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Sacrum morphology supports taxonomic heterogeneity of *Australopithecus africanus* at Sterkfontein Member 4

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Abstract

The presence of multiple *Australopithecus* species at Sterkfontein Member 4, South Africa (2.07 to 2.61 Ma) is highly contentious. Quantitative assessments of craniodental and postcranial variability remain inconclusive. Using geometric morphometrics, we compared the sacrum of the small-bodied, presumed female subadult *Australopithecus africanus* skeleton Sts 14 and the large, alleged male adult StW 431 against a geographically diverse sample of modern humans, and two species for each of the genera *Gorilla*, *Pan* and *Pongo*. The probabilities of sampling morphologies as distinct as Sts 14 and StW 431 from a single species ranged from 1.3 to 2.5% for the human sample, and from 0.0 to 4.5% for the ape sample, depending on the analysis performed. Neither differences in developmental or geologic age nor sexual dimorphism could account for the differences between StW 431 and Sts 14 sacra. These findings support earlier claims of taxonomic heterogeneity at Sterkfontein Member 4.

Main

Traditionally, all early hominin fossils from Taung, Sterkfontein Member 4 and Makapansgat have been attributed to *Australopithecus africanus*, although several authors noted the remarkably high morphological variability within these assemblages [1–10]. This led Clarke [1–3,11] to propose the presence of a second *Australopithecus* species at Sterkfontein Member 4 and Makapansgat, which he named *A. prometheus* after [12]. Recent studies of the StW 573 “Little foot” skeleton from Sterkfontein Member 2 renewed debates on the functional biology and taxonomy of the Plio-Pleistocene hominins from South Africa [11,13–15]. Nevertheless, the presence of two closely related *Australopithecus* taxa at Sterkfontein Member 4 is not widely accepted [16,17] because of the ambiguous research evidence and the fragmentary preservation of the fossils. Moreover, quantitative studies focused mainly on the craniodental remains and rarely considered morphological variation within a broad comparative setting.

Sts 14 [18–20] and StW 431 [21–25] are the best-preserved partial skeletons from Sterkfontein Member 4. The unfused apophyses of the iliac crests and ischial tuberosities and the partially fused epiphyseal plates of the sacral alae of Sts 14 suggest an age of about 15 years compared to modern human standards [23,26,27]. Its acetabulum, which already reached adult dimensions, predicts a body size of 25.4 kg [28], suggesting a female sex. StW 431, an adult individual possibly of male sex based on its greater robusticity and large body size, probably weighed considerably more than 40 kg [28,29]. Both Sts 14 and StW 431 are traditionally attributed to *A. africanus*. However, the StW 431 sacrum is narrower and more elongated while that of Sts 14 is rather gracile and wide relative to its small sacral body [25,30] (Fig. 1). The superior tips of the transverse processes of the sacrum are prominent in both StW 431 and Sts 14, though they project superiorly in StW 431 while they are laterally oriented in Sts 14, resulting in a smooth and elongated superior aspect of the sacral wings [23]. This contrasts to the sacrum of A.L. 288-1 (*Australopithecus afarensis*), which lacks well-developed tips of the transverse processes [31].

Here, we used different geometric morphometric approaches based on 113 3D landmarks to compare the morphological differences between the StW 431 and Sts 14 sacra to all pairwise differences within our sample of extant species, including a geographically diverse sample of juvenile and adult modern humans (*N* = 74) and an extensive sample of extant great ape species (*N* = 94). Additionally, the *A. afarensis* A.L. 288-1 'Lucy' was considered. Because the size and shape of the sacral wings varied strongly and largely independently from that of the sacral body, we used two different morphometric approaches, one in which we registered the landmark configurations by a Generalized Procrustes Analysis (GPA) of all 113 landmarks, and one in which all landmarks were registered based on a GPA of the landmarks on the body of the first sacral vertebra only. Both datasets were analyzed separately in shape space and form space [32,33].

Results And Discussion

In the principal component analysis (PCA) of the shape coordinates based on the full GPA, Sts 14 and StW 431 plotted at the opposite sides of the modern human distribution, whereas all extant great apes clearly separated from modern humans along PC1 (accounting for 50% of the total variance) (Fig. 2 and Supplementary data file S1). StW 431 resembled the great apes in having a considerably narrower and more elongated sacrum compared to that of humans, whereas Sts 14 possessed relatively wider and superiorly flatter alae. Nevertheless, StW 431 was overall more similar to modern humans than great apes (see the quadratic discriminant analysis in Supplementary Note 1). The two reconstructions of the A.L. 288-1 sacrum were close to Sts 14. Shape variation along PC2 (11%) was driven by the supero-inferior orientation of the sacral alae relative to the sacral body. StW 431 differed along PC2 from Sts 14 and A.L. 288-1 for its caudally directed sacral portion of the linea terminalis. PC3 (6%) reflected changes in the antero-posterior orientation of the sacral alae and did not add considerably to the differences between StW 431 and Sts 14. Some *Pongo* specimens were intermediate between the human and great ape clusters; one *Pongo pygmaeus* female even overlapped with the *Homo* cluster because of its relatively broad shape. *Pongo* and *Gorilla* separated from one another quite well, whereas *Pan* displayed considerable overlap with the two other ape genera.

The different species within the genera *Gorilla*, *Pan*, and *Pongo* did not separate based on sacral morphology (Fig. 3A), nor did the different modern human populations (Fig. 3B). The sacral shape of the subadult modern humans—with ages comparable to that of Sts 14—tended to separate from adult modern humans along PC2, while Sts 14 and StW 431 separated along PC1. Even though modern human males and females overlapped in the PCA plot, the mean shapes differed significantly in full shape space (p=0.0005). Size-related shape variation accounted for 12.3% of total sacral shape variation within the full sample but for only 3.3% within the hominin sample (see also Supplementary Fig. 1).

Since sacrum morphology of *Australopithecus* more closely resembled that of *Homo* than that of great apes, we repeated the geometric morphometric analysis by excluding the great apes (Fig. 3B). In this reduced sample, the main axis of variation was driven by the supero-inferior orientation of the alae, which again distinguished StW 431 from Sts 14. The A.L. 288-1 sacrum deviated from modern humans and the

other *Australopithecus* specimens for its more posteriorly oriented alae and the weakly developed superior tips of the transverse processes (PC2). The Procrustes distance (a measure of shape difference) between StW 431 and Sts 14 was among the largest observed distances within the modern human sample, including both adults and subadults (Table 1, Fig. 4). Only 2.5% of the Procrustes shape distances between all pairwise male-female comparisons within modern humans were higher than the Procrustes distance between Sts 14 and StW 431. A very similar result (2.4%) was obtained when all pairwise Procrustes distances of modern humans, regardless of their sex, were considered. Procrustes distances in form space (comprising differences in both shape and size; see Supplementary Fig. 2) resulted in slightly higher percentages (3.4% and 3.3%, respectively). Within great apes, a greater percentage of pairwise Procrustes distances exceeded that between Sts 14 and StW 431 (Table 1).

To explore the contribution of sexual dimorphism to sacral shape, we also performed a PCA for modern human adults and the two fossils Sts 14 and StW 431 only (Supplementary Fig. 3). Sexual dimorphism was represented by PC2 and PC3, despite a large overlap between males and females, whereas both sexes showed the same range of variation along PC1. Importantly, the differences between Sts 14 and StW 431 along PC2 and PC3 resembled the average sexual dimorphism in humans, both in pattern and magnitude. However, the two fossils mainly differed along PC1, which is unrelated to sexual dimorphism. Along this PC1, 1.0% of all pairwise differences and 1.1% of male-female pairwise differences exceeded the distance between Sts 14 and StW 431.

Additionally, with the aim to better capture the relative dimensions of the transverse processes, we compared the sacral shape of StW 431 and Sts 14 to those of the recent species after the registration of the landmark configurations based on the corpus landmarks only. The resulting PCA plot (Supplementary Fig. 4) was similar to that presented above in Fig. 2 for the separation of hominins from great apes along PC1, but showed a more pronounced overlap between the great apes. The percentages of pairwise Procrustes distances in Homo exceeding the distance between Sts 14 and StW 431 ranged from 2.1% to 2.6%. Importantly, the corresponding percentages in the great ape species were considerably lower than for the full GPA, ranging from 0% in P. troglodytes to 4.5% in G. gorilla for male-female pairs (Table 1).

Our study uses a comprehensive geometric morphometric approach to quantitatively assess the morphological variation within the Sterkfontein Member 4 *Australopithecus* sacrum sample against the background of a large, worldwide sample of modern humans and six great ape species. We restricted our comparative sample to specimens without lumbosacral transitional vertebrae because Sts 14 and StW 431 do not patently show sacral segmentation anomalies. However, since these fossils preserve only the first two and a half sacral vertebrae, it is impossible to completely rule out transitional vertebrae in either of these specimens, hence this aspect should be investigated further. In fact, Sts 14 shows a segmentation anomaly at the thoracolumbar transition. Border shifts of the thoracolumbar junction are frequent in hominin fossils and are often associated with border shifts at the lumbosacral junction [34]. The morphological differences between the partial sacra of StW 431 and Sts 14 are remarkable when compared to the range of variation in modern humans and great apes. Although these morphological discrepancies can be partly explained by individual variation, further exploration of the impact of sexual

dimorphism, allometry, different individual and geological age, and, eventually, taxonomic heterogeneity are necessary.

Sexual dimorphism, allometry, and individual age. In modern humans, sexual dimorphism of the sacrum is low compared to that of other parts of the pelvis [35]. Although we found a significant shape dimorphism in the human sacrum, which is also reflected by the shape differences between StW 431 and Sts 14, the very large overall shape difference between the two fossils remained very high when compared to the morphological distances of all possible male-female pairwise combinations. As expected, we did not observe considerable sexual dimorphism in the great ape sacrum shape. In addition, size-related shape differences within hominins were of small magnitude (3.3% allometry shape variation) and, hence, are unlikely to account for the differences in sacral shape between StW 431 and Sts 14. It is also unlikely that the shape differences between the fossils result from differences in individual age because in our PCA analysis the vector between StW 431 and Sts 14 was almost perpendicular to the vector of average human ontogenetic shape change. Moreover, if Sts 14 had developed to full adult age, the fusion of the lateral epiphyseal plates would have resulted in an even wider sacrum, and thus would have further increased the observed morphological distance from StW 431.

Geological age. The deposits of Sterkfontein Member 4 accumulated between 2.61 and 2.07 Ma [36,37], and Sts 14 and StW 431 can thus differ up to 540,000 years in chronological age. The Sts 14 skeleton was found within a single block of breccia 2.4 m away from and 0.4 m deeper than Sts 5 ('Mrs. Ples') [38,39]. As Sts 5 is associated with the flowstone topping Sterkfontein Member 4 [37], Sts 14 might also date close to 2.07 Ma. On the other hand, almost all fragments of the StW 431 skeleton were found in two adjacent square yards at a mean depth of 7 m below datum, and thus at the same depth as the bulk of the Member 4 fossils recovered between 1966 and the late 1990s by teams of the University of the Witwatersrand. However, parts of the StW 431 skeleton were vertically distributed between a depth of 6.5 m below datum (some vertebrae) and a depth of 9.0 m (right pubis fragment) [23]. This distribution does not conform to that of a simple talus cone resulting from bones and debris falling into a cave from an above opening as suggested previously [40,41]. Rather, it indicates the presence of deep crevasses into which the fragments have been dislocated. This complex taphonomy makes it challenging to date the StW 431 skeleton, but suggests a rather young age compared to other Member 4 fossils.

However, a possible difference in geological age between StW 431 and Sts 14 can only partially, if at all, account for the differences in sacrum shape. The human populations in our sample completely overlapped in the PCA of sacrum shape, even though they diverged at least 260 to 350 ka years ago [42]. Similarly, *P. pygmaeus* and *P. abelii* diverged about 400,000 years ago [43] but were indistinguishable in the PCA. Even *Pan troglodytes* and *P. paniscus* were comparable in sacrum shape although they diverged 1.6 Ma ago, with extensive gene flow until at least 200 ka ago [44]. *Gorilla gorilla* and *G. beringei* diverged 1.75 Ma ago, with substantial gene flow until at least 20 ka ago [45], but also largely overlapped in sacrum shape. Thus, sacrum shape appears to be evolutionary conserved, presumably due to stabilizing selection imposed by biomechanical and obstetric demands e.g., [46].

In conclusion, our results show that, under the assumption that the *A. africanus* sacrum was as variable in shape as that of modern humans and extant great ape species, it is possible but unlikely that Sts 14 and StW 431 belong to a single species, supporting earlier claims of taxonomic heterogeneity at Sterkfontein Member 4. Yet, as neither Sts 14 nor StW 431 is associated with craniodental remains, it is at the moment impossible to infer which one of these partial skeletons, if any, belongs to *A. africanus*.

Methods

The fossil and comparative samples

We compared the partial sacrum of StW 431 and Sts 14 to a sample of 157 sacra from adult modern humans and great apes with known sex. In addition, we included the sacrum of A.L. 288-1 (*A. afarensis*), an alleged female. Our worldwide sample 63 modern humans including Central Europeans (*N*=28), Western Africans (*N*=13), Khoe-Sān (*N*=7) and Pygmies (*N*=2), Indians (*N*=8), and Fuegians (*N*=5). The great ape sample included *G. beringei* (*N*=10), *G. gorilla* (*N*=23), *P. paniscus* (*N*=8), *P. troglodytes* (*N*=22), *P. abelii* (*N*=7), and *P. pygmaeus* (*N*=24) (Table 2). Since Sts 14 died prior to fusion of the lateral epiphyseal plate and of the ring apophysis of the superior surface of the sacral body [23,47,48], we included also six male and five female juvenile modern humans (Central Europeans, *N*=10, Khoe-Sān, *N*=1) with a developmental age similar to that of Sts 14 (16-17 years). Individuals with lumbosacral transitional vertebrae such as lumbarisations and sacralisations were excluded.

3D surface models of the sacra were generated via a high-resolution optical 3D-surface scanner (QT Sculptor PT-M4, Polymetrics, Darmstadt, Germany) [49]. In instances where CT data were available, the meshes were generated by segmentation using Amira software (www.fei.com). The skeletal collections and the source of the surface models are listed in Table 2.

Virtual reconstruction of the Australopithecus *specimens*

The StW 431 sacrum preserves most of the first two and a half sacral vertebrae on the left side, while the right side is more damaged. The most inferior portion of the left auricular surface is also broken off and was restored based on the shape of the auricular surface of the ilium (Fig. 1). This resulted in an approximately 2 mm longer auricular surface than the one originally preserved. Afterwards, the restored left side of the fossil was mirrored with respect to the mid-sagittal plane to replace the incomplete right side.

The Sts 14 sacrum preserves the left side of the first two sacral vertebrae. We reconstructed it virtually by removing the restoration by Robinson [19] in plaster of Paris on the right side, and mirroring the originally preserved left side with respect to the mid-sagittal plane.

Since the A.L. 288-1 sacrum is taphonomically distorted, we used the same virtual protocol to obtain two symmetrised versions of the fossil, one for the mirrored right side and the other for the mirrored left side.

Geometric morphometric analyses

The landmark configuration (Supplementary Fig. S5) included 29 anatomical landmarks, 36 semilandmarks on five curves, and 48 surface semilandmarks. In particular, the curves described the margins of the superior sacral surface and of the auricular surfaces, the anterior aspect and the superior aspect of the alae, and the posterior corner of the alae. The anterior and superior aspects of the upper portion of the sacrum were represented by surface semilandmarks. The posterior surface of the sacrum is highly variable and heavily reconstructed in Sts 14. Therefore, only few landmarks and curve semilandmarks were gathered on the dorsal aspect. The analysis was repeated both with and without the surface semilandmarks to explore the contribution of the inter-landmark surface patches. Since the anterior aspect of the sacrum consists of a rather smooth surface between the chosen landmarks, we did not obtain relevant differences in the outcomes and thus presented the results for the complete landmark configuration.

Standard geometric morphometric analyses were performed using principal component analysis (PCA) of the Procrustes shape coordinates both in shape space and form space by augmenting the shape coordinates with the natural logarithm of centroid size (lnCS) [32,50-52]. The landmarks were collected in Viewbox 4 (www.dhal.com), and analysed in the Evan Toolbox (www.evan-society.org) and R software package [53]. PAST software was used for generating the PCA plots. The morphological differences between StW 431 and Sts 14 were evaluated with respect to the rest of the sample by running a pairwise comparison of the Procrustes distances (i.e., the square root of the summed squared differences between the corresponding shape coordinates of two landmark configurations) after the full GPA analysis in both shape and full space, and after the Procrustes fit based on the subset of 13 landmarks on the body of the first sacral vertebra. The percentages of higher Procrustes distances with respect to that observed between StW 431 and Sts 14 were computed for all pairwise comparisons and separately also for male-female pairs only, both on the genus and species level, if at least 20 individuals could be included. A comparative evaluation of size was performed by visualization of the lnCS using box plots R software package, [53] (Supplementary Fig. 2). The influence of size on shape (i.e., allometry) was evaluated by regressing the Procrustes shape variables on lnCS. The male and female group mean differences were tested for the modern humans using a permutation test of the Procrustes distances (10,000 random permutations. Since StW 431 plotted between modern humans and *Pongo* in the PCA analysis after full GPA for the entire sample, the likelihood of classifying StW 431 to either groups was evaluated using Quadratic Discriminant Analysis.

Declarations

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Author Contributions: M.H. initiated and organized the project. C.F. and M.H. designed the research protocol. C.F., V.A.K., M.H. gathered the image data. C.F. and V.A.K. segmented the CT data, generated the surface models and collected the landmark data. C.F. virtually reconstructed the fossil specimens. C.F. and P.M. performed the statistical analyses supported by N.M.W. All authors discussed the results. C.F. and M.H. wrote the manuscript; all authors edited it.

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Data and materials availability: All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Information.

References

1 Clarke, R. J. in *Evolutionary History of the "Robust" Australopithecines* (ed F. E. Grine) 285-292 (Aldine de Gruyter, 1988).

2 Clarke, R. J. in *Contemporary Issues in Human Evolution* Vol. Memoir 21 (eds W. E. Meikle, F. K. Howell, & N. G. Jablonski) (California Academy of Sciences, 1996).

3 Clarke, R. J. Latest information on Sterkfontein's *Australopithecus* skeleton and a new look at *Australopithecus*. *South African Journal of Science* **104**, 443-449 (2008).

4 Kimbel, W. H. & White, T. D. in *Evolutionary History of the "Robust" Australopithecines* (ed F. E. Grine) 259–268 (Aldine de Gruyter, 1988).

5 Lockwood, C. A. & Tobias, P. V. Morphology and affinities of new hominin cranial remains from Member 4 of the Sterkfontein Formation, Gauteng province, South Africa. *Journal of Human Evolution* **42**, 389-450, doi:10.1006/jhev.2001.0532 (2002).

6 Schwartz, J. H. & Tattersall, I. (Wiley-Liss, New York, 2005).

7 Moggi-Cecchi, J. & Boccone, S. in *Dental Perspectives on Human Evolution* (eds S. E. Bailey & J.-J. Hublin) 53-64 (Springer, 2007).

8 Grine, F. E., Delanty, M. M. & Wood, B. A. in *The Paleobiology of Australopithecus* (eds Kaye E. Reed, John G. Fleagle, & Richard E. Leakey) 125-146 (Springer, 2013).

9 Fornai, C., Bookstein, F. L. & Weber, G. W. Variability of *Australopithecus* second maxillary molars from Sterkfontein Member 4. *Journal of Human Evolution* **85**, 181-192, doi:10.1016/j.jhevol.2015.05.013 (2015).

10 Fornai, C., Bookstein, F. L. & Weber, G. W. Corrigendum to “Variability of *Australopithecus* second maxillary molars from Sterkfontein Member 4” [J Hum Evol 85 (2015) 181–192]. *Journal of Human Evolution* **88**, 180, doi:https://doi.org/10.1016/j.jhevol.2015.10.004 (2015).

11 Clarke, R. J. & Kuman, K. The skull of StW 573, a 3.67 Ma *Australopithecus prometheus* skeleton from Sterkfontein Caves, South Africa. *Journal of Human Evolution* **134**, doi:10.1016/j.jhevol.2019.06.005 (2019).

12 Dart, R. A. The Makapansgat proto-human *Australopithecus prometheus*. *American Journal of Physical Anthropology* **6**, 259-283 (1948).

13 Beaudet, A. *et al.* The bony labyrinth of StW 573 (“Little Foot”): Implications for early hominin evolution and paleobiology. *Journal of Human Evolution* **127**, 67-80, doi:https://doi.org/10.1016/j.jhevol.2018.12.002 (2019).

14 Beaudet, A. *et al.* The endocast of StW 573 (“Little Foot”) and hominin brain evolution. *Journal of Human Evolution* **126**, 112-123, doi:https://doi.org/10.1016/j.jhevol.2018.11.009 (2019).

15 Clarke, R. J. Excavation, reconstruction and taphonomy of the StW 573 *Australopithecus prometheus* skeleton from Sterkfontein Caves, South Africa. *Journal of Human Evolution* **127**, 41-53, doi:https://doi.org/10.1016/j.jhevol.2018.11.010 (2019).

16 Grine, F. E. in *The Paleobiology of Australopithecus* (eds Kaye E. Reed, John G. Fleagle, & Richard E. Leakey) 73-104 (Springer, 2013).

17 Grine, F. E. The alpha taxonomy of *Australopithecus* at Sterkfontein: The postcranial evidence. *Comptes Rendus Palevol* **18**, 335-352, doi:https://doi.org/10.1016/j.crpv.2019.01.004 (2019).

18 Broom, R. & Robinson, J. T. Further remains of the Sterkfontein Ape-Man, *Plesianthropus*. *Nature* **160**, 430-431 (1947).

19 Robinson, J. T. *Early Hominid Posture and Locomotion*. (University of Chicago Press, 1972).

20 Häusler, M. & Schmid, P. Comparison of the pelves of Sts 14 and AL 288-1: implications for birth and sexual dimorphism in australopithecines. *Journal of Human Evolution* **29**, 363-383 (1995).

21 Tobias, P. V. 21st Annual Report of PARU and its Precursors. (Department of Anatomy, University of the Witwatersrand, Johannesburg, 1987).

22 Haeusler, M. F. New insights into the locomotion of *Australopithecus africanus* based on the pelvis. *Primatology and Anthropology: Into the Third Millennium* **11**, 53-57 (2002).

23 Haeusler, M. F. & Ruff, C. B. in *Hominid Postcranial Remains from Sterkfontein, South Africa, 1936-1995* (eds B. Zipfel, B.G. Richmond, & C.V. Ward) 181-201 (Oxford University Press, 2020).

24 Kibii, J. M. & Clarke, R. J. A reconstruction of the Stw 431 *Australopithecus* pelvis based on newly discovered fragments. *South African Journal of Science* **99**, 225-226 (2003).

25 Toussaint, M., Macho, G. A., Tobias, P. V., Partridge, T. C. & Hughes, A. R. The third partial skeleton of a late Pliocene hominin (Stw 431) from Sterkfontein, South Africa. *South African Journal of Science* **99**, 215-223 (2003).

26 Berge, C. & Gommery, D. Le sacrum de Sterkfontein Sts 14 Q (*Australopithecus africanus*): nouvelles données sur la croissance et sur l'âge osseux du spécimen (hommage à R. Broom et J.T. Robinson). *Comptes rendus de l'académie des sciènces de Paris, Sciences de la Terre et des planètes* **329**, 227-232 (1999).

27 Häusler, M. & Berger, L. R. Stw 441/465: A new fragmentary ilium of a small-bodied *Australopithecus africanus* from Sterkfontein, South Africa. *Journal of Human Evolution* **40**, 411-417 (2001).

28 Ruff, C. B., Burgess, M. L., Squyres, N., Junno, J.-A. & Trinkaus, E. Lower limb articular scaling and body mass estimation in Pliocene and Pleistocene hominins. *Journal of Human Evolution* **115**, 85-111, doi:https://doi.org/10.1016/j.jhevol.2017.10.014 (2018).

29 McHenry, H. M. & Berger, L. R. Body proportions in *Australopithecus afarensis* and *A. africanus* and the origin of the genus *Homo*. *Journal of Human Evolution* **35**, 1-22 (1998).

30 Haeusler, M. F. *New insights into the locomotion of Australopithecus africanus: Implications of the partial skeleton Stw 431 (Sterkfontein, South Africa)*, Universität Zürich, (2001).

31 Stern, J. T. J. & Susman, R. L. The locomotor anatomy of *Australopithecus afarensis*. *American Journal of Physical Anthropology* **60**, 279-317, doi:10.1002/ajpa.1330600302 (1983).

32 Bookstein, F. L. *Morphometric Tools for Landmark Data: Geometry and Biology*. (Cambridge University Press, 1991).

33 Mitteroecker, P., Gunz, P., Windhager, S. & Schaefer, K. A brief review of shape, form, and allometry in geometric morphometrics, with applications to human facial morphology. *Hystrix, the Italian Journal of Mammalogy* **24**, 59-66, doi:10.4404/hystrix-24.1-6369 (2013).

34 Haeusler, M. in *Spinal Evolution: morphology, function, and pathology of the spine in hominoid evolution* (eds Ella Been, A. Gómez-Olivencia, & P.A. Kramer) Ch. 10, 213-245 (Spinger, 2019).

35 Flander, L. B. & Corruccini, R. S. Shape differences in the sacral alae. *American Journal of Physical Anthropology* **52**, 399-403 (1980).

36 Pickering, R. *et al.* U–Pb-dated flowstones restrict South African early hominin record to dry climate phases. *Nature*, doi:10.1038/s41586-018-0711-0 (2018).

37 Pickering, R. & Herries, A. I. R. in *Hominin Postcranial Remains from Sterkfontein, South Africa, 1936-1995* (eds Zipfel. B., B. Richmond, & C. Ward) (Oxford University Press, 2020).

38 Broom, R. & Robinson, J. T. Further evidence of the structure of the Sterkfontein ape-man *Plesianthropus*. *Transvaal Museum Memoir* **4**, 1-83 (1950).

39 Thackeray, F., Gommery, D. & Braga, J. Australopithecine postcrania (Sts 14) from the Sterkfontein Caves, South Africa: the skeleton of'Mrs Ples'? *South African journal of science* **98**, 211-212 (2002).

40 Robinson, J. T. Sterkfontein stratigraphy and the significance of the extension site. *S. Afr. Archaol. Bull.* **17**, 87-107 (1962).

41 Kuman, K. & Clarke, R. J. Stratigraphy, artefact industries and hominid associations for Sterkfontein, Member 5. *Journal of Human Evolution* **38**, 827-847 (2000).

42 Schlebusch, C. M. *et al.* Southern African ancient genomes estimate modern human divergence to 350,000 to 260,000 years ago. *Science* **358**, 652-655, doi:10.1126/science.aao6266 (2017).

43 Locke, D. P. *et al.* Comparative and demographic analysis of orang-utan genomes. *Nature* **469**, 529-533, doi:10.1038/nature09687 (2011).

44 de Manuel, M. *et al.* Chimpanzee genomic diversity reveals ancient admixture with bonobos. *Science* **354**, 477-481, doi:10.1126/science.aag2602 (2016).

45 Scally, A. *et al.* Insights into hominid evolution from the gorilla genome sequence. *Nature* **483**, 169-175, doi:10.1038/nature10842 (2012).

46 Pavličev, M., Romero, R. & Mitteroecker, P. Evolution of the human pelvis and obstructed labor: new explanations of an old obstetrical dilemma. *American journal of obstetrics and gynecology* **222**, 3-16, doi:10.1016/j.ajog.2019.06.043 (2020).

47 Gommery, D. & Thackeray, J. F. Sts 14, a male subadult partial skeleton of *Australopithecus africanus*? *South African Journal of Science* **102**, 91-92 (2006).

48 Bonmatí, A., Arsuaga, J. L. & Lorenzo, C. Revisiting the developmental stage and age-at-death of the "Mrs. Ples" (Sts 5) and Sts 14 specimens from Sterkfontein (South Africa): do they belong to the same individual? *Anat Rec* **291**, 1707-1722, doi:10.1002/ar.20795 (2008).

49 Haeusler, M. F., Schweitzer, W., Braun, M., Brüschweiler, W. & Bär, W. Evaluation von 3D-Scanner für den Einsatz in der Rechtsmedizin. *Rechtsmedizin* **14**, 356-357 (2004).

50 Bookstein, F. L. *A Course in Morphometrics for Biologists: Geometry and Statistics for Studies of Organismal Form*. (Cambridge University Press, 2018).

51 Weber, G. W. & Bookstein, F. L. *Virtual Anthropology: A Guide to a New Interdisciplinary Field*. (Springer, 2011).

52 Mitteroecker, P., Gunz, P., Bernhard, M., Schaefer, K. & Bookstein, F. L. Comparison of cranial ontogenetic trajectories among great apes and humans. *Journal of Human Evolution* **46**, 679-698, doi:https://doi.org/10.1016/j.jhevol.2004.03.006 (2004).

53 R Development Core Team. *R: A language and environment for statistical computing*, <http://www.R-project.org> (2008).

Tables

Table 1: Percentages of the pairwise Procrustes distances that exceeded the Procrustes distance between StW 431 and Sts 14. The computations were performed for male-female pairs only as well as for all pairwise comparisons. m/f = male-female; S1 = first sacral vertebra

Groups	Full GPA shape space		Full GPA form space		Procrustes fit on S1 body shape space	
	m/f pairs	all pairs	m/f pairs	all pairs	m/f pairs	all pairs
Modern human adults (*N*=63)	1.5	1.3	3.8	3.7	2.6	2.1
Modern human adults and subadults (*N*=74)	2.5	2.4	3.4	3.3	2.6	2.3
Gorilla (*N*=33)	18.8	18.8	54.2	39.4	5.4	4.2
Pan (*N*=30)	24.1	21.8	6.0	6.9	0.9	1.1
Pongo (*N*=31)	26.7	28.8	39.5	28.2	2.4	4.5
G. gorilla (*N*=23)	15.2	15.8	47.7	32.0	4.5	3.6
P. troglodytes (*N*=22)	24.2	22.1	0.8	0.4	0.0	0.0
P. pygmaeus (*N*=24)	30.5	31.2	43.8	31.5	3.9	6.2

Table 2: List of fossil sacra and modern comparative material

	Individuals / taxa	Females	Males	Collections
Australopithecus	Sts 14q	1		a
	StW 431h		1	b
	A.L. 288-1an	1		c
Modern humans	adults	28	35	d, e, f, g, h, i, j
	subadults	5	6	k
Great apes	*Gorilla beringei*	2	8	d, h, l, m
	Gorilla gorilla	11	12	d, h, l, m, n
	Pan paniscus	6	2	o
	Pan troglodytes	12	10	d, h, l, m, n, p, q
	Pongo abelii	5	2	d, h
	Pongo pygmaeus	16	8	d, h, l, n, q
Total modern comparative sample (*N*=168)		85	83	

a) Ditsong National Museum of Natural History, Pretoria; b) Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa; c) National Museum of Ethiopia, Addis Ababa, Ethiopia; d) Anthropological Institute and Museum, University of Zurich, Switzerland; e) Department of Anthropology and Narrenturm, Natural History Museum of Vienna, Austria; f) Department of Evolutionary Anthropology, University of Vienna, Austria; g) Institute of Evolutionary Medicine, University of Zurich, Switzerland; h) Laboratory of Prehistoric Archaeology and Anthropology, University of Geneva, Switzerland; i) Museum of Natural History, University of Florence, Italy; j) Smithsonian National Museum of Natural History, Washington, USA; k) Hospital Timone, Marseille, France; l) Department of Zoology, Natural History Museum of Vienna, Austria; m) Zoological Museum, University of Zurich, Switzerland; n) Digital Morphology Museum, KUPRI, Kyoto University, Japan; o) Royal Museum for Central Africa, Tervuren, Belgium; p) Museum of Primatology, University of California, San Diego; q) Natural History Museum Basel, Switzerland.

Figures

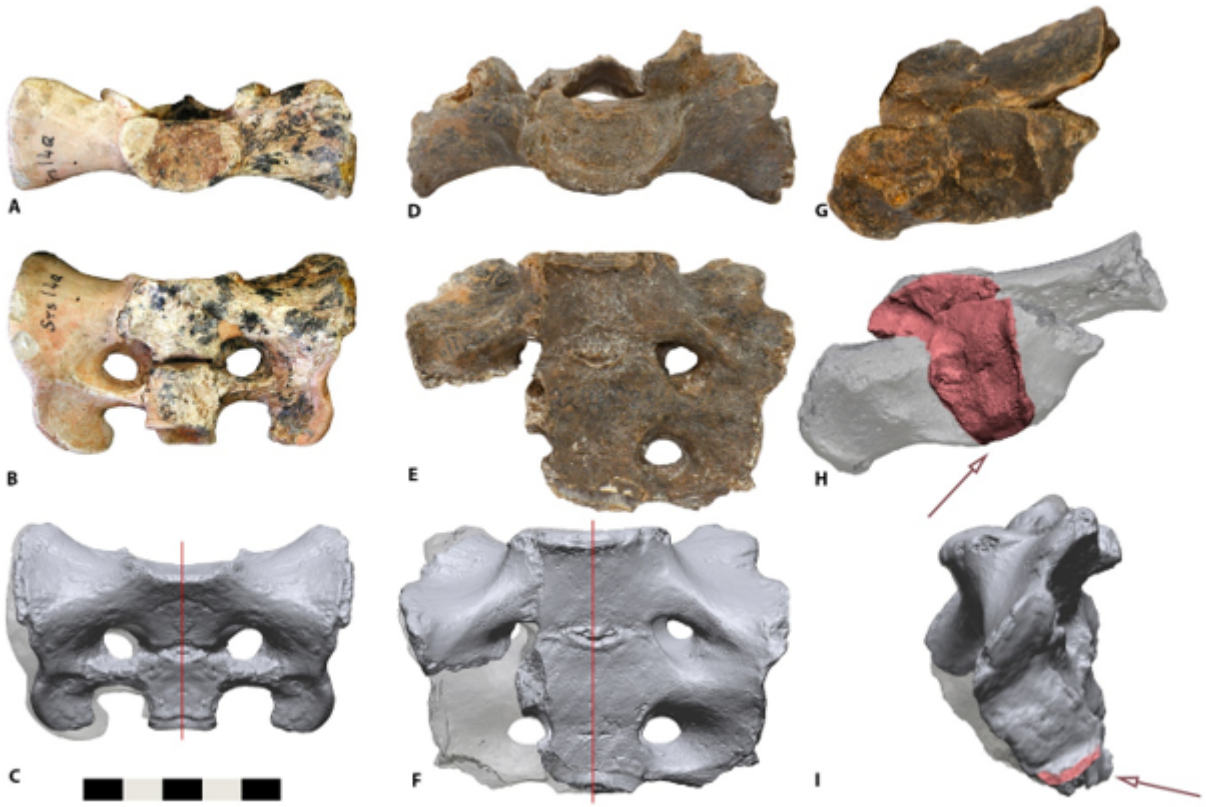

Figure 1

The sacrum of Sts 14 and StW 431, both traditionally attributed to A. africanus. (A) Photograph of the Sts 14 sacrum, superior view and (B) anterior view. (C) 3D surface model of the reconstructed Sts 14 sacrum produced by mirroring the left side with respect to the midsagittal plane (red line), thereby removing the plaster reconstruction of 19 (shown in transparent). (D) Photograph of the StW 431 sacrum, superior view and (E) anterior view. (F) Reconstructed 3D surface model of StW 431 (in transparent) obtained by mirroring the left side of the sacrum at the mid-sagittal plane (red line). (G) Photograph and (H) 3D surface model of the left ilium fragment of StW 431; the sacroiliac joint surface is colored in red. (I) The most inferior portion of the sacral auricular surface (arrow) was restored using the auricular surface of the ilium.

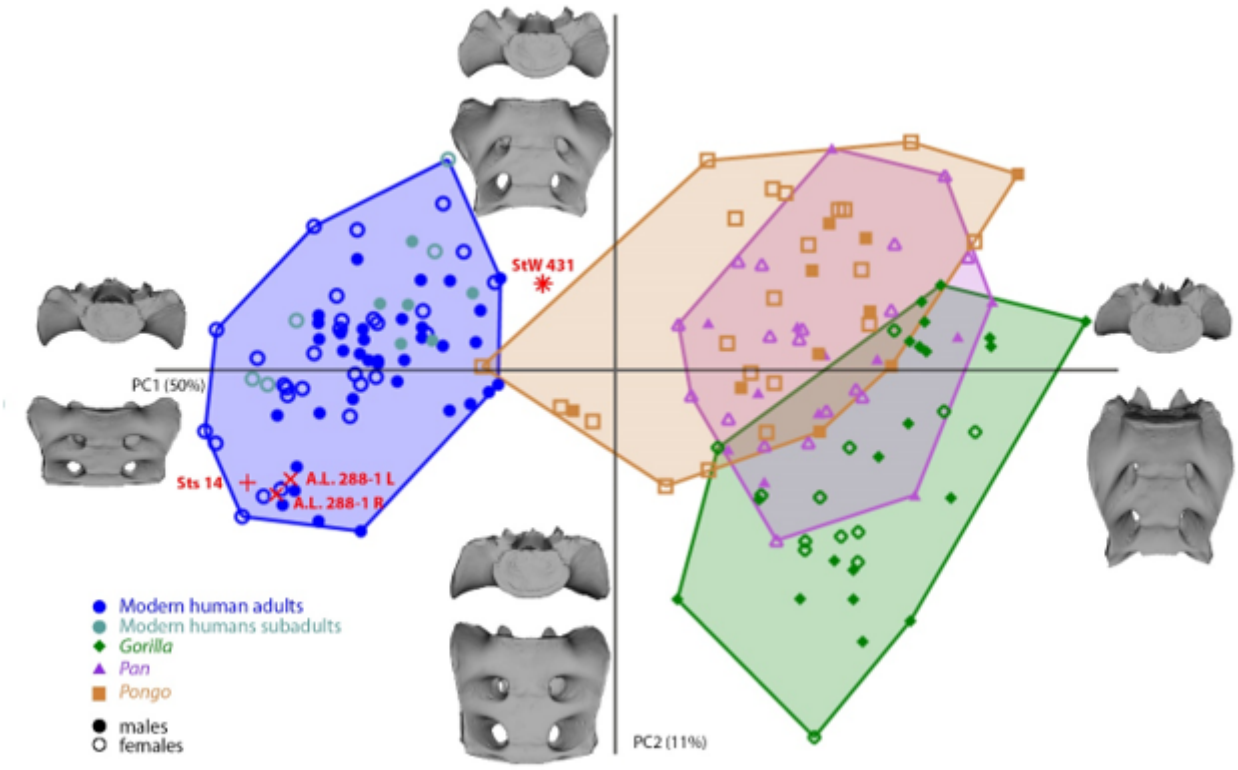

Figure 2

PCA plot of the shape coordinates of the first two sacral vertebrae and auricular surface after a full Generalized Procrustes Analysis (GPA). Sts 14 and StW 431 (both attributed to Australopithecus africanus) plot at opposite sides of the modern human distribution, while the two reconstructions of the A.L. 288-1 (A. afarensis) sacrum are close to Sts 14. The great apes are separated from the hominins along PC1. PC1 is driven by the overall height-to-width ratio of the sacrum, and PC2 represents the orientation and relative antero-posterior width of the sacral alae.

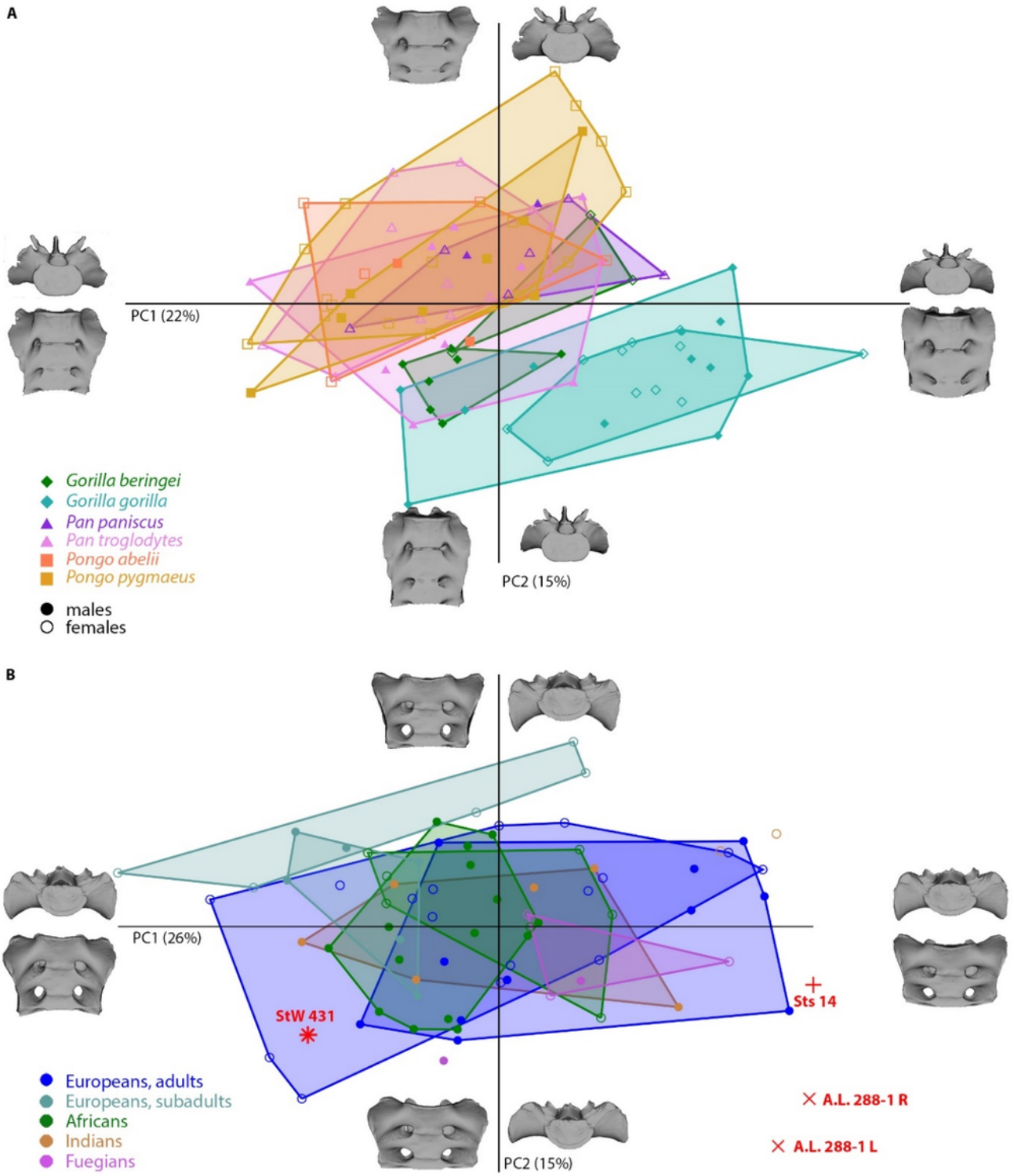

Figure 3

PCA plot of the Procrustes shape coordinates for the upper portion of the sacrum (full GPA) in great apes and modern humans. (A) PCA plot of great apes, labelled by species and sex. Within each genus, the species and sexes largely overlap, except for G. beringei. (B) PCA plot for the upper portion of the sacrum (full GPA) in modern humans and Australopithecus, labelled by sex, age, and ethnicity. Along PC1, the sacral portion of the linea terminalis varies from more horizontal, as in Sts 14 and A.L. 288-1, to more

caudally oriented, as in StW 431. A.L. 288-1 differs from StW 431 and Sts 14 along PC2 for its posterior orientation of the alae. The various modern human populations do not separate, but the subadult females tend to differ from the adults along PC2, while StW 431 and Sts 14 differ along PC1.

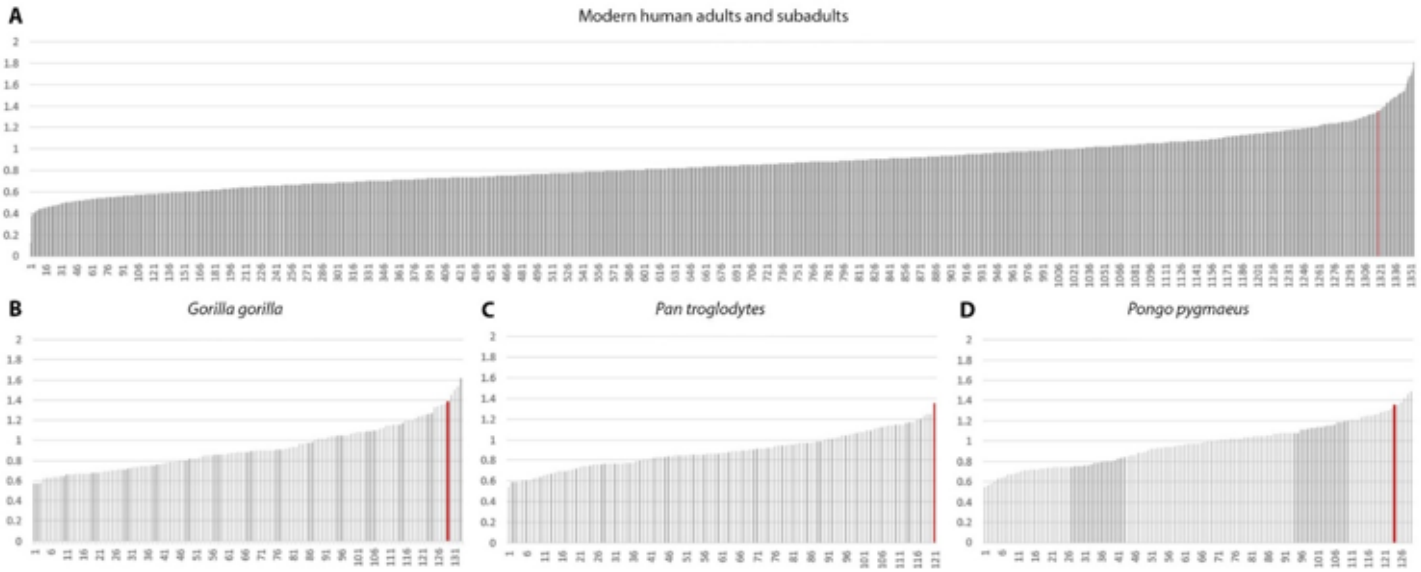

Figure 4

Column distribution of the male-female pairwise Procrustes distances after Procrustes fit based on 13 landmarks on the first sacral vertebra. The red lines indicate the Procrustes distance between Sts 14 and StW 431. (A) In modern humans only 35 out of 1353 Procrustes distances (2.6%) exceeded that between Sts 14 and StW 431. (B) In Gorilla gorilla 4.5% (6 out of 132) distances exceeded that between the fossils, in Pan troglodytes 0% (0 out of 120), and in Pongo pygmaeus 3.9% (5 out of 128).

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Fornaietal3dAnimatedScatterplot.gif
- FornaietalSacrummorphologyofAustralopithecusafricanusSupplements.docx
- ReadMeLandmarkdata.txt
- FornaietalLandmarkdataMorphologika.txt