doi:10.1038/nature17999

Homo floresiensis-like fossils from the early Middle Pleistocene of Flores

Gerrit D. van den Bergh[1]*, Yousuke Kaifu[2]*, Iwan Kurniawan[3], Reiko T. Kono[2], Adam Brumm[4,5], Erick Setiyabudi[3], Fachroel Aziz[3] & Michael J. Morwood[1]‡

The evolutionary origin of *Homo floresiensis*, a diminutive hominin species previously known only by skeletal remains from Liang Bua in western Flores, Indonesia, has been intensively debated. It is a matter of controversy whether this primitive form, dated to the Late Pleistocene, evolved from early Asian *Homo erectus* and represents a unique and striking case of evolutionary reversal in hominin body and brain size within an insular environment[1–4]. The alternative hypothesis is that *H. floresiensis* derived from an older, smaller-brained member of our genus, such as *Homo habilis*, or perhaps even late *Australopithecus*, signalling a hitherto undocumented dispersal of hominins from Africa into eastern Asia by two million years ago (2 Ma)[5,6]. Here we describe hominin fossils excavated in 2014 from an early Middle Pleistocene site (Mata Menge) in the So'a Basin of central Flores. These specimens comprise a mandible fragment and six isolated teeth belonging to at least three small-jawed and small-toothed individuals. Dating to ∼0.7 Ma, these fossils now constitute the oldest hominin remains from Flores[7]. The Mata Menge mandible and teeth are similar in dimensions and morphological characteristics to those of *H. floresiensis* from Liang Bua. The exception is the mandibular first molar, which retains a more primitive condition. Notably, the Mata Menge mandible and molar are even smaller in size than those of the two existing *H. floresiensis* individuals from Liang Bua. The Mata Menge fossils are derived compared with *Australopithecus* and *H. habilis*, and so tend to support the view that *H. floresiensis* is a dwarfed descendent of early Asian *H. erectus*. Our findings suggest that hominins on Flores had acquired extremely small body size and other morphological traits specific to *H. floresiensis* at an unexpectedly early time.

This paper reports morphological analyses of hominin fossil materials excavated from the open site of Mata Menge in 2014 (ref. 7) (Extended Data Table 1). Mata Menge is one of the Middle Pleistocene fossil-bearing localities in the So'a Basin, and is situated 74 km east-southeast of Liang Bua. The specimens ($n = 7$) under study were recovered *in situ* from the upper part of a lens-shaped fluvial sandstone unit (Layer II) measuring up to 30 cm in thickness. Layer II is capped by a 6.5 m thick sequence of clay-rich volcanic mudflows (Layer Ia–f) that filled in the stream valley and effectively sealed off Layer II (ref. 7). All hominin fossils were excavated within a maximum linear distance of 15 m. They are associated with stone tools and the fossil remains of dwarfed proboscideans (*Stegodon florensis*), murine rodents, Komodo dragons, and other insular fauna of Flores. The age of Layer II is constrained to between 0.65 and 0.8 Ma, using $^{40}Ar/^{39}Ar$ dating and other methods of age determination[7]. The hominin fossils display some minor dissolution pitting; generally, however, the surface preservation of these specimens is quite good.

SOA-MM4 is a right mandibular corpus (Fig. 1). Despite its small size, we conclude that this partial mandible comes from an adult individual, and that the preserved alveoli represent M_1 to M_3. Only the lingual wall of the mesial alveolus remains for M_1 (Extended Data Fig. 1a). This is not for P_3 because the mandibular canal that normally exits in the area below P_3—M_1 of a hominin mandible further continues anteriorly beyond this level (Extended Data Fig. 1c, h). Micro computed tomography (CT) scan data indicates that the alveolus for the last molar supported a plate-like mesial root and a conical distal root which together tilt distally, a form typical for a hominin M_3 root (Extended Data Fig. 1h, i). Distally to it, the alveolar bone bears no evidence of a tooth germ. The bottoms of the long M_3 alveoli come close to the mandibular canal and display tapering shapes, indicating that its root formation was fully or at least nearly completed.

The lateral corpus is the smallest in our sample, being 21–28% lower and narrower than in the two existing *H. floresiensis* mandibles from Liang Bua (LB1, LB6/1: Extended Data Fig. 2a, b). The lateral corporal surface of SOA-MM4 is damaged, but its cross-sectional shape (Fig. 1d, Extended Data Fig. 1e) clearly indicates the absence of an *Australopithecus*-like hollow, and the presence of a prominent superior lateral torus, a feature characteristic of *Homo*[8,9]. Mandibles of *Australopithecus* and to a lesser extent those of *H. habilis sensu lato* are characterized by a robust and strongly everted lateral corpus as well as a wide extramolar sulcus, in association with their narrow dental arcades and the resultant horizontal separation between the lateral mandibular corpus and the ramus[10,11]. These features are lacking in SOA-MM4, which has a comparatively thin, vertically oriented lateral corpus with a narrow extramolar sulcus that is evident from the medially located anterior ramus root (Extended Data Fig. 1). Such features became apparent in post-1.7-million-year-old (Myr old) *Homo*, including early Javanese *H. erectus* and *H. floresiensis* (Extended Data Fig. 3). Similarities between SOA-MM4 and the corresponding morphology of *H. floresiensis* extend to other features such as the near parallel alveolar margin and mandibular base, a moderate lateral prominence, and a gently hollowed masseteric fossa with a coarse, curved line for the masseter muscle attachment (Extended Data Fig. 4). Multivariate analyses based on the small number of the available linear measurements also support our hypothesis that SOA-MM4 is at least different from *Au. afarensis*, and is similar to *H. floresiensis* in the corpus shape (Extended Data Fig. 5).

The 2014 fossil assemblage from Mata Menge includes six isolated hominin teeth from three or more individuals (Fig. 2; Extended Data Fig. 1j,k; Extended Data Table 1; Supplementary Information). Crown and root measurements available from three permanent teeth (left I^1, right P^3, and left M_1 (or M_2)[12]) are small and similar to or slightly smaller than those of *H. floresiensis* (Extended Data Table 2,

[1]Centre for Archaeological Science, School of Earth & Environmental Sciences, University of Wollongong, Wollongong, New South Wales 2522, Australia. [2]Department of Anthropology, National Museum of Nature and Science, 4-1-1 Amakubo, Tsukuba-shi, Ibaraki 305-0005, Japan. [3]Geology Museum Bandung, Geological Agency, Jalan Diponegoro 57, Bandung 40122, Indonesia. [4]Research Centre of Human Evolution, Environmental Futures Research Institute, Griffith University, Nathan, Queensland 4111, Australia. [5]School of Earth & Environmental Sciences, University of Wollongong, Wollongong, New South Wales 2522, Australia.
*These authors contributed equally to this work.
‡Deceased.

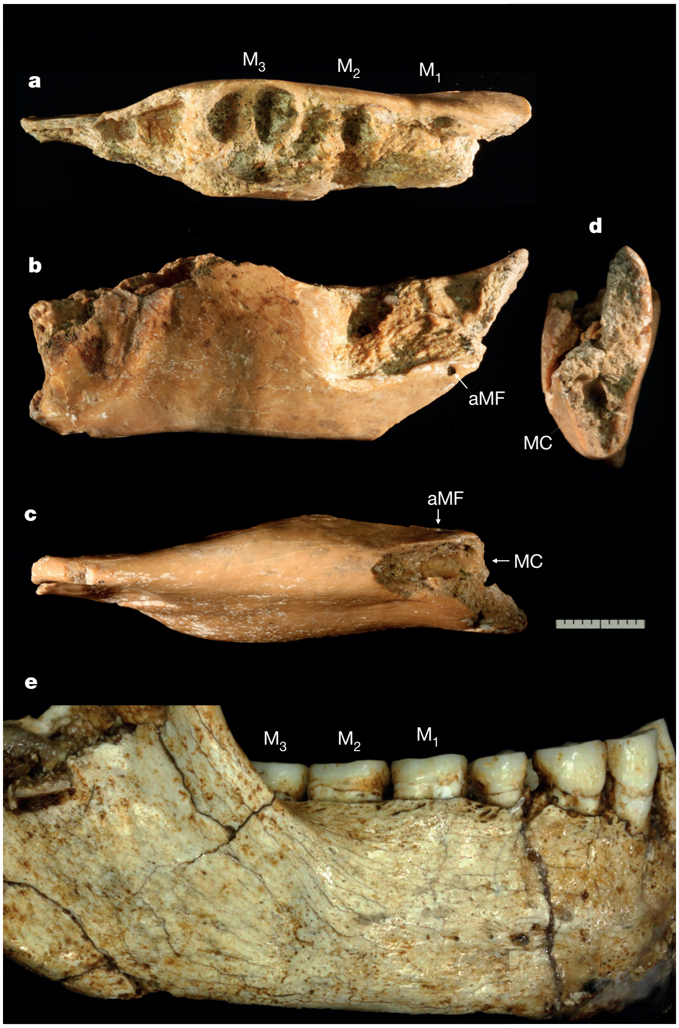


Figure 1 | SOA-MM4 mandible compared with a Liang Bua *H. floresiensis* specimen. a–d, Superior (**a**), lateral (**b**), inferior (**c**), and anterior (**d**) views. **e**, Lateral view of the LB6/1 mandible. M_1, first molar; M_2, second molar; M_3, third molar; MC, mandibular canal; aMF, accessory mental foramen. Scale bar, 10 mm.

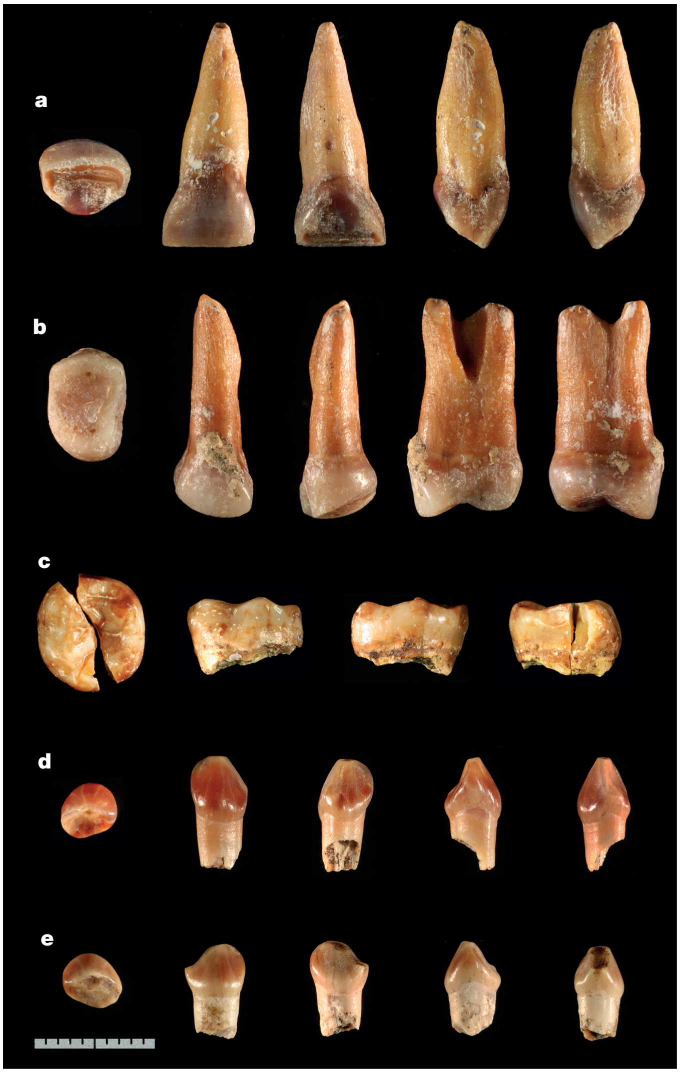


Figure 2 | Isolated teeth from Mata Menge. a, SOA-MM2 (left I^1). **b**, SOA-MM5 (right P^3). **c**, SOA-MM1 (left M_1). **d**, SOA-MM7 (left d_c). **e**, SOA-MM8 (right d_c). In each row, from left to right, occlusal, buccal (labial), lingual, mesial, and distal (except for **c**) views. Scale bar, 10 mm.

Extended Data Fig. 2c–f). The broken root of the $I_{1/2}$ is also equally small (Extended Data Fig. 1k), although comparative measurements are unavailable from this specimen, which was used for direct uranium-series dating[7]. Morphologically, the Mata Menge teeth display the following primitive features: (i) a lingually (I^1, $I_{1/2}$) or distally (P^3) beveled, worn occlusal surface that suggests tilted anterior dentition and substantial prognathism (Extended Data Fig. 1j); (ii) a pronounced P^3 lingual cusp whose mesiodistal diameter compares with that of the buccal cusp[13,14]; and (iii) a mid-trigonid crest on M_1. These features are frequently observed in Early Pleistocene African and Eurasian *Homo* (that is, *H. habilis sensu lato* and *H. erectus sensu lato*), and the third character became frequent in *H. erectus* and some later groups of archaic *Homo*[3,15]. Liang Bua *H. floresiensis* shares the first and probably the third characteristics, although the second is not evident on the worn Liang Bua premolars[16]. Most features of the Mata Menge I^1 and P^3 are not useful for assessing taxonomic affinities relative to *H. habilis* or *H. erectus* (Supplementary Information), although the absence of the P^3 buccal groove is a condition appeared in post-*habilis* grade *Homo*[3]. The Mata Menge and Liang Bua hominins also share a bifurcated, fused P^3 root form.

We digitally reconstructed the broken M_1 (or M_2) crown (SOA-MM1) based on its micro-CT scan (Fig. 3a). Both linear metric and crown contour analyses of the M_1s showed that this five-cusped tooth is moderately long and is close to the average M_1 shape of early Javanese *H. erectus*, but is different from the elongated *H. habilis*-like forms[17] (Fig. 3b, Extended Data Fig. 2e). SOA-MM1 lacks two of the most peculiar, derived characteristics of the Liang Bua *H. floresiensis* M_1s: a reduced cusp number (five to four) and a MD shortened crown configuration[3]. The above comparative morphology remains largely the same even if SOA-MM1 is a M_2, although these analyses do not clearly separate *H. floresiensis* from early Javanese *H. erectus* (Fig. 3c; Extended Data Fig. 2f).

The two deciduous canines (d_cs) from Mata Menge are much smaller than *H. sapiens* ($n = 63$), *H. erectus* ($n = 1$), and *Australopithecus* ($n = 6$), but do not display the relatively high crown shape that characterizes the latter genus (Extended Data Fig. 6a, b). In a principal component analysis (PCA) based on five size-adjusted linear measurements (Extended Data Fig. 6c–e), PC1 separates *Australopithecus*-like primitive (a high crown with a low distal shoulder) and modern human-like derived (a low crown with a high distal shoulder) morphologies. Allometry does not explain this inter-taxon difference because the d_c crown sizes are similar between the two taxa. SOA-MM7, the minimally worn d_c from Mata Menge, is positioned in between *Australopithecus* and *H. sapiens* in PC1. There are no deciduous teeth in the existing *H. floresiensis* assemblage from Liang Bua.

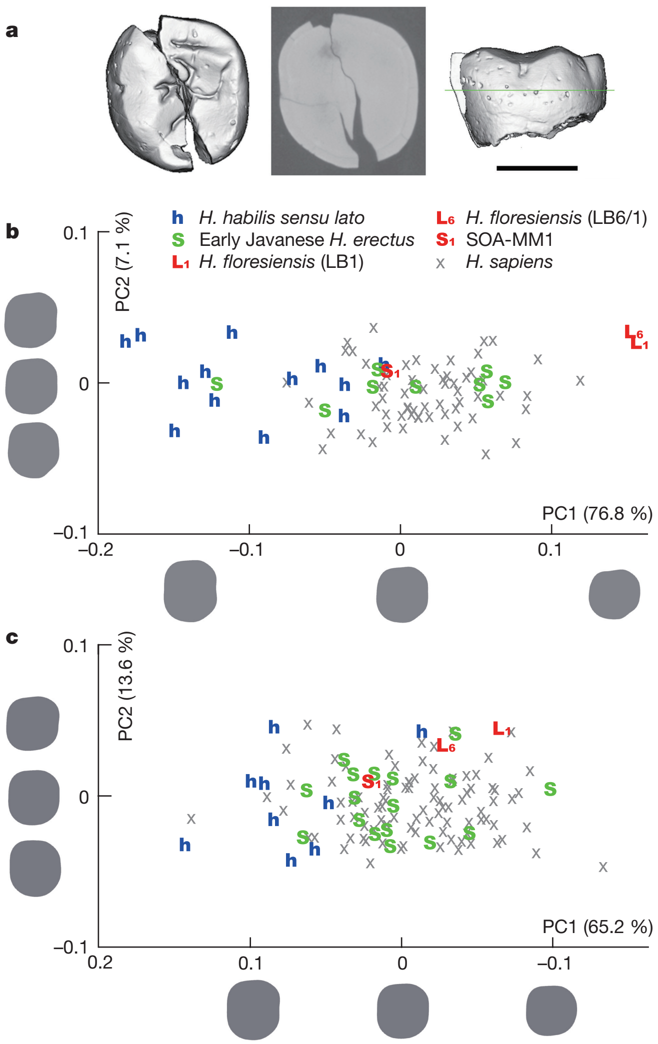


Figure 3 | CT-based reconstruction of SOA-MM1 and the results of Elliptic Fourier Analysis of the molar crown contour. a, Occlusal (left) and buccal (right) views of the reconstructed SOA-MM1, and a horizontal CT section (central) at the level indicated in the buccal view. Scale bar, 5 mm. Plots of the PC scores for the first molar (**b**) and the second molar (**c**) analyses. Proportions of the variance explained by each PC is in the parentheses.

The above findings shed new light on the origin and evolution of Late Pleistocene *H. floresiensis*. Notably, the 0.7-Myr-old Mata Menge hominins are similar to Late Pleistocene *H. floresiensis* of Liang Bua in dentognathic size and morphology, but the former lacks several derived molar morphologies of the latter. This suggests that the early Middle Pleistocene hominins of the So'a Basin were directly ancestral to Liang Bua *H. floresiensis*. Further support for this view is provided by the following observations: (i) stone technologies at Mata Menge and Liang Bua are markedly similar, implying a period of technological continuity spanning at least several hundred millennia[18]; (ii) there is no evidence for a faunal turnover during the time interval separating the fossil records of the So'a Basin and Liang Bua[19]; and (iii) *H. floresiensis* lacks a series of derived cranial features of chronologically late *H. erectus* from Java, such as specimens from Ngandong, Sambungmacan, and Ngawi (all of which are presumably from the late Middle to Late Pleistocene period)[2,20]. We conclude that the most reasonable taxonomic assignment for the Mata Menge fossils is to *H. floresiensis*, although this remains a provisional interpretation until new skeletal materials are found.

Concerning the origins and evolutionary relationships of *H. floresiensis*, we note that the Mata Menge mandible and teeth are morphologically derived compared with *Australopithecus* and *H. habilis*, with their primitive aspects comparable to post-*habilis* grade Early Pleistocene *Homo*. This is most consistent with the hypothesis that *H. floresiensis* originated from a population whose closest affinities are with early Javanese *H. erectus* (≥1.2–0.8 Ma), whose femoral length is 55–61% longer, and absolute brain size about twice as large, as *H. floresiensis*[21–23]. Additional support for this includes reports that the earliest evidence for hominins on Flores (~1.0 Ma)[24] does not exceed the oldest record of *H. erectus* on Java (≥1.2 Ma)[25,26], and recent detailed analyses of the craniodental morphology of Liang Bua *H. floresiensis*[2,3,16]. Given how little is known about the distribution of early *H. erectus* on the ancient 'Sunda' shelf, it remains an open question whether the founding population crossed to Flores in a west-to-east direction from Java, or via a northern route from the Wallacean island of Sulawesi[27–29].

It is noteworthy that the mandible and teeth from Mata Menge are slightly smaller than the two *H. floresiensis* individuals from Liang Bua (LB1 and LB6/1). While this could indicate a slight body size increase over time, it may also simply reflect intra-population variation in the Mata Menge and Liang Bua hominin groups. Whichever the case, it would appear that the Flores hominins had acquired extremely small dentognathic size during the time span of at least 300 millennia following the initial colonization of Flores, assuming that the oldest artefacts from Flores—dated to at least ~1 Ma[24]—were produced by large-bodied ancestors of the Mata Menge hominins. This apparently very fast transformation in hominin body size is surprising. Although no other documented examples of rapid island dwarfing exist for primates, we note that red deer from the island of Jersey had reduced to one-sixth of the body size in the ancestral population within about six millennia[30]. Flores may have been an exceptional case; however, the fossil evidence from Mata Menge highlights how quickly major evolutionary changes could have occurred in hominin populations cut off on isolated and impoverished islands of Wallacea.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

Received 30 December 2015; accepted 13 April 2016.

1. Brown, P. *et al.* A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. *Nature* **431,** 1055–1061 (2004).
2. Kaifu, Y. *et al.* Craniofacial morphology of *Homo floresiensis*: description, taxonomic affinities, and evolutionary implication. *J. Hum. Evol.* **61,** 644–682 (2011).
3. Kaifu, Y. *et al.* Unique dental morphology of *Homo floresiensis* and its evolutionary implications. *PLoS ONE* **10,** e0141614 (2015).
4. Sutikna, T. *et al.* Revised stratigraphy and chronology for *Homo floresiensis* at Liang Bua in Indonesia. *Nature* **532,** 366–369 (2016).
5. Morwood, M. J. & Jungers, W. L. Conclusions: implications of the Liang Bua excavations for hominin evolution and biogeography. *J. Hum. Evol.* **57,** 640–648 (2009).
6. Brown, P. & Maeda, T. Liang Bua *Homo floresiensis* mandibles and mandibular teeth: a contribution to the comparative morphology of a new hominin species. *J. Hum. Evol.* **57,** 571–596 (2009).
7. Brumm, A. *et al.* Age and context of the oldest known hominin fossils from Flores. *Nature* http://dx.doi.org/10.1038/nature17663 (2016).
8. White, T. D., Johanson, D. C. & Kimbel, W. H. *Australopithecus africanus*: its phyletic position reconsidered. *S. Afr. J. Sci.* **77,** 445–470 (1981).
9. Villmoare, B. *et al.* Early *Homo* at 2.8 Ma from Ledi-Geraru, Afar, Ethiopia. *Science* **347,** 1352–1355 (2015).
10. Rosas, A. & Bermudez de Castro, J. M. On the taxonomic affinities of the Dmanisi mandible (Georgia). *Am. J. Phys. Anthropol.* **107,** 145–162 (1998).
11. Kaifu, Y. *et al.* Taxonomic affinities and evolutionary history of the Early Pleistocene hominids of Java: dentognathic evidence. *Am. J. Phys. Anthropol.* **128,** 709–726 (2005).
12. Suwa, G. Serial allocations of isolated mandibuar molars of unknown taxonomic affinities from the Shungra and Usno Formations, Ethiopia, a combined method approach. *Hum. Evol.* **11,** 269–282 (1996).
13. Kimbel, W. H., Johanson, D. C. & Rak, Y. Systematic assessment of a maxilla of *Homo* from Hadar, Ethiopia. *Am. J. Phys. Anthropol.* **103,** 235–262 (1997).
14. Gómez-Robles, A., Martinón-Torres, M., Bermúdez de Castro, J. M., Prado-Simon, L. & Arsuaga, J. L. A geometric morphometric analysis of hominin upper premolars. Shape variation and morphological integration. *J. Hum. Evol.* **61,** 688–702 (2011).

15. Martinón-Torres, M. *et al.* Dental remains from Dmanisi (Republic of Georgia): morphological analysis and comparative study. *J. Hum. Evol.* **55,** 249–273 (2008).
16. Kaifu, Y. *et al.* Descriptions of the dental remains of *Homo floresiensis*. *Anthropol. Sci.* **123,** 129–145 (2015).
17. Tobias, P. V. *Olduvai Gorge, 4: The Skulls, Endocasts and Teeth of Homo habilis.* Vol. 4 (Cambridge Univ. Press, 1991).
18. Brumm, A. *et al.* Early stone technology on Flores and its implications for *Homo floresiensis*. *Nature* **441,** 624–628 (2006).
19. van den Bergh, G. D. *et al.* The Liang Bua faunal remains: a 95k.yr. sequence from Flores, East Indonesia. *J. Hum. Evol.* **57,** 527–537 (2009).
20. Kaifu, Y. *et al. Homo erectus* calvaria from Ngawi (Java) and its evolutionary implications. *Anthropol. Sci.* **123,** 161–176 (2015).
21. Puymerail, L. *et al.* Structural analysis of the Kresna 11 *Homo erectus* femoral shaft (Sangiran, Java). *J. Hum. Evol.* **63,** 741–749 (2012).
22. Ruff, C. B., Puymerail, L., Macchiarelli, R., Sipla, J. & Ciochon, R. L. Structure and composition of the Trinil femora: functional and taxonomic implications. *J. Hum. Evol.* **80,** 147–158 (2015).
23. Kubo, D., Kono, R. T. & Kaifu, Y. Brain size of *Homo floresiensis* and its evolutionary implications. *Proc. R. Soc. Lond. B* **280,** 20130338 (2013).
24. Brumm, A. *et al.* Hominins on Flores, Indonesia, by one million years ago. *Nature* **464,** 748–752 (2010).
25. Larick, R. *et al.* Early Pleistocene ^{40}Ar/^{39}Ar ages for Bapang Formation hominins, Central Jawa, Indonesia. *Proc. Natl Acad. Sci. USA* **98,** 4866–4871 (2001).
26. Hyodo, M. *et al.* High-resolution record of the Matuyama–Brunhes transition constrains the age of Javanese *Homo erectus* in the Sangiran dome, Indonesia. *Proc. Natl Acad. Sci. USA* **108,** 19563–19568 (2011).
27. Morwood, M. & van Oosterzee, P. *The Discovery of the Hobbit* (Random House, 2007).
28. van den Bergh, G. D. *et al.* Earliest hominin occupation of Sulawesi, Indonesia. *Nature* **529,** 208–211 (2016).
29. Dennell, R. W., Louys, J., O'Regan, H. J. & Wilkinson, D. M. The origins and persistence of *Homo floresiensis* on Flores: biogeographical and ecological perspectives. *Quat. Sci. Rev.* **96,** 98–107 (2014).
30. Lister, A. M. Rapid dwarfing of red deer on Jersey in the last interglacial. *Nature* **342,** 539–542 (1989).

Supplementary Information is available in the online version of the paper.

Acknowledgements Funding for the So'a Basin project was provided by an Australian Research Council (ARC) *Discovery* grant (DP1093342) awarded to M.J.M. and A.B., and the project was directed by M.J.M. (2010-2013) and G.D.v.d.B. (2013-2015). The Japan Society for the Promotion of Science provided a grant (No. 24247044) to Y.K. Financial and technical support was provided by the Geological Survey Centre of Indonesia. The Indonesian State Ministry of Research and Technology granted permission to undertake this research, and we thank the successive directors of the Geological Survey Centre, Y. Kusumahbrata, A. Wibowo and A. Pribadi, the Heads of the Geological Agency (R. Sukyiar and Surono), and the successive directors of the Geology Museum in Bandung (S. Baskoro and O. Abdurahman) for facilitating and supporting this research. In addition, we acknowledge support and advice provided by I. Setiadi, D. Pribadi and Suyono. We also thank M. R. Puspaningrum, H. Insani, I. Sutisna, S. Sonjaya, U. P. Wibowo, A. Gunawan, A. M. Saiful, S. Hayes, B. Burhan, E. Sukandar, A. Rahman, A. Rahmadi and E. E. Laksmana for their assistance in the field (2014–2015), and G. Suwa, T. Djubiantono, F. Aziz, T. Jacob, E. Mbua, F. Schrenk, I. Tattersall, K. Mowbray, J. de Vos, P. Mennecier, F. Demeter, Nguyen Kim Thuy, and Nguyen Lan Cuong for access to the specimens in their care.

Author Contributions G.D.v.d.B. is co-director of the So'a Basin project with A.B. and I.K. M.J.M. (deceased) was also a co-director of the So'a Basin project. The project was initiated by M.J.M. and F.A. G.D.v.d.B. and I.K. undertook initial identification and analyses of the hominin fossils. Y.K. conducted the morphological analysis together with R.T.K. Fieldwork was planned and directed by G.D.v.d.B., I.K., A.B. and E.S.. Y.K., G.D.v.d.B. and A.B. wrote the manuscript.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to Y.K. (kaifu@kahaku.go.jp).

METHODS

Comparative samples. Comparative fossil samples include the proposed two major ancestral candidates for *H. floresiensis*, *H. habilis sensu lato* (East Africa) and early Javanese *H. erectus* (Java), as well as other Asian archaic *Homo* (Dmanisi *Homo* and Middle Pleistocene Asian *Homo*), and *H. floresiensis* from the Late Pleistocene of Liang Bua (Extended Data Table 3). No *Australopithecus* molar samples were included in the comparison with SOA-MM1 because the latter is obviously derived in having a well-developed mid-trigonid crest[15] and a gently convex, non-bilobed, buccal crown outline[8]. However, in view of the previous claim that the *H. floresiensis* mandibles resemble *Australopithecus afarensis* (ref. 6, but see ref. 2), the mandibular analysis includes specimens belonging to this species as well as the recently reported 'earliest *Homo*' specimen from Ethiopia[9]. The deciduous tooth analyses also include *Australopithecus* specimens because no measurable mandibular deciduous canines are represented in the existing fossil collections of *H. habilis* to represent the primitive condition in this tooth. Two worn *H. erectus* specimens from the Zhoukoudian Lower Cave are included in the metrical comparison, but could not be included in the PCA; nor are there any Javanese *H. erectus* specimens of this tooth known.

Debate continues over whether *H. habilis sensu lato* includes diverse evolving lineages[31–34], but we pooled the relevant specimens from East Africa for the present purpose to recognize primitive morphological condition in *Homo*.

The early Javanese *H. erectus* sample is from the varying stratigraphic levels at Sangiran, Central Java, which are dated to between $\geq$1.2 and 0.8 Ma[25,26]. Previous studies demonstrated significant temporal decrease in tooth crown size within this sample[11,35,36], but we nevertheless pooled these chronological subgroups for the purposes of this study because their crown shapes are remarkably similar to each other[3].

The other Asian archaic *Homo* samples (such as Dmanisi *Homo*, and various groups of the Middle Pleistocene East Asian *Homo*, as listed in Extended Data Table 3) were included in the linear metric analyses of the mandible and teeth.

Our *H. sapiens* sample is from Africa, Europe, Asia, and Oceania, with particular emphasis on prehistoric individuals from Southeast Asia, including Flores, as well as modern small-bodied populations (such as Philippine 'Negrito', Andaman, African 'Pygmy', and 'Bushman') (Extended Data Table 4). This choice was made to reflect species-wide variation of *H. sapiens*, and to respond to the claim that Liang Bua *H. floresiensis* resembles a local short-statured Australomelanesian population[37]. Sexes were pooled due to general difficulties in sex assignment for various fragmentary hominin fossils.

Materials. The data of the mandibles were taken from the original specimens, but some notes should be made on the materials for the dental analyses. Dental specimens with severe tooth wear were excluded from the metric analyses. Metric and non-metric data were obtained from the original specimens, plaster casts, or published studies (Extended Data Table 3). For all the *H. floresiensis*, early Javanese *H. erectus*, and *H. sapiens* specimens, high-quality 'isolated' plaster casts were prepared by Y.K. with partial assistance from Hisao Baba. Silicone was used for molding and the produced plaster cast of a dentition was then cut with a saw to isolate individual teeth. Such isolated casts can be measured more easily and accurately than the original specimens when the teeth are embedded in the jaw bones and measurement equipment is difficult to apply to the original specimens. Thus, we used these isolated casts for linear measurement and crown contour extraction. Non-isolated, high-quality plaster casts were used for most of the *H. habilis* and *H. ergaster* specimens. These were prepared by Gen Suwa with dimensional accuracies being within $\pm$0.1 mm[38].

Measurements. A digital sliding caliper (Mitutoyo) was used for linear measurements. Mesiodistal (MD) and buccolingual (BL) tooth crown diameters were recorded with allowance for wear, following the methods outlined in ref. 39. Values from the right and left sides are averaged for the fossil specimens, while the data for *H. sapiens* are from the better-preserved and/or less-worn side. All the metric data were taken by Y.K., with the exception of those cited from the literature (refs. 15, 39–42).

CT scan. The Mate Menge hominin fossils reported here were CT scanned using the microfocal X-ray CT system TXS320-ACTIS (TESCO, Japan) at the National Museum of Nature and Science, Tokyo, in 2014. Original scans were taken at 189 kV and 0.23 mA with a 0.5-mm-thick copper plate prefilter to lessen beam-hardening effects. Scanned images were reconstructed into a 512 $\times$ 512 matrix of 150 μm pixel size with 150 μm slice interval and thickness (mandible), or 512 $\times$ 512 matrices of 32 μm pixels with 32 microns slice interval and 34.63 microns slice thickness (isolated teeth).

Size-adjusted PCAs of the mandibular corpus measurements. Principal component analysis (PCA) was performed using mandibular corpus heights and widths as variables (Extended Data Fig. 5). The size adjustment was done by dividing each raw measurement by the geometric mean of all the measurements used for each individual.

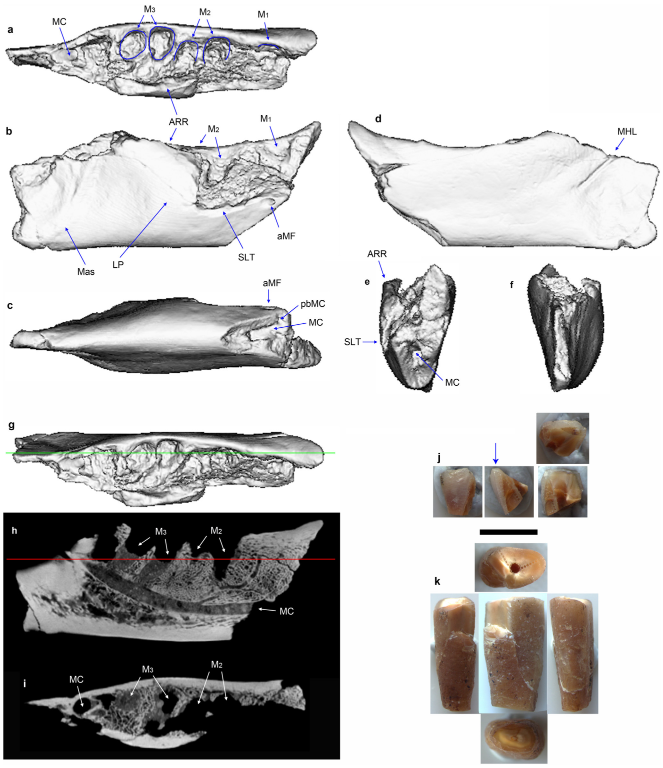
Elliptic Fourier analysis (EFA) of the mandibular molar. Occlusal crown contours of the mandibular molar were analysed by normalized (size-standardized) EFA[43,44] (Fig. 3), following the previous analysis of the teeth of *H. floresiensis*[3]. This method was chosen in that study because the *H. floresiensis* teeth are moderately worn and retain few homologous landmarks. We performed EFAs for both M_1s and M_2s, because the position of SOA-MM1 is indeterminate.

The comparative samples were *H. floresiensis*, the two major ancestral candidates of *H. floresiensis* (*H. habilis sensu lato* and early Javanese *H. erectus*), and *H. sapiens*. Comparisons were made on the images from the right side teeth, or horizontally flipped images of the left teeth if the latter side is better preserved. The crown contour of each tooth was captured by photography with a dental cast placed so that its cervical line is vertical to the axis of the camera lens[45–47]. Local fluctuations of the cervical lines were ignored[38]. A 100 mm macro lens was set to a Canon D40 digital camera to minimize the parallax effect. Interproximal wear was corrected on each photograph before extracting the crown contour. Capturing of crown contours from the digital images, obtaining EFDs, and PCA of the normalized EFDs were conducted using the software SHAPE 1.3 (ref. 48). Other methodological details for the EFA are available in ref. 3.

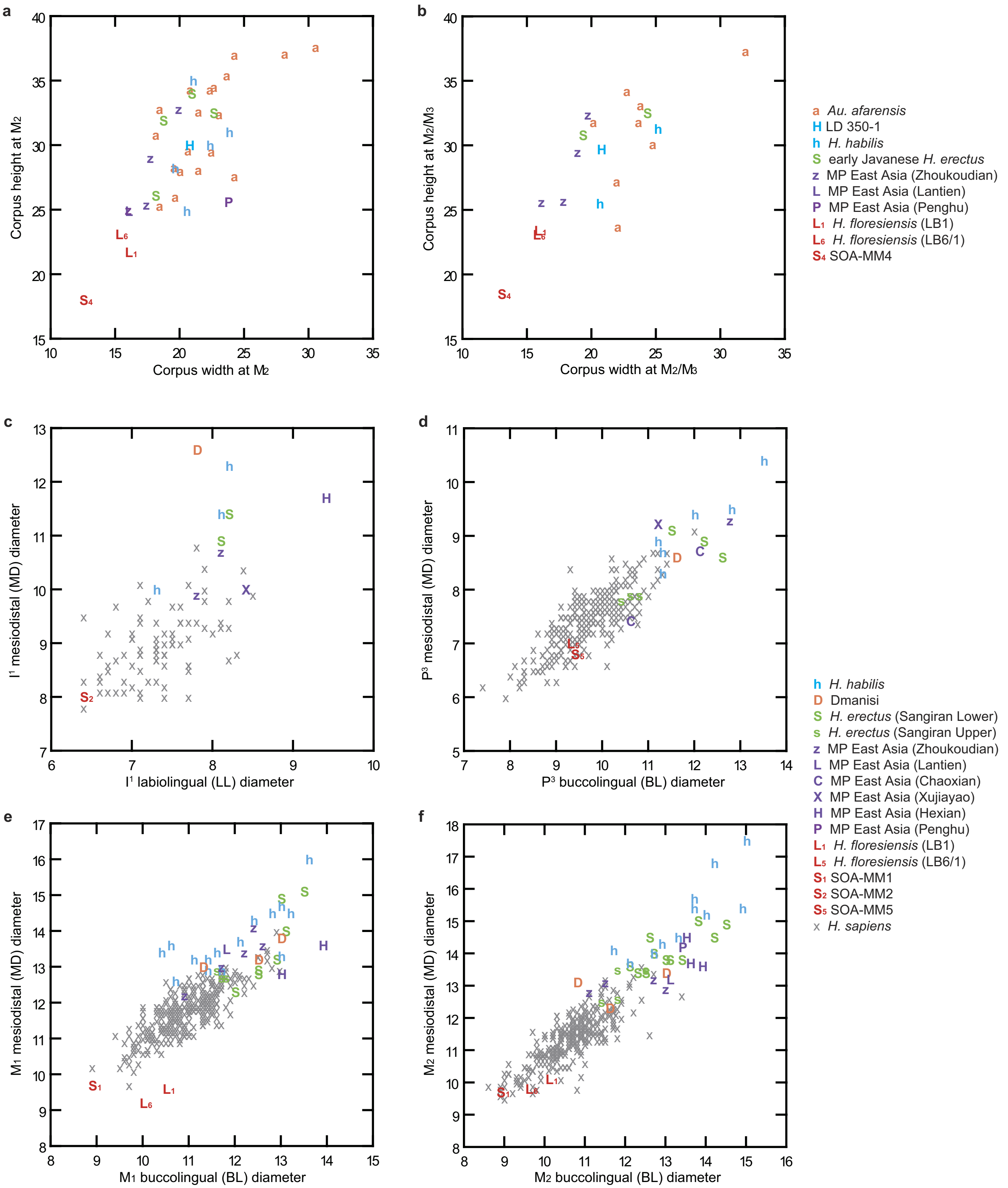
Size-adjusted PCAs of the mandibular deciduous canine (d_c). Principal component analysis (PCA) was undertaken using five size-adjusted linear crown diameters (mesiodistal diameter, buccolingual diameter, mesial crown shoulder height, crown height, and distal crown shoulder height), as shown in Extended Data Fig. 6c–e. The size adjustment was done by dividing each raw measurement by the geometric mean of the five measurements for each individual. Crown height of the less worn SOA-MM7 can be estimated with some confidence, but moderately worn SOA-MM8 was excluded from this analysis.

Data reporting. No statistical methods were used to predetermine sample size. The experiments were not randomized. The investigators were not blinded to allocation during experiments and outcome assessment.

31. Lordkipanidze, D. *et al.* A complete skull from Dmanisi, Georgia, and the evolutionary biology of early *Homo*. *Science* **342,** 326–331 (2013).
32. Wood, B. Fifty years after *Homo habilis*. *Nature* **508,** 31–33 (2014).
33. Antón, S. C., Potts, R. & Aiello, L. C. Human evolution. Evolution of early *Homo*: an integrated biological perspective. *Science* **345,** 1236828 (2014).
34. Spoor, F. *et al.* Reconstructed *Homo habilis* type OH 7 suggests deep-rooted species diversity in early *Homo*. *Nature* **519,** 83–86 (2015).
35. Kaifu, Y. Advanced dental reduction in Javanese *Homo erectus*. *Anthropol. Sci.* **114,** 35–43 (2006).
36. Zanolli, C. Additional evidence for morpho-dimensional tooth crown variation in a new Indonesian *H. erectus* sample from the Sangiran Dome (Central Java). *PLoS ONE* **8,** e67233 (2013).
37. Jacob, T. *et al.* Pygmoid Australomelanesian *Homo sapiens* skeletal remains from Liang Bua, Flores: population affinities and pathological abnormalities. *Proc. Natl Acad. Sci. USA* **103,** 13421–13426 (2006).
38. Suwa, G. *A Comparative Analysis of Hominid Dental Remains from the Sungura and Usno Formations, Omo Valley, Ethiopia* Ph.D. thesis, University of California, Berkeley (1990).
39. Wood, B. *Koobi Fora Research Project 4: Hominid Cranial Remains.* Vol. 4 (Clarendon Press, 1991).
40. Leakey, M. G. *et al.* New fossils from Koobi Fora in northern Kenya confirm taxonomic diversity in early Homo. *Nature* **488,** 201–204 (2012).
41. Weidenreich, F. The dentition of *Sinanthropus pekinensis*: a comparative odontography of the hominids. *Palaeontologia Sinica New Series D* **1,** 1–180 (1937).
42. Xing, S., Martinón-Torres, M., Bermúdez de Castro, J. M., Wu, X. & Liu, W. Hominin teeth from the early Late Pleistocene site of Xujiayao, Northern China. *Am. J. Phys. Anthropol.* **156,** 224–240 (2015).
43. Kuhl, F. P. Elliptic Fourier features of a closed contour. *Computer Graphics and Image Processing* **18,** 236–258 (1982).
44. Lestrel, P. E., Wolfe, C. A. & Bodt, A. Mandibular shape analysis in fossil hominins: Fourier descriptors in *norma lateralis*. *Homo* **64,** 247–272 (2013).
45. Wood, B. A. & Abbott, S. A. Analysis of the dental morphology of Plio-Pleistocene hominids. I. Mandibular molars: crown area measurements and morphological traits. *J. Anat.* **136,** 197–219 (1983).
46. Bailey, S. E. & Lynch, J. M. Diagnostic differences in mandibular P4 shape between Neandertals and anatomically modern humans. *Am. J. Phys. Anthropol.* **126,** 268–277 (2005).
47. Martinón-Torres, M. *et al.* Hominin lower second premolar morphology: evolutionary inferences through geometric morphometric analysis. *J. Hum. Evol.* **50,** 523–533 (2006).
48. Iwata, H. & Ukai, Y. SHAPE: a computer program package for quantitative evaluation of biological shapes based on elliptic Fourier descriptors. *J. Hered.* **93,** 384–385 (2002).
49. Smith, B. H. Patterns of molar wear in hunter-gathers and agriculturalists. *Am. J. Phys. Anthropol.* **63,** 39–56 (1984).
50. Hillson, S., Fitzgerald, C. & Flinn, H. Alternative dental measurements: proposals and relationships with other measurements. *Am. J. Phys. Anthropol.* **126,** 413–426 (2005).
51. Kimbel, W. H., Rak, Y. & Johanson, D. C. *The Skull of Australopithecus afarensis* (Oxford Univ. Press, 2004).
52. Kaifu, Y., Aziz, F. & Baba, H. Hominid mandibular remains from Sangiran: 1952–1986 collection. *Am. J. Phys. Anthropol.* **128,** 497–519 (2005).
53. Chang, C. H. *et al.* The first archaic *Homo* from Taiwan. *Nature Commun.* **6,** 6037 (2015).



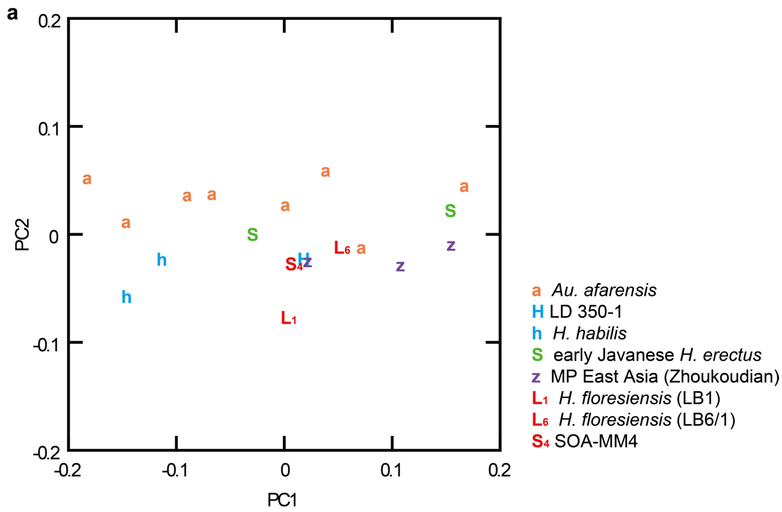
Extended Data Figure 1 | CT-based images of the SOA-MM4 mandible and photos of the SOA-MM6 incisor. a–i, SOA-MM4 mandible. Surface-rendered images of superior (**a**), lateral (**b**), inferior (**c**), lingual (**d**), anterior (**e**), and posterior (**f**) views. Sagittal (**h**) and horizontal (**i**). CT sections at the plane indicated by the green (**g**) and red (**h**) lines. aMF, a branch of the mandibular foramen; ARR, anterior ramus root; LP, lateral prominence; M_1, M_1 alveolus; M_2, M_2 alveolus, M_3, M_3 alveolus; MC, mandibular canal; Mas, line for the masseter muscle attachment; MHL, mylohyoid line; pbMC, posterior branch of the mandibular canal; SLT, superior lateral torus. **j**–**k**, SOA-MM6 mandibular incisor ($I_{1/2}$) fragments. The crown (**j**, SOA-MM6a) and a root (**k**, SOA-MM6b) fragments were used for laser ablation uranium-series dating. The specimen was deposited before at least 0.55 Ma[7]. Note the bevelled occlusal wear surface (arrow). Scale bar, 5 mm.



Extended Data Figure 2 | Linear metric comparisons of the mandibles and permanent teeth. a–e, Scatter plots of the mandibular corporal dimensions (**a**, **b**) and permanent tooth crown diameters (**c**–**e**). We identify SOA-MM1 as M_1 (**e**), but there remains a slight possibility that this tooth is M_2 (**f**). Metric data of SOA-MM4: corpus height at M2, 18 mm; corpus height at M2/3, 18.5 mm; corpus width at M2, 12.5 mm; corpus width at M2/3, 13 mm.

Extended Data Figure 3 | Mandibular comparisons. a–m, *H. habilis sensu lato*: OH 13 (**a**, late adolescent), OH 37 (**b**, horizontally flipped image), KNM-ER 1802 (**c**, late adolescent), KNM-ER 3734 (**d**, horizontally flipped image), KNM-ER 60000 (**e**, horizontally flipped image) (photo by F. Spoor, copyright National Museums of Kenya); early Javanese *H. erectus*, Sangiran 1b (**f**), Sangiran 9 (**g**), Sangiran 22 (**h**), Sb 8103 (**i**), Sangiran 21 (**j**); Liang Bua *H. floresiensis*: LB1 (**k**), LB6/1 (**l**, horizontally flipped image; the corpus is distorted); (**m**) SOA-MM4. Scale bar, 30 mm. Note that the *H. habilis* mandibles tend to exhibit a thicker corpus, the position of the basal ramus (filled arrow) that is shifted laterally relative to the corpus midline axis, a prominent posterior part of the alveolar prominence (filled triangle), and a wider extramolar sulcus between the anterior ramus root (open arrow) and the molar row. The early Javanese *H. erectus* sample is variable but includes specimens with weaker expressions in these traits. The Liang Bua *H. floresiensis* and the SOA-MM4 mandibles share such derived features with early Javanese *H. erectus*.

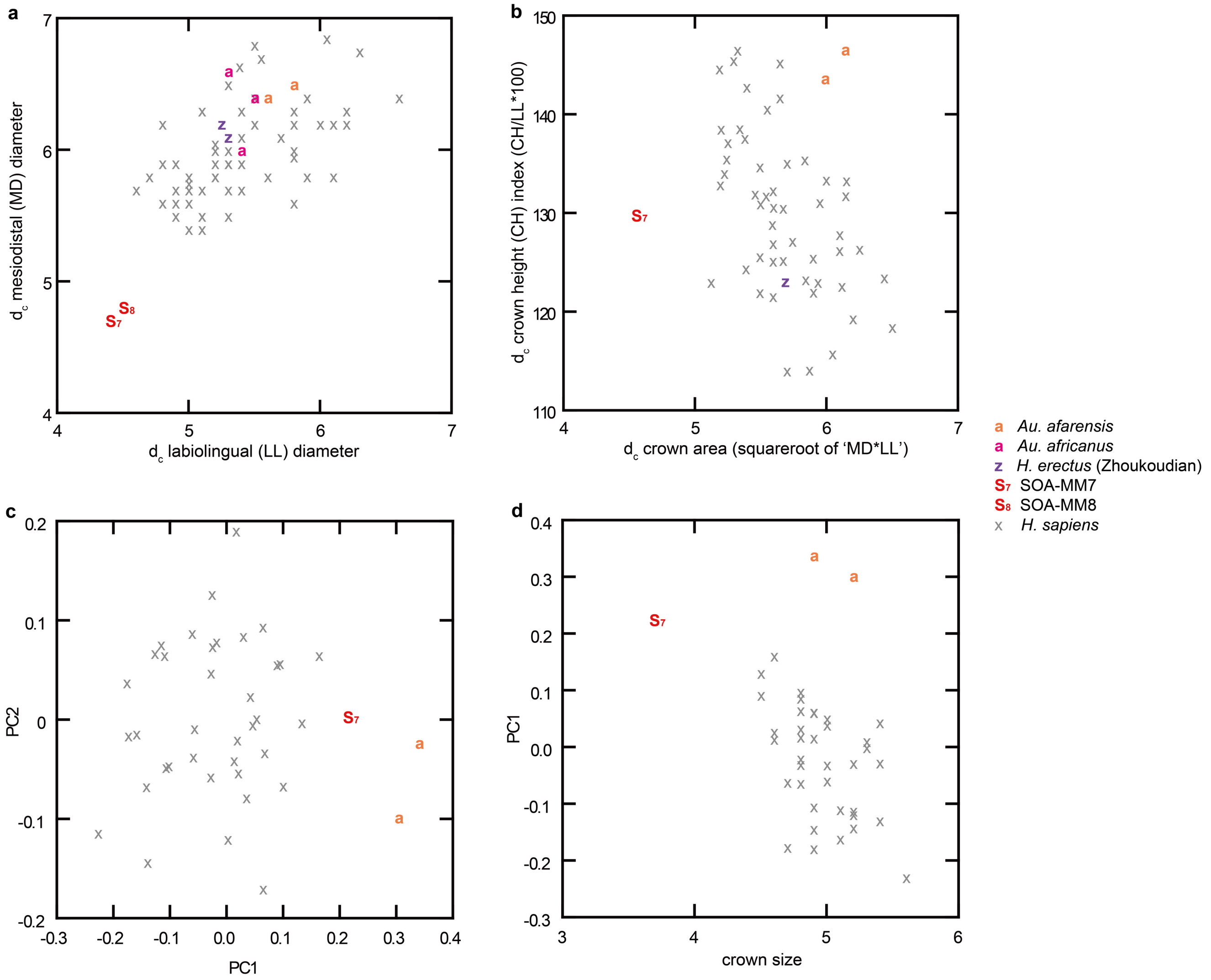
Extended Data Figure 4 | Comparisons of the hominin mandibles and teeth from So'a Basin (Mata Menge) and *H. floresiensis* from Liang Bua. **a**, SOA-MM4 mandible. **b**, **c**, Right lateral and left lateral (horizontally flipped) views of LB1. **d**, Right lateral view of LB6/1. **e**, **f**, The SOA-MM3 and LB1 P_3s, respectively. **g**, SOA-MM1 M_1. **h**–**j**, Occlusal views of SOA-MM4 (**h**), LB1 (**i**), and LB6/1 (**j**) mandibles. Scale bar, 10 mm.



b

Variable (size-standardized)	PC1	PC2	PC3	PC4
Corpus height at M_2	0.936	0.313	-0.160	0.013
Corpus height at $M_{2/3}$	0.955	-0.222	0.198	0.016
Corpus width at M_2	-0.803	-0.528	-0.275	0.034
Corpus width at $M_{2/3}$	-0.934	0.325	0.145	0.022
Proportion (%)	86	11	3	0
Cumulative proportion (%)	86	97	100	100

Extended Data Figure 5 | Principal component analyses of the four size-standardized mandibular measurements. a, Scatter plot of the PC scores. **b**, Component loading of each PC. PC1 does not distinguish *Homo* from *Au. afarensis*, but *Au. afarensis* and post-*habilis Homo* are relatively well-separated in PC2. SOA-MM4 belongs to the cluster of *Homo* in this PC. SOA-MM4 occupies the space in between the two Liang Bua *H. floresiensis* mandibles, suggesting their shared lateral corporal shape.



e

Variable (size-standardized)	PC1	PC2	PC3	PC4	PC5
Mesiodistal diameter	0.599	0.166	-0.554	0.553	0.031
Labiolingual diameter	0.497	0.798	-0.084	-0.328	0.031
Crown height	0.859	-0.232	0.456	0.027	0.015
Mesial shoulder height	-0.163	-0.788	-0.496	-0.320	0.054
Distal shoulder height	-0.893	0.135	0.404	0.141	0.038
Proportion (%)	53	21	18	8	0
Cumulative proportion (%)	53	74	92	100	100

Extended Data Figure 6 | Metric analyses of mandibular deciduous canines. a–e, Comparisons of the crown length and breadth (**a**), and relative crown height (**b**). Results of the PCA based on size-adjusted five crown diameters (**c**, **d**) and the component loadings of each PC (**e**). 'Crown size' = geometric mean of the five crown diameters used. *Au. afarensis* and *H. sapiens* are indistinguishable in crown size (**d**) but they are discriminated from each other by PC1 ($P < 0.00002$, *t*-test). SOA-MM7 occupies an intermediate position between *Au. afarensis* and *H. sapiens*, suggesting its moderately primitive crown configuration. The other PCs did not discriminate *Au. afarensis* and *H. sapiens*.

Extended Data Table 1 | 2014 Hominin fossil collection from Mata Menge

Specimen No.	Catalogue No.	Date of discovery	Portion
SOA-MM1	MM14-T32D-F191	2014 Oct 08	broken crown of left M_1 (or M_2)
SOA-MM2	MM14-T32C-F234	2014 Oct 14	complete crown and root of left I^1
SOA-MM3	MM14-T32D-F384	2014 Oct 14	hominin cranial fragment?
SOA-MM4	MM14-T32C-F277	2014 Oct 14	right mandibular body
SOA-MM5	MM14-T32C-F452	2014 Oct 16	complete crown and root of right P^3
SOA-MM6	MM14-T32B-F94	2014 Oct 18	broken root and crown fragments of right $I_{1/2}$
SOA-MM7	MM14-T32C-dry sieve	2014 Oct 21	nearly complete left d_c
SOA-MM8	MM14-T32B-dry sieve	2014 Oct 24	nearly complete right d_c

All specimens are housed in the Geology Museum in Bandung.

Extended Data Table 2 | Hominin teeth from Mata Menge as compared to those of Liang Bua *H. floresiensis*[a]

Specimen	Tooth	Side	Wear[b]	Crown diam.				Cervical diam.[e]		Root length[f]
				MD[c] as measured	MD[c] corrected	BL[c]	Height[d]	MD	BL	
SOA-MM2	**I^1**	**L**	**5**	**7.6**	**8.0**	**6.4**	**–**	**5.5**	**5.7**	**12.0**
LB15/2	I^1	L	7	–	–	≥ 6.2	–	5.2	6.2	12.0–13.0
SOA-MM5	**P^3**	**R**	**3**	**6.6**	**6.8**	**9.4**	**–**	**4.4**	**(8.4)**	**(12.5)**
LB1/1[i]	P^3	R & L	3.5	6.85	7.0	9.25	–	4.85	9.0	14.95
SOA-MM6	**$I_{1/2}$**	**R**	**5?**	**–**	**–**	**–**	**–**	**–**	**–**	**–**
SOA-MM1	**M_1 (or M_2)**	**L**	**2**	**9.7**	**9.7**	**8.9**	**–**	**–**	**–**	**–**
LB1[i]	M_1	R & L	4.75	9.25	9.6	10.5	–	8.2	9.1	12.4, 12.45[g]
LB6/1[i]	M_1	R & L	4.5	8.9	9.2	10.0	–	–	8.8	–
LB1[i]	M_2	R & L	3.75	9.8	10.1	10.2	–	8.8	8.9	12.5, 11.75[g]
LB6/1[i]	M_2	R & L	3.5	9.45	9.7	9.55	–	–	–	–
SOA-MM7	**d_c**	**L**		**4.7**	**4.7**	**4.4**	**(5.8)**	**3.9**	**3.4**	**–**
SOA-MM8	**d_c**	**R**		**4.8**	**4.9**	**4.5**	**–**	**3.9**	**3.4**	**–**

[a]Measurements of the Liang Bua hominins cited from ref. 16.
[b]Scored following ref. 49.
[c]Measured following the method of ref. 39.
[d]Buccal crown height.
[e]Cervical diameters as defined by ref. 50.
[f]Buccal root length.
[g]Lengths for mesial and distal roots, respectively.
[i]Average of the right and left sides.

Extended Data Table 3 | Comparative fossil samples

Sample	Age (Ma)	Portion	Composition	Data source
H. floresiensis (Liang Bua)	0.1-0.06	Mandible	LB1#, 6/1#	Originals
		Teeth	LB1*, 6/1*	Ref. 16
Au. afarensis	3.6-3.0	Mandible	A.L. 198-22#, 225-8, 315-22, 330-5#, 417-1a#, 436-1#, 437-2, 438-1#, 444-2, 620-1, 188-1#, 198-1, 207-13, 266-1, 333w1a,b, 333w-32+60, MAL1/12#, MAK1/2#, LH4	Ref. 51
"Earliest *Homo*"	2.8	Mandible	LD350-1#	Ref. 9
H. habilis	2.3-1.6	Mandible	KNM-ER 3734, 1805, 60000; OH 13#, 37#	Originals, Ref.40
		Teeth	A.L. 666-1; KNM-ER 1502*, 1507*, 1508*, 1590, 1801*, 1802*, 1805*, 1813; 2597*, 2601*, 60000; OH7*, 13*, 16*, 37*, 39; L7-279*, 628-10, 894-1; Omo 75-14*, 75s-15*, 195-1630*	Refs. 3,13, 40
Dmanisi *Homo*	1.75	Teeth	D211, 2600, 2700, 2735	Ref.15
Early Javanese *H. erectus* (older)	≥1.2-1.0	Mandible	Sangiran 1b#, 5, 9#, 22	Originals, Ref.52
		Teeth	Sangiran 1b*, 4, 5*, 6b*, 6b, 7-35, 7-42*, 7-43*, 7-58, 7-61*, 7-62*, 7-63*, 7-64*, 7-65*, 7-76*, 7-78*, 7-84*, 7-85, 7-86, 22*; Bk 7905*	Ref. 3
Early Javanese *H. erectus* (younger)	1.0-0.8	Teeth	Sangiran 7-20*, 7-21*, 7-22*, 7-27, 7-31, 7-32; Sb 8103*, Ng 8503*	Ref. 3
Middle Pleistocene East Asian *Homo*	c. 0.75-0.05	Mandible	Lantian; Zhoukoudian G1#, H1#, K1#, PA86; Penghu 1	Originals, casts, Ref.53
		Teeth	Zhoukoudian 1/2, 4, 19, 34, 35, 36/37, 43, 44, 45, 97, 98, 99, 107, 108, 137'; Lantian PA102; Hexian PA834, 835, 838, 839, AN1644; Chaoxian; Xujiayao PA1480-1, 1480-3	Refs.3, 41, 42

#Specimens included in the PCAs.
*Specimens included in the EFAs.
Refs. 51–53 are cited in this table.

Extended Data Table 4 | Comparative *Homo sapiens* dental sample

	Remarks	N[a]	Repository[b]
Prehistoric Southeast Asia			
Flores*	Aimere, Gua Alo, Gua Nempong, Liang Bua, Liang Momer, Liang Toge, Liang X	9	NBC, ARKENAS
Java*	Hoekgrot, Wajak	3	NBC
Malaysia*	Guar Kepah	19	NBC
Vietnam*	Mai Da Dieu, Mai Da Nuoc, Hang Chim, Dong Cang, Con Co Ngua	73	IAH
Australia/Melanesia			
New Guinea*		30	AMNH, MH
Indigenous Australian/Tasmanian*		19	AMNH
Southeast Asia			
Philippine Negrito*		20	MH
Others	Andaman, Indonesia, Malaysia, Nicobar, Philippine, Singapore, Thailand	57	AMNH, MH
Northeast Asia			
Northeast Asia	China, Chukuci, Korea, Mongol, Yukagir	18	AMNH
Africa			
Bushman		17	AMNH, MH
African Pygmy		20	MH
South Africa	Excluding Bushman	26	AMNH
East Africa		45	AMNH
West Africa	Excluding Pygmy	55	AMNH
Indo/Europe			
India		6	AMNH
German		65	AMNH
Others	Hungary, Poland, Sweden	8	AMNH
Total		490	

[a]Number of individuals.
[b]NBC, Naturalis Biodiversity Center, Leiden; ARKENAS, National Research and Development Centre for Archaeology, Jakarta; AMNH, American Museum of Natural History, New York; MH, Musée de l'Homme, Paris, IAH, Institute of Archaeology, Hanoi.
*Samples included in the EFAs.