more primitive species than *H. erectus* s.l. (18, 39). The specimens StW 80/81, representing a single individual, preserve crushed and fragmentary portions of the mandibular bone with little morphological information (1). The EDJ of

the postcanine teeth of StW 80/81 displays affinities with *Homo*, as well as some features reminiscent of the australopith condition (mesiodistally elongated P₄ and M₃, and developed protostylid on the M₂). This combination of *Australopithecus*-like and *Homo*-like traits detected in some specimens investigated here can be interpreted in different ways: 1) These individuals could represent some of the earliest members of the genus *Homo*, retaining some primitive features of the dentition; 2) they could belong to an *Australopithecus* group evolving directly or convergently toward the *Homo* condition; or 3) they could be an australopith-*Homo* hybrid of the kind hypothesized by Thackeray (61). With respect to the first and second scenarios, StW 80/81 comes from member 5 west of Sterkfontein, likely dating to 1.7 Ma to 1.4 Ma (1). If this individual represents an early member of our genus with a morphology reminiscent of *Australopithecus*, it could imply that a stem group of early *Homo* remained genetically isolated for some time from *H. erectus*/*H. ergaster*. If it represents *Australopithecus*, it is more recent than *A. sediba*, and future studies of the EDJ of the postcanine dentition could resolve whether StW 80/81 morphology is compatible with *A. sediba*. The third hypothesis cannot be discarded either, and, while the influence of interbreeding on hominin tooth morphology is poorly understood, molecular analyses such as paleoproteomics should be soon able to test this and investigate phylogenetic relationships of Pliocene and Early Pleistocene hominins (62).

The case of the specimens SE 1508 and StW 669, from Sterkfontein, is more ambiguous, as they have a central position in the bgPCA and/or CVA plots (Fig. 2 and *SI Appendix, Fig. S11*), indicating the need for more caution in the interpretation of their group affiliation. The EDJ of the M² SE 1508 is similar to that of SK 27, albeit with a lower and broader crown base with respect to the occlusal basin. In the DSM analyses, these differences drive the specimen away from the *Homo* morphology represented in our sample and make it closer to *Paranthropus*. However, together with the marked similarities with SK 27, the position of the dentine horns and relatively simple crown morphology (i.e., absence of accessory traits) suggest that SE 1508 could represent early *Homo*. The M¹ StW 669 shows external crown morphological features similar to those of *H. habilis* (63), and preliminary analyses of the internal tooth structure also show affinities with *Homo* (64). However, our comparative analyses reveal that the EDJ retains some *Australopithecus*-like features, such as a markedly waisted occlusal outline, a buccal shelf, and a mesial lateral aspect that is strongly oriented inwardly (as in StW 283, for example). While an attribution to early *Homo* cannot be rejected, the specimen may represent *Australopithecus* with derived features resembling the *Homo* condition.

All the other purported early *Homo* specimens analyzed here show a dominant australopith signature of the EDJ morphology, and statistical analyses suggest that their inclusion in the *Homo* hypodigm is poorly supported based on EDJ morphology. As many of these are isolated teeth, additional analyses will be necessary to more clearly establish their taxonomic status (e.g., proteomic and ancient DNA evidence, and/or isotopic data [see below]). This also implies that the species *H. gautengensis*, created to accommodate the large morphodimensional variation of the southern African “early *Homo*” material (40), is invalid, as it includes specimens belonging to *Homo* (e.g., SKX 21204 and SK 27), *Australopithecus* (e.g., SE 255 and StW 53), and *Paranthropus* (e.g., KB 5223 and DNH 70).

SK 96 has a relatively central position in the bgPCA (Fig. 3), while the CVA place it close to *Paranthropus* (*SI Appendix, Fig.*

Table 1. Typicality probabilities of the investigated specimens computed for the bgPCA and CVA of shape analyses

	HOM		AUS		PAR	
	bgPCA	CVA	bgPCA	CVA	bgPCA	CVA
M ¹						
DNH 39					0.19	0.25
DNH 62					0.34	0.08
DNH 70					0.37	0.11
SE 255			0.82	0.18		
SK 27 L	0.16	0.42				
SK 27 R	0.18	0.55				
SKX 268			0.24	0.07		
StW 151 L			0.39	0.68		
StW 151 R			0.28	0.58		
StW 669			0.19	0.01		
M ²						
SE 1508					0.06	0.39
SK 27	0.80	0.75				
StW 151					0.29	0.52
M ³						
SK 847	0.22			0.02		
StW 19			0.50	0.30	0.24	0.09
StW 53 L			0.46			0.26
StW 53 R					0.50	0.76
P ₃						
SK 18a			0.21			0.16
SK 96					0.03	0.07
SKX 21204	0.36	0.89				
StW 80	0.05	0.74				
P ₄						
SK 18a			0.26	0.32		
SKX 21204	0.31	0.32				
StW 80			0.25	0.58		
StW 87			0.11	0.06		
StW 151 L			0.79	0.31		
StW 151 R			0.38	0.73		
M ₁						
DNH 67					0.99	0.99
KB 5223					0.14	0.12
SKX 257			0.52	0.63		
Sts 9	0.84	0.47				
StW 151 L			0.71	0.77		
StW 151 R			0.60	0.76		
M ₂						
SK 15					0.81	0.53
StW 80			0.19	0.62		
M ₃						
SK 15 L					0.61	0.10
SK 15 R			0.31	0.42		
StW 53h			0.37	0.01		

For each specimen, typicality probabilities are shown only for the group with which that specimen was affiliated. Values in bold are below the 0.05 threshold and are regarded as outliers for the groups included here. AUS, *Australopithecus*; HOM, Early and Middle Pleistocene *Homo*; PAR, *Paranthropus*.

SI Appendix, Fig. S12), as also indicated by the typicality probabilities (Table 1). The bgPCA probabilities are below the statistical threshold of classification within any of the comparative groups ($P < 0.05$), suggesting that SK 96 could either be an outlier for any of the comparative genera or represent another genus that is not represented in the reference samples. It was suggested by Davies et al. (50) that SK 96 EDJ shares similarities with *Paranthropus* and also approximates that of *Homo naledi*. The taxonomic

Table 2. Summary of taxonomic evidence for specimens previously attributed to *Homo*

Specimen	Tooth	EDJ area	Nonmetric traits	cv-bgPCA	cv-CVA	Bone morphology	Revised assessment
DNH 39	RM¹	UND	UND	PAR	PAR	n/a	PAR
DNH 62	LM ¹	UND	UND	PAR	PAR	n/a	PAR
DNH 67	RM₁	AUPITH	UND	PAR	PAR	n/a	PAR
DNH 70	LM ¹	UND	UND	PAR	PAR	n/a	PAR
KB 5223	LM₁	AUPITH	AUPITH	PAR	PAR	n/a	PAR
SE 255	RM ¹	UND	UND	AUS	AUS	n/a	AUS
SE 1508	RM²	HOM	UND	INT	PAR	n/a	PAR?
StW 19b	RM ³	AUPITH	UND	AUS	AUPITH	n/a	AUS
StW 53	LM³	AUPITH	UND	AUPITH	PAR	HOM?	AUPITH
StW 53	RM³	AUPITH	UND	AUPITH	PAR	HOM?	AUPITH
StW 53	LM₃	AUPITH	UND	AUS	AUS	HOM?	AUS
StW 80	RP ₃	UND	UND	HOM	HOM	UND	HOM
StW 80	RP ₄	HOM?	UND	AUS?	AUS	UND	AUS/HOM
StW 80	RM ₂	UND	UND	AUS?	AUS	UND	AUS?
StW 81	RM ₃	AUPITH	UND	INT	HOM	UND	HOM
StW 87	RP₄	HOM?	UND	AUS?	AUS	n/a	AUS
StW 151	LM ¹	UND	UND	AUS	AUS	UND	AUS
StW 151	RM ¹	UND	UND	AUS	AUS	UND	AUS
StW 151	RM ²	HOM	UND	PAR	PAR	UND	AUPITH
StW 151	LP ₄	HOM	UND	AUS	AUS	UND	AUS
StW 151	RP ₄	HOM	UND	AUS?	AUS	UND	AUS
StW 151	LM ₁	UND	AUPITH?	AUS	AUS	UND	AUS
StW 151	RM ₁	UND	AUPITH?	AUS	AUS?	UND	AUS
StW 669	RM¹	UND	UND	AUS?	AUS	n/a	AUS?
Sts 9	RM ₁	AUPITH	UND	HOM	HOM	n/a	HOM
SK 15	RM₂	AUPITH	UND	PAR	PAR	HOM?	PAR
SK 15	LM₃	AUPITH	UND	PAR	PAR	HOM?	PAR
SK 15	RM₃	AUPITH	UND	AUS?	AUS?	HOM?	AUPITH
SK 18a	LP ₃ or LP ₄	HOM?	UND	AUS	AUPITH	HOM?	AUPITH
SK 27	LM¹	UND	UND	HOM	HOM	HOM	HOM
SK 27	RM¹	UND	UND	HOM?	HOM	HOM	HOM
SK 27	RM²	HOM	UND	HOM	HOM	HOM	HOM
SK 96	LP ₃	UND	UND	AUPITH	PAR?	n/a	AUPITH
SK 847	LM³	AUPITH	UND	HOM	AUS?	HOM	HOM
SKX 257	RM ₁	UND	UND	AUS	AUS	n/a	AUPITH
SKX 268	RM ¹	UND	AUPITH	AUS	AUS	n/a	AUPITH
SKX 21204	RP₃	HOM	UND	HOM	HOM	HOM	HOM
SKX 21204	RP₄	HOM	UND	HOM	HOM	HOM	HOM

Bold and nonbold rows separate the different individuals represented here. AUS, *Australopithecus*; AUPITH, australopith; HOM, Early and Middle Pleistocene *Homo*; INT, intermediate; PAR, *Paranthropus*; UND, undiagnostic.

attribution of this specimen thus remains problematic. If SK 96 belongs to *Paranthropus*, it differs from the morphology of *P. robustus*, and it raises questions regarding possible affinities with *H. naledi*. There is a chronological gap of more than 1 My between the Swartkrans member 2 specimen and the Rising Star Cave hominin, and phylogenetic relationships of *H. naledi* with other hominin taxa are still uncertain (50, 65), and could be a focus of future studies. Our results also indicate that SK 15, holotype of the *nomen oblitum* *T. capensis* (15), as well as SK 18a that is supposedly associated with this mandible, actually represent an australopith taxon and not *Homo*. Although generally regarded as a representative of *H. erectus* s.l (9), the specimen is extremely robust, with proportions of the mandibular corpus that markedly differ from those of *H. erectus*/*H. ergaster* and other Pleistocene *Homo* species (66). The EDJ of SK 15 molars shows strong affinities with *Paranthropus* but differs in size and in relevant morphological aspects from the species *P. robustus* (e.g., absence of protostylid and accessory features) (Fig. 1). Interestingly, SK 15 molar root morphology has been linked with *H. naledi* and is, to some extent, also comparable with the

Paranthropus condition (67). If SK 15 belongs to *P. robustus*, then it either suggests high levels of variation in mandible size/shape with implications for sexual dimorphism within the genus or a higher degree of taxonomic diversity than currently recognized in the genus. The currently available evidence from dental structural organization suggests that SK 15 possibly belongs to *Paranthropus*, but its taxonomic status should be investigated further.

Based on morphology and dimensions of the craniodental remains, the specimens StW 53 and StW 151 were both suggested to represent early *Homo* or *Australopithecus* individuals more derived toward *Homo* than the rest of the australopith hypodigm (2, 28, 29, 68). StW 53 preserves partial aspects of the face and cranium (69). The most recent reconstruction shows a small endocranial volume and an intermediate morphology between *Australopithecus* and *H. habilis* (37), even if it has been criticized for the anatomically unrealistic shape, indicating that the reconstruction of the cranium would be closer to *Australopithecus* (29). The juvenile specimen StW 151 only preserves small bone fragments of the jaw and cranium that are not very informative for taxonomy (68). Our results show

Sterkfontein		Drimolen		Swartkrans	
STK-MH1 T1 (2.2-2.0 Ma)	StW 669 (M ¹) ?		DNH 39 (M ¹) ✗	Member 2 (~1.4 Ma)	SK 15-SK 18a (P _{3/4} , M ₂ , LM ₃ , RM ₃) ✗ SKX 257-SKX 268 (M ¹ , M ₁) ✗
	SE 255 (M ¹) ✗	Main Quarry (~2.0 Ma)	DNH 62 (M ¹) ✗ DNH 67 (M ₁) ✗ DNH 70 (M ¹) ✗		SK 27 (LM ¹ , RM ¹ , M ²) ✓
Member 5 (2.2-2.0 Ma)	SE 1508 (M ²) ?			Member 1 (2.2-1.8 Ma)	SK 96 (P ₃) ✗ SK 847 (M ³) ✓ SKX 21204 (P ₃ , P ₄) ✓
	StW 80-StW 81 (P ₃ , P ₄ , M ₂ , M ₃) ?				
	StW 87 (P ₄) ✗				
Member 4/5?	StW 19b (M ³) ✗				
	StW 53 (LM ³ , RM ³ , M ₃) ✗				
	Sts 9 (M ₁) ✓				
Member 4 (~2.8-2.2 Ma)	StW 151 (LM ¹ , RM ¹ , M ² , LP ₄ , RP ₄ , LM ₁ , RM ₁) ✗	Kromdraai B	Member 3/2? (early Early Pleistocene)		
			KB 5223 (M ₁) ✗		

Fig. 4. Chronostratigraphic distribution of the investigated purported *Homo* remains. In light of the results of the present study, only four specimens are likely to represent *Homo* (green ticks), four are possibly *Homo* (light green question marks), and the others more likely belong to *Australopithecus* or *Paranthropus* (red crosses).

that EDJ morphology of both specimens is on the margins of *Australopithecus* variation or even approximates the *Paranthropus* condition. Interestingly, the analysis of bony labyrinth shape shows that the two specimens represent the two extremes of the *Australopithecus* variation, where StW 53 appears as an outlier of the taxon (70).

All the Drimolen specimens investigated here that were suggested to represent early *Homo* (DNH 39, DNH 62, DNH 67, and DNH 70) show EDJ morphology that is more similar to *P. robustus*. Interestingly, the M₁ KB 5223, whose crown shows small dimensions comparable to those of early *Homo* (26) and smaller than in *P. robustus*, likely belongs to the latter taxon. Indeed, the EDJ of this specimen displays a marked protostylid that is similar to that of *P. robustus*. It is noteworthy that the analysis of enamel microstructure of KB 5223 revealed an overall pattern compatible with *Paranthropus* (71). The above specimens from Drimolen are relatively small and are dated to around 2 Ma (6), and KB 5223 from Kromdraai comes from early Early Pleistocene sediments (25), again suggesting that a smaller morph of *P. robustus* than that from Swartkrans coexisted in southern Africa for some time. However, the chronology of the deposits from these sites is debated, and the small *Paranthropus* dental specimens from Drimolen and Kromdraai that were previously identified as *Homo* could represent the early condition of the *P. robustus* morphocline (72, 73).

Most of the Early Pleistocene southern African teeth that our analyses identify as misattributed to *Homo* are smaller than those typical of *Australopithecus* and *Paranthropus*, while those compatible with *Homo* in shape are relatively large (SI Appendix, Fig. S13). It is possible that, besides the smaller dimensions, the external crown shape initially used to classify these teeth is also less diagnostic. In this respect, allometric changes could be considered as a potential factor. In our PCA, bgPCA, and CVA, allometric changes could be considered as a potential factor. However, even after controlling for allometry, group differences remain large (R² ranging from 9 to 29%) and significant (SI Appendix, Table S5). This suggests that differences between EDJ morphology of the specimens mostly represent shape variation and are only modestly influenced by size. This study also demonstrates that, at many postcanine tooth positions, crown dimensions overlap in *Australopithecus*, *Homo*, and *Paranthropus* (SI Appendix, Fig. S13). Using the natural logarithm of the EDJ as a proxy for crown size, Early to Middle Pleistocene *Homo* generally has significantly smaller postcanine teeth than *Paranthropus* (except for the M¹) and slightly smaller

teeth than *Australopithecus*, on average (but only partially, as indicated by the small determination coefficient and SI Appendix, Fig. S13 and Table S7). In fact, some of the investigated specimens show small dimensions, close to those of *Homo*, but the EDJ shape unambiguously displays an australopith morphology (e.g., DNH 70 and StW 151), and vice versa (SK 27 and SK 847 have large molars but a *Homo*-like EDJ shape). This result thus indicates that tooth size alone should not be used for taxonomic diagnosis in this lineage.

Following our revision, among the 23 specimens previously labeled as *Homo*, only between 4 and 7 specimens very likely belong to this taxon. It is possible that some of the southern African purported *Homo* specimens that, in our analysis, exhibit an australopith-like signal actually do belong to *Homo*. This would mean that, dentally speaking, the typical tooth morphology of specimens attributed as *H. erectus*/*H. egaster* around 2 Ma did not emerge with the genus or was not ubiquitous among all early *Homo* groups. However, the diversity of *Australopithecus*-like and *Paranthropus*-like signals that we have found in the southern African purported *Homo* hypodigm suggests that it is unlikely that all of these specimens belong to *Homo*. We propose that, in addition to the four that display a *Homo* signal, a number of other individuals that show australopith affinities (e.g., SE 1508, StW 80 and 81, and StW 669) should be investigated further and compared with the hominin specimens from Olduvai Gorge, Tanzania, currently under study for internal tooth structure (74). The presence of another hominin taxon not included in the reference sample and represented by one or more of these intermediate specimens cannot be discarded either. This revision of the purported early *Homo* dental material reduces its frequency and representation in the Early Pleistocene southern African fossil record (Fig. 4), and this has implications for the interpretation of the fossil hominin paleodiversity, paleoecology, and dietary behavior at macroregional scale (75).

As an example, if a specimen is regarded as *Homo* whereas it belongs to *Australopithecus* or *Paranthropus*, the interpretations of the biological signal that can be extracted from the mineralized tissues are erroneous. This leads to the false impression that *Homo* was more variable in growth, development, morphology, behavior, and ecology than it really was, and prevents understanding of how it biologically differed from other hominin genera. To illustrate this, we analyzed here the geochemical profile of three teeth previously regarded as *Homo*: SK 96, whose taxonomic identity remains uncertain, and KB 5223 and SKX 268, reattributed, in this study, to *Paranthropus* and *Australopithecus*,

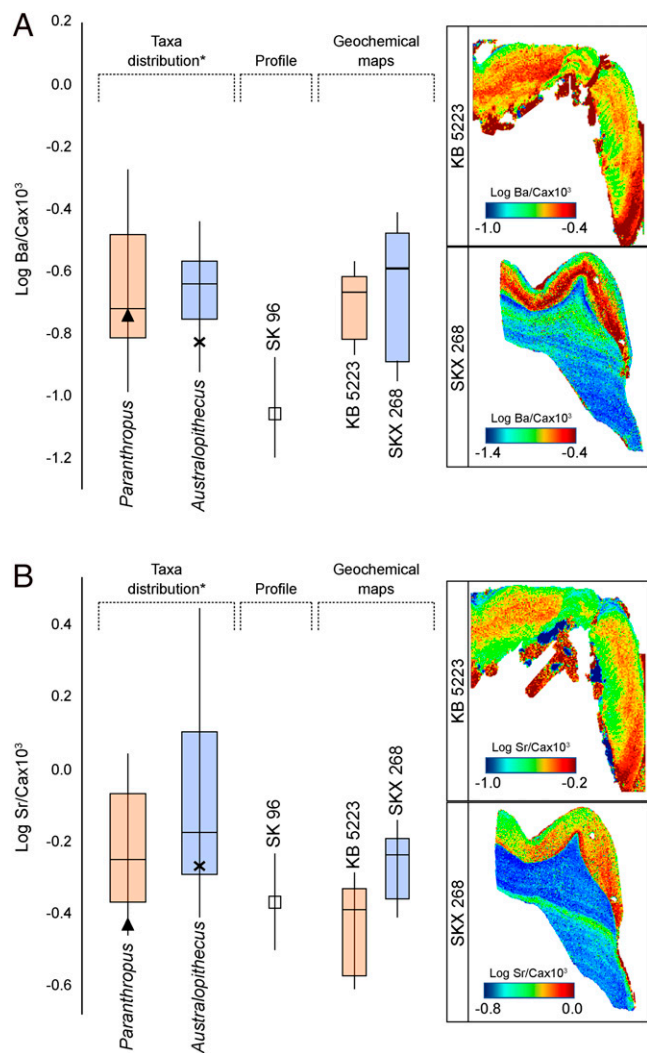


Fig. 5. Ba/Ca (A) and Sr/CA (B) ratios and elemental mapping of SK 96, KB 5223, and SKX 268 compared with the distributions of *Australopithecus* and *Paranthropus*. Asterisks denote that data for taxa distribution were calculated using a combination of new data and a previously published datasets (80, 81), with the average values of KB 5223 (triangles) and SKX 268 (crosses) extracted from Balter et al. (76). SK 96 profile analysis was realized on the enamel for this study, as well as the geochemical maps of KB 5223 and SKX 268. All error bars are 2 sigma.

respectively (Fig. 5). We also conducted elemental mapping of Sr/Ca and Ba/Ca ratios on the latter two specimens. Our geochemical results confirm those of a previous analysis of KB 5223 and SKX 268 that aimed to infer early *Homo* dietary preferences (76). Both SK 96 and KB 5223 have low Sr/Ca ratios, close to the mean value of TM 1517, holotype of *P. robustus*, with a range of variation compatible with the values of pencontemporaneous browser taxa (76). The elemental maps of KB 5223 are highly affected by diagenesis, showing large areas of uniform density and few structured areas indicative of a biogenic signal (i.e., of biological origin, as opposed to diagenetic that is related to taphonomy and fossilization processes). In the M¹ SKX 268, the Ba/Ca and Sr/Ca ratios are higher than in the other two specimens, more closely approximating the condition of the *Australopithecus*. The overall distribution of Ba/Ca in the enamel indicates a dominance of biogenic signal (some of the highest concentrations follow the striation pattern of the Retzius lines), while the Sr/Ca ratio is more influenced by diagenetic processes (with low and high values distributed homogeneously). Conversely, for both variables, the dentine shows pristine, biogenic banding typical of the growth

layering architecture of tooth formation, mimicking the profiles obtained by a previous study on *Australopithecus* (77). SKX 268 preserves part of the nursing sequence, which is comparable with the breastfeeding timing previously proposed for *Australopithecus* (77). Lactation behavior—with the infant relying more on solid food during periods of abundance, allowing the mother to replenish her energetic and calcium reserves to support lactation during periods of food scarcity—was proposed to represent a versatile adaptive trait to survive challenging ecological niches (77). Taxonomically misattributing SKX 268 would thus skew our understanding of the intrataxic/intertaxic variability of this feature.

Regardless of the robustness of the biogeochemical studies arising from the southern African hominin fossil record, accurate interpretations are contingent on correct taxonomic classification of hominin dental specimens. Our results highlight the need to continually interrogate taxonomic attributions of Early Pleistocene hominins in light of new evidence, such as shifts in first appearance dates [i.e., necessitated by the classification of the Ledi-Geraru mandible as *Homo* (78)], the unresolved taxonomic status of numerous specimens from Omo, Ethiopia (79), and Koobi Fora, Kenya (36), and the recent discovery of rather primitive *Homo* dentitions from Rising Star Cave, South Africa (65), Liang Bua, Indonesia (80), and Callao Cave, Philippines (81). This will facilitate paleobiological reconstructions and our understanding of the timing, location, and nature of the selective pressures that resulted in a shift between australopith-like and *Homo*-like grades during hominin evolution.

Materials and Methods

Thirty-seven southern African postcanine teeth previously attributed to early *Homo*, as well as one isolated lower molar, Sts 9, generally attributed to *Australopithecus* but recognized here as *Homo* (SI Appendix, Table S1), were compared with *Australopithecus* ($n = 123$), *Paranthropus* ($n = 97$), and African and Asian Early to mid-Middle Pleistocene *Homo* ($n = 66$; SI Appendix, Supplementary Note 1 and Table S2). We combined nonmetric trait and DSM GM approaches to investigate the EDJ shape of the purported early *Homo* sample, and we conducted geochemical analyses on three of the investigated specimens (for more detailed information, see SI Appendix, Supplementary Material and Methods).

Data Availability. All study data are included in the article and/or SI Appendix. The microCT scans of fossil specimens are available by research application to the relevant curatorial institution.

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