**Early Neolithic genomes from the eastern Fertile Crescent**

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**Abstract (~125 words):** We sequenced Early Neolithic genomes from the Zagros region of Iran (eastern Fertile Crescent), where some of the earliest evidence for farming is found, and identify a previously uncharacterized population that is neither ancestral to the first European farmers nor has contributed significantly to the ancestry of modern Europeans. These people are estimated to have separated from Early Neolithic farmers in Anatolia some 51- 77,000 years ago and show affinities to modern day Pakistani and Afghan populations, but particularly to Iranian Zoroastrians. We conclude that multiple, genetically differentiated hunter-gatherer populations adopted farming in SW-Asia, that components of pre-Neolithic population structure were preserved as farming spread into neighboring regions, and that the Zagros region was the cradle of eastward expansion.

**One Sentence Summary:** Neolithic genomes from Zagros region of Iran are ancestral to modern South Asians but distinct from early NW-Anatolian and European farmers.

The earliest evidence for cultivation and stock-keeping is found in the Neolithic core zone of the Fertile Crescent (*1, 2*); a region stretching north from the southern Levant through E-Anatolia and N-Mesopotamia then east into the Zagros Mountains on the border of modern-day Iran and Iraq (Fig. 1). From there farming spread into surrounding regions, including Anatolia and later Europe, southern Asia, and parts of Arabia and N-Africa. Whether the transition to agriculture was a homogenous process across the core zone, or a composite of localized domestications is unknown. Likewise, the extent to which core zone farming populations were genetically homogenous, or exhibited structure that may have been preserved as agriculture spread into surrounding regions, is undetermined.

Ancient DNA (aDNA) studies indicate that early Aegean farmers dating to c. 6,500-6,000 BCE are the main ancestors of early European farmers (*3, 4*), although it is not known if they were predominantly descended from core zone farming populations. We sequenced four Early Neolithic (EN) genomes from Iran, including a well preserved sample from the central Zagros site of Wezmeh Cave (WC1, 7,455-7,082 cal BCE), the latter to a coverage of 10x. The three other individuals from Tepe Abdul Hosein were less well preserved (genome coverage between 0.6 and 1.2 x) but are around 10,000 years old, and therefore among the earliest Neolithic human remains in the world (Table S1 and S3).

Despite a lack of a clear Neolithic context, the radiocarbon inferred chronological age, and palaeodietary data support WC1 being an early farmer (Tables S1-S3, Fig. S7). WC1 bone collagen δ13C and δ15N values are indistinguishable from that of a securely assigned Neolithic individual from Abdul Hosein and consistent with a diet rich in cultivated C3 cereals rather than animal protein. Specifically, collagen from WC1 and Abdul Hosein is 13C depleted compared to those from contemporaneous wild and domestic fauna from this region (*5*), which consumed C4 plants. Crucially, WC1 and the Abdul Hosein farmers exhibit very similar genomic signatures.

The four EN Zagros genomes form a distinct cluster in the first two dimensions of a principal components analysis (PCA; Fig. 2); they plot closest to modern-day Pakistanis and Afghans and are separated from European hunter-gatherers (HG) and other Neolithic farmers. In an outgroup *f3*-test (*6, 7*) (Fig. S17-S21), all four Neolithic Iranian individuals are genetically more similar to each other than to any other prehistoric genome except a Chalcolithic genome from NW-Anatolia (see below). Despite 14C dates spanning around 1,000 years, these data are consistent with all four genomes being sampled from a single eastern Fertile Crescent EN population.

We obtained the distribution of runs of homozygosity (ROH) above 500 kb in length and compared other relevant ancient and modern genomes (Fig. 3A, B). WC1 shares a similar ROH distribution with European and Aegean Neolithics, and modern day Europeans. However, of all ancient samples considered, WC1 displays the lowest total length of short ROH suggesting he was descended from a relatively large HG population. In sharp contrast, the ROH distributions of the HG Kotias from Georgia, and Loschbour from Luxembourg indicate prolonged periods of small ancestral population size (*8*).

We developed an unbiased method to estimate heterozygosity (𝜃) in 1Mb windows that takes post mortem damage fully into account, even at low coverages (*9*; Fig. 3C, D). The mean WC1 diversity was higher than for HG individuals (Bichon and Kotias), but similar to Bronze Age individuals from Hungary and modern Europeans, and lower than for ancient (*10*) and modern Africans. Multidimensional scaling on a matrix of centered Spearman correlations of local heterozygosity estimates across the whole genome again puts WC1 closer to modern populations than to ancient foragers, indicating that the mean diversity and pattern of diversity distribution over the genome is similar to modern populations (Fig. 3E). However, WC1 does have an excess of long ROH segments (>1.6 Mb), relative to Aegean and European Neolithics (Fig. 3B). This includes several substantially long (7-16 Mb) ROH segments (Fig. 3A), consistent with low 𝜃 estimates in those regions (Fig. 3C). These regions do not show reduced coverage in WC1 nor a reduction in diversity in other samples, except for the longest such segment where we find a similar, but less extended region of reduced diversity in modern and HG individuals (*7*; Figs. 3B). Such long segments of reduced heterozygosity can result from cultural practices, such as consanguinity and endogamy, or demographic constraints such as a recent or ongoing bottleneck (*11*).

The extent of population structure in Neolithic SW-Asia has important implications for the origins of farming. High structuring would be expected under a scenario of localized independent domestication processes by distinct populations, whereas low structure would be more consistent with a single population origin of farming or a diffuse homogeneous domestication process, perhaps involving high rates of gene flow across the Neolithic core zone. The ancient Zagros individuals show stronger affinities to Caucasus HGs (Table S17.1) whereas Aegeans showed affinities to other European HGs (Tables S17.2 and S17.3). Formal tests of admixture of the form f3(Neo\_Iranian, HG; Anatolia\_Neolithic) were all positive with Z-scores above 15.78 (Table S17.6), indicating that Neolithic NW-Anatolians did not descend from a population formed by the mixing of Zagros Neolithics and known HG groups. These results suggest that Neolithic populations from NW-Anatolia and the Zagros descended from distinct ancestral populations. Furthermore, while the Caucasus HGs are genetically closest to EN Zagros individuals, they also share unique drift with eastern, western, and Scandinavian European HGs (Table S16.1), indicating that they are not the direct ancestors of Zagros Neolithics.

The significant differences between ancient Iranians, Anatolian/European farmers and European HGs suggest a separation before the Neolithic. Assuming a mutation rate of 5 x 10-10 per site per year (*12*), the inferred mean split time for Anatolian/European farmers (as represented by Bar8) and European hunter-gatherers (LOS; Loschbour) ranged from 33-39 kya (combined 95% CI 16-61), and for the Neolithic Iranians (WC1) 46-77 kya (combined 95% CI 38-104) (13). Furthermore, the European hunter-gatherers were inferred to have an effective population size (*Ne*)that was ~10-20% of either Neolithic farming group.

Levels of inferred Neanderthal ancestry in WC1 are low (Fig. S22, Table S21), but fall within the general trend described in Fu *et al.* (*14*). Fu *et al.* (*14*) also inferred a basal Eurasian ancestry component in the Caucasus HG sample Satsurblia when examined within the context of a “base model” for various ancient Eurasian genomes dated from ~45,000-7,000 years ago. We examined this base model using ADMIXTUREGRAPH (*6*) and inferred almost twice as much basal Eurasian ancestry for WC1 as for Satsurblia (62% versus 32%) (Fig. S52), with the remaining derived from Ancient north Eurasians such as Mal`ta1 (*15*). Thus Neolithic Iranians appear to derive predominantly from the earliest known Eurasian population branching event (*7*).

We applied ‘chromosome painting’ and a Bayesian mixture model (*7*) to infer which individuals from160-220 modern groups are most recently related to WC1 on the basis of shared haplotypes. WC1 was inferred to share a high proportion (>95%) of recent ancestry with groups sampled from the Middle East, Caucasus and India. We compared WC1's profile of haplotype sharing with modern groups to that of three high coverage Neolithic genomes from Barcın, NW-Anatolia (Fig 4), Germany (LBK, Stuttgart) and Hungary (NE1, Polgár-Ferenci-hát). In stark contrast to WC1, these Anatolian and European Neolithics shared ~60-90% of recent ancestry with modern groups sampled from South Europe (Figs. S24, S30, S32-S37, Table S22).

We examined recent haplotype sharing between each modern group and ancient Neolithic genomes from Iran (WC1) and Europe (LBK, NE1), two ancient HG genomes sampled from Luxembourg (LOS) and the Caucasus (KK1; Kotias), a 4.5k-year old genome from Ethiopia (Mota) and Ust’-Ishim, a 45k-year old genome from Siberia. Modern groups from S-, C and NW-Europe shared haplotypes predominantly with European Neolithic samples LBK and NE1, and European HGs, while modern Near and Middle Eastern, and Indian samples had higher sharing with WC1 (Fig. S28-29). Modern Pakistani, Iranian, Armenian, Tajikistani, Uzbekistani and Yemeni samples were inferred to share >10% of haplotypes most recently with WC1; even when we include modern groups from neighboring geographic regions as ancestry surrogates (Fig. S26-27, Table S23). This includes Iranian Zoroastrians, having the highest inferred sharing with WC1 out of all modern groups (Table S23). Consistent with this, *f3* statistics indicate Iranian Zoroastrians are the most genetically similar to all four Neolithic Iranians, followed by other modern Iranians (Fars), Balochi (border region of Iran, Pakistan and Afghanistan), Brahui (Pakistan and Afghanistan), Kalash (Pakistan) and Georgians (Figs. S12-15). Interestingly, WC1 most likely had brown eyes, relatively dark skin, and black hair, although Neolithic Iranians do carry reduced pigmentation-associated alleles in several genes, and display derived alleles at 7 of the 12 loci showing the strongest signatures of selection in ancient Eurasians (*3*) (Tables S29-S33). While there is a strong Neolithic component in these modern S-Asian populations, simulation of allele sharing rejected full population continuity under plausible ancestral population sizes, indicating some population turnover in Iran since the Neolithic (*7*).

Early Neolithic samples from eastern and western SW-Asia differ conspicuously, but comparisons to genomes from Chalcolithic Anatolia and Iron Age Iran indicate a degree of subsequent homogenization. Kumtepe6, a ~6,750 year old genome from NW-Anatolia (*16*), was more similar to Neolithic Iranians than any other non-Iranian ancient genome (Fig. S17-20; Table S18.1). Furthermore, our Iron Age genome (F38; 971-832 BCE; sequenced to 1.9x) from Tepe Hasanlu in NW-Iran shares greatest similarity with Kumtepe6 (Fig. S21) even compared to Neolithic Iranians (Table S20). We inferred additional non-Iranian or non-Anatolian ancestry in F38 from sources such as European Neolithics and even post-Neolithic Steppe populations (Table S20). Consistent with this, the F38 individual carried a N1a sub-clade mtDNA, which is common in early European and NW-Anatolian farmers (*3*). In contrast, his Y-chromosome belongs to sub-haplogroup R1b1a2a2, also found in five Yamnaya individuals (*17*) and in two individuals from the Poltavka culture (*3*). These patterns indicate that post-Neolithic homogenization in SW-Asia involved substantial bidirectional gene flow between the East and West of the region, as well as possible gene flow from the Steppe.

Migration of people associated with the Yamnaya culture has been implicated in the spread of Indo-European languages (*17, 18*) and some level of Near Eastern ancestry was inferred in southern Russian pre-Yamnaya populations (*3*). Our tests suggest that Neolithic Iranians were unlikely to be the main source of Near Eastern ancestry in the Steppe population (Table S20), and that ancestry in pre-Yamnaya populations originated primarily in the west of SW-Asia.

We also inferred shared ancestry between Steppe and Hasanlu Iron Age genomes, distinct from that in EN Iranians (Table S20, (*7*)). In addition, modern Middle Easterners and South Asians appear to possess mixed ancestry from ancient Iranian and Steppe populations (Table S19 and S20). However, Steppe-related ancestry may also have been acquired indirectly from other sources (*7*) and it is not clear if this is sufficient to explain the spread of Indo-European languages from a hypothesized Steppe homeland to the region where Indo-Iranian languages are spoken today. On the other hand, the affinities of Zagros Neolithic individuals to modern populations of Pakistan, Afghanistan, Iran and India is consistent with a spread of Indo-Iranian languages, or of Dravidian languages (which includes Brahui), from the Zagros into southern Asia, in association with farming (*19*).

The Neolithic transition in SW-Asia involved the appearance of different domestic species, particularly crops, in different parts of the Neolithic core zone, with no single center (*20*). Early evidence of plant cultivation and goat management between the 10th and the 8th millennium BCE highlight the Zagros as a key region in the Neolithisation process (*1*). Given evidence of domestic species movement from East to West across SW-Asia (*21*), it is surprising that EN human genomes from the Zagros are not closely related to those from NW-Anatolia and Europe. Instead they represent a previously undescribed Neolithic population. Our data show that the chain of Neolithic migration into Europe does not reach back to the eastern Fertile Crescent, also raising questions about whether intermediate populations in southeastern and Central Anatolia form part of this expansion. On the other hand, it seems probable that the Zagros region was the source of an eastern expansion of the SW-Asian domestic plant and animal economy. Our inferred persistence of ancient Zagros genetic components in modern day S-Asians lends weight to a strong demic component to this expansion.

**References**

1. S. Riehl, M. Zeidi, N. Conard, Emergence of Agriculture in the Foothills of the Zagros Mountains of Iran . *Science* **341**, 65-57 (2013)

2. R. Mattews, W. Mattews, Y. Mohammadifar, Eds., *The Earliest Neolithic of Iran: 2008 Excavations at Sheikh-e Abad and Jani Central Zagros*, vol. 1 (Oxbow Books,Oxford, 2013)

3. I. Mathieson *et al.*, Genome-wide patterns of selection in 230 ancient Eurasians. *Nature* **528**, 499-503 (2015)

4. Z. Hofmanová *et al.*, Early farmers from across Europe directly descended from Neolithic Aegeans. *PNAS*, 1523951113 (2016)

5. G. Müldner, " Isotope Analysis of Animal Bone" in *The Earliest Neolithic of Iran: 2008 Excavations at Sheikh-e Abad and Jani.* R. Matthews, W. Matthews, Y.Mohammadifar, Eds. (Oxbow Books, 2013)

6. N. Patterson *et al.*, Ancient admixture in human history. *Genetics* **192**, 1065-1093 (2012)

7. Materials and methods are available as supplementary material at the Science website.

8. E. R. Jones *et al.*, Upper Palaeolithic genomes reveal deep roots of modern Eurasians. *Nat Commun* **6**, (2015)

9. A. Kousathanas *et al.*, Inferring heterozygosity from ancient and low coverage genomes. *bioRxiv*, 046748 (2016)

10. M. G. Llorente *et al*., Ancient Ethiopian genome reveals extensive Eurasian admixture in Eastern Africa. *Science* **350**, 820-822 (2015)

11. T. J. Pemberton *et al.*, Genomic Patterns of Homozygosity in Worldwide Human Populations. *Am J Hum Genet* **91**, 275-292 (2012)

12. A. Kong *et al.*, Rate of de novo mutations, father’s age, and disease risk. *Nature* **488**, 471-475 (2012)

13. M. W. Nachman, S. L. Crowell, Estimate of the mutation rate per nucleotide in humans. *Genetics* **156**, 297-304 (2000)

14. Fu, Q. *et al.* The genetic history of Ice Age Europe. *Nature* **534***,*200–205 (2016)

15. M. Raghavan *et al*., Upper Palaeolithic Siberian genome reveals dual ancestry of Native Americans. *Nature* **505**, 87-91 (2014)

16. A. Omrak *et al.*, Genomic Evidence Establishes Anatolia as the Source of the European Neolithic Gene Pool. *Curr Biol* **26**, 270-275 (2016)

17. W. Haak *et al.*, Massive migration from the steppe was a source for Indo-European languages in Europe. *Nature* **522**, 207-211 (2015)

18. M. E. Allentoft *et al.*, Population genomics of Bronze Age Eurasia. *Nature* **522**, 167- 172 (2015)

19. DQ. Adams, [*Encyclopedia of Indo-European Culture*](https://books.google.com/books?id=tzU3RIV2BWIC) (Taylor & Francis, London, 1997)

20. D. Q. Fuller, G. Willcox, R. G. Allaby, Early agricultural pathways: moving outside the 'core area' hypothesis in Southwest Asia. *J Exp Bot* **63**, 617-633 (2012)

21. A. Scheu *et al.*, The genetic prehistory of domesticated cattle from their origin to the spread across Europe. *Bmc Genet* **16**, (2015)

 **Supplementary references**

22. R. J. Braidwood, The Agricultural Revolution. *Scientific American* **203**, 130-152 (1960)

23. J. Pullar, *Tepe Abdul Hosein: A Neolithic site in western Iran, excavations 1978*. (BAR Int Ser 563, Oxford, 1990)

24. J. Pullar, Tepe Abdul Hossein. *Iran* **17**, 153-155 (1979)

25. P. Mortensen, *Excavations at Tepe Guran. The Neolithic Period*. (vol. 55, Acta Iranica, 2014), pp. 145.

26. P. E. L. Smith, Reflexion on four seasons of excavations at Tappeh Ganj Dareh. *Proceedings of the Annual Symposium on Archaeological Research in Iran* **4**, 11-22 (1976).

27. M. A. Zeder, B. Hesse, The Initial Domestication of Goats (*Capra hircus*) in the Zagros Mountains 10,000 years Ago. *Science* **287**, 2254-2257 (2000)

28. B. Hesse, Thesis, Columbia University (1977)

29. M. A. Zeder, "A view from the Zagros: new perspectives on livestock domestication in the Fertile Crescent" in *First steps of animal domestication,* J.-D. Vigne, J. Peters, D. Helmer, Eds. (Oxbow, Oxford, 2005), pp. 125-146.

30. F. Hole, K. V. Flannery, J. A. Neely, *Prehistory and Human Ecology of the Deh Luran Plain. An Early Village Sequence from Khuzistan, Iran*. (vol. 1, Memoirs of the Museum of Anthropoplogy University of Michigan, Ann Arbor, 1969)

31. F. Hole, Thesis, University of Michigan (1977)

32. A. Alizadeh, *Excavations at the Prehistoric Mound of Chogha Bonut, Khuzestan, Iran, Seasons 1976/77, 1977/78, and 1996*. (vol. 120, Oriental Institute Publications, University of Chicago, 2003)

33. H. B. J. Peters, G. Grupe, K. Schmidt, N. Pöllath, "The long and winding road: ungulate exploitation and domestication in Early Neolithic Anatolia (10,00-7,000 cal.BC)" in *The Origins and Spread of Domestic Animals in Southwest Asia and Europe,* J. C. S. Colledge, K. Dobney, K. Manning, S. Shennan, Ed. (Walnut Creek, CA: Left Coast Press, 2013), pp. 83-114.

34. B. Moradi *et al.*, "A Short Account on Kelek Asad Morad, a Pre-Pottery Neolithic Site in Pol-e Dokhtar, Luristan" in *The Neolithic of the Iranian Plateau. Recent Research,* K. Roustaei, M. Mashkour, Eds. (ex oriente, Berlin, 2016 ).

35. J. Daujat, M. Mashkour, A. Emery-Barbier, R. Neef, R. Bernbeck, "Qale Rostam: Reconsidering the "Rise of a Highland Way of Life". An integrated bioarchaeological analysis" in *The Neolithic of the Iranian Plateau. Recent Research,* K. Roustaei, M. Mashkour, Eds. (ex oriente, Berlin, 2016 )

36. K. Roustaei, M. Mashkour, M. Tengberg, Tappeh Sang-e Chakhmaq and the Beginning of the Neolithic in north-east Iran. *Antiquity* **89**, 573-595 (2015).

37. K. Roustaei, An Emerging Picture of the Neolithic of Northeast Iran. *Iranica Antiqua* **51**, 21-56 (2016).

38. R. Matthews, H. Fazeli Nashli, Eds., *The Neolithisation of Iran. The formation of new societies*, (BANEA, Owbow Books, Oxford, 2013), pp. Pages

39. K. O. Lorentz, "Ubaid headshaping: negotiations of identity through physical appearance?" in *Beyond the Ubaid: Transformation and integration in the late prehistoric societies of the Middle East. ,* R. Carter, G. Philip, Eds. (Oriental Institute of Chicago, Chicago, 2010), pp. 125-147.

40. R. Hubbard, " "Archaeobotany of Abdul Hosein"" in *Tepe Abdul Hosein: A Neolithic site in western Iran, excavations 1978*. (Oxford: BAR International, 1990), pp. 217-222.

41. J. Bruzek, A Method for Visual Determination of Sex, Using the Human Hip Bone. *American Journal of Physical Anthropology* **117**, 157-168 (2002).

42. L. Scheuer, S. Black, *Developmental juvenile osteology*. (Elsevier, ed. Academic Press, 2000).

43. M. Trotter, "Estimation of stature from intact long limb bones" in *Personal Identification in Mass Disasters,* T. D. Steward, Ed. (Smithsonian Institution, Washington, D.C, 1970), pp. 71-83.

44. P. S. Ungar, F. E. Grine, M. F. Teaford, A. Perez-Perez, A review of interproximal wear grooves on fossil hominin teeth with new evidence from Olduvai Gorge. *Archives of Oral Biology* **46**, 285–292 (2001).

45. J. R. Lukacs, R. F. Pastor, Activity-induced patterns of dental abrasion in prehistoric Pakistan: evidence from Mehrgarh and Harappa. *American Journal of Physical Anthropology* **76**, 377-398 (1988).

46. C. F. A. Moorrees, E. A. Fanning, E. E. j. Hunt, Age variation of formation stages for ten permanent teeth. *Journal of dental Research* **42**, 1490-1502 (1963a)

47. P. Murail, J. Bruzek, F. Houët, E. Cunha, DSP: a probabilistic sex diagnosis tool using worldwide variability in hip bone measurements. *Bulletins et Mémoires de la Société d'Anthropologie de Paris* **17**, 167-176 (2005).

48. K. Abdi, F. Biglari, S. Heydari, Islamabad Project 2001. Test Excavations at Wezmeh Cave. *Archäologische Mitteilungen aus Iran und Turan.* **34**, 171-194 (2002).

49. M. Mashkour *et al.*, Carnivores and their Prey in the Wezmeh Cave (Kermanshah, Iran): A Late Pleistocene Refuge in the Zagros. *Int J Osteoarchaeol* **19**, 678-694 (2009).

50. E. Trinkhaus *et al.*, Late pleistocene human remains from Wezmeh Cave, western Iran. *Am J Phys Anthropol* **135**, 371-378 (2008).

51. M. D. Danti, "The late Bronze and early Iron age in northwestern Iran" in *The Oxford Handbook of Ancient Iran,* D. T. Potts Ed. (2013), vol. Oxford University Press, pp. 327-376.

52. O. W. Muscarella, The Excavation of Hasanlu: An Archaeological Evaluation. *Bulletin of the American Schools of Oriental Research*, 69-94 (2006).

53. R. H. Dyson, The Iron Age Architecture at Hasanlu: an Essay. *Expedition* **31**, 107-127 (1989).

54. R. H. Dyson, O. W. Muscarella, Constructing the Chronology and Historical Implications of Hasanlu IV. *Iran*, 1-27 (1989).

55. P. Selinsky, Thesis, University of Pennsylvania (2009).

56. M. Danti, M. Cifarelli, Iron II Warrior Burials at Hasanlu Tepe, Iran. *Iranica Antiqua* **50**, 61-157 (2015).

57. O. W. Muscarella, Hasanlu in the Ninth Century B.C. and its Relations with Other Cultural Centers of the Near East. *American Journal of Archaeology* **75**, 263-266 (1971)

58. M. I. Marcus, Emblems of authority, the seals and sealings from Hasanlu IVB. *Expedition* **31**, 53-63 (1989).

59. M. I. Marcus, Glyptic style and seal function: the Hasanlu connection. . *Aegean Seals, Sealings and Administration*, (1990).

60. M. Cifarelli, "Personal ornaments at Hasanlu, Iran. " in *Polish Archaeology in the Mediterranean* **XXIII/2***,* 297-316 (2014).

61. P. Magee, Deconstructing the Destruction of Hasanlu: an Archaeological Evaluation. *Bulletin of the American Schools of Oriental Research* **342**, 69-94 (2008).

62. G. J. Van Klinken, Bone collagen quality indicators for palaeodietary and radiocarbon measurements. *Journal of Archaeological Science* **26**, 687-695 (1999)

63. M. Kircher, S. Sawyer, M. Meyer, Double indexing overcomes inaccuracies in multiplex sequencing on the Illumina platform. *Nucleic Acids Res* **40**, (2012)

64. I. Gronau, M. J. Hubisz, B. Gulko, C. G. Danko, A. Siepel, Bayesian inference of ancient human demography from individual genome sequences. *Nature genetics* **43**, 1031-1034 (2011)

65. M. Kuhlwilm *et al.*, Ancient gene flow from early modern humans into Eastern Neanderthals. *Nature* **530**, 429-433 (2016).

66. D. F. Conrad *et al.*, A worldwide survey of haplotype variation and linkage disequilibrium in the human genome. *Nature Genetics* **38**, 1251-1260 (2006).

67. G. Hellenthal, A. Auton, D. Falush, Inferring human colonization history using a copying model. *PLoS Genetics* **4**, e1000078 (2008).

68. S. Leslie *et al.*, The fine scale genetic structure of the British population. *Nature* **519**, 309-314 (2015).

69. H. Jonsson, A. Ginolhac, M. Schubert, P. L. F. Johnson, L. Orlando, mapDamage2.0: fast approximate Bayesian estimates of ancient DNA damage parameters. *Bioinformatics* **29**, 1682-1684 (2013)

70. C. Gamba *et al.*, Genome flux and stasis in a five millennium transect of European prehistory. *Nat Commun* **5**, (2014)

71. E. Aronesty, Comparison of sequencing utility programs. *The Open Bioinformatics Journal* **7**, (2013).

72. H. Li, R. Durbin, Fast and accurate short read alignment with Burrows-Wheeler transform. *Bioinformatics* **25**, 1754-1760 (2009).

73. M. A. DePristo *et al.*, A framework for variation discovery and genotyping using next-generation DNA sequencing data. *Nat Genet* **43**, 491-498 (2011).

74. D. Vianello *et al.*, HAPLOFIND: A New Method for High-Throughput mtDNA Haplogroup Assignment. *Hum Mutat* **34**, 1189-1194 (2013).

75. A. Gomez-Carballa, J. Pardo-Seco, J. Amigo, F. Martinon-Torres, A. Salas, Mitogenomes from The 1000 Genome Project Reveal New Near Eastern Features in Present-Day Tuscans. *Plos One* **10**, (2015).

76. M. Derenko *et al.*, Complete Mitochondrial DNA Diversity in Iranians. *Plos One* **8**, (2013).

77. B. Malyarchuk, M. Derenko, G. Denisova, O. Kravtsova, Mitogenomic Diversity in Tatars from the Volga-Ural Region of Russia. *Mol Biol Evol* **27**, 2220-2226 (2010).

78. M. Pala *et al.*, Mitochondrial DNA Signals of Late Glacial Recolonization of Europe from Near Eastern Refugia. *Am J Hum Genet* **90**, 915-924 (2012).

79. A. Al-Abri *et al.*, Pleistocene-Holocene boundary in Southern Arabia from the perspective of human mtDNA variation. *Am J Phys Anthropol* **149**, 291-298 (2012).

80. L. Quintana-Murci *et al.*, Where west meets east: The complex mtDNA landscape of the southwest and Central Asian corridor. *Am J Hum Genet* **74**, 827-845 (2004).

81. Q. Fu *et al.*, Genome sequence of a 45,000-year-old modern human from western Siberia. *Nature* **514**, 445-449 (2014).

82. I. Lazaridis *et al.*, Ancient human genomes suggest three ancestral populations for present-day Europeans. *Nature* **513**, 409-413 (2014).

83. G. Brandt *et al.*, Ancient DNA Reveals Key Stages in the Formation of Central European Mitochondrial Genetic Diversity. *Science* **342**, 257-261 (2013).

84. A. Szecsenyi-Nagy *et al.*, Tracing the genetic origin of Europe's first farmers reveals insights into their social organization. *P Roy Soc B-Biol Sci* **282**, (2015).

85. A. Ralf, M. van Oven, K. Y. Zhong, M. Kayser, Simultaneous Analysis of Hundreds of Y-Chromosomal SNPs for High-Resolution Paternal Lineage Classification using Targeted Semiconductor Sequencing. *Hum Mutat* **36**, 151-159 (2015).

86. H. Li *et al.*, The Sequence Alignment/Map format and SAMtools. *Bioinformatics* **25**, 2078-2079 (2009).

87. C. Cinnioglu *et al.*, Excavating Y-chromosome haplotype strata in Anatolia. *Hum Genet* **114**, 127-148 (2004).

88. I. Nasidze, D. Quinque, M. Rahmani, S. A. Alemohamad, M. Stoneking, Close genetic relationship between Semitic-speaking and Indo-European-speaking groups in Iran. *Ann Hum Genet* **72**, 241-252 (2008)

89. S. Firasat *et al.*, Y-chromosomal evidence for a limited Greek contribution to the Pathan population of Pakistan. *Eur J Hum Genet* **15**, 121-126 (2007)

90. S. Sengupta *et al.*, Polarity and temporality of high-resolution Y-chromosome distributions in India identify both indigenous and exogenous expansions and reveal minor genetic influence of central Asian pastoralists. *Am J Hum Genet* **78**, 202-221 (2006).

91. M. Haber *et al.*, Afghanistan's Ethnic Groups Share a Y-Chromosomal Heritage Structured by Historical Events. *Plos One* **7**, (2012)

92. D. M. Behar *et al.*, Contrasting patterns of Y chromosome variation in Ashkenazi Jewish and host non-Jewish European populations. *Hum Genet* **114**, 354-365 (2004).

93. D. M. Behar *et al.*, The genome-wide structure of the Jewish people. *Nature* **466**, 238-U112 (2010).

94. N. M. Myres *et al.*, A major Y-chromosome haplogroup R1b Holocene era founder effect in Central and Western Europe. *Eur J Hum Genet* **19**, 95-101 (2011)

95. V. Grugni *et al.*, Ancient Migratory Events in the Middle East: New Clues from the Y-Chromosome Variation of Modern Iranians. *Plos One* **7**, (2012)

96. Q. M. Fu *et al.*, A Revised Timescale for Human Evolution Based on Ancient Mitochondrial Genomes. *Curr Biol* **23**, 553-559 (2013).

97. T. S. Korneliussen, A. Albrechtsen, R. Nielsen, ANGSD: Analysis of Next Generation Sequencing Data. *Bmc Bioinformatics* **15**, (2014).

98. M. Rasmussen *et al.*, An Aboriginal Australian Genome Reveals Separate Human Dispersals into Asia. *Science* **334**, 94-98 (2011).

99. G. B. J. Busby *et al.*, The Role of Recent Admixture in Forming the Contemporary West Eurasian Genomic Landscape. *Curr Biol* **25**, 2518-2526 (2015)

100. A. Seguin-Orlando *et al.*, Genomic structure in Europeans dating back at least 36,200 years. *Science* **346**, 1113-1118 (2014).

101. I. Olalde *et al.*, Derived immune and ancestral pigmentation alleles in a 7,000-year-old Mesolithic European. *Nature* **507**, 225-228 (2014)

102. L. M. Cassidy *et al.*, Neolithic and Bronze Age migration to Ireland and establishment of the insular Atlantic genome. *P Natl Acad Sci USA* **113**, 368-373 (2016)

103. C. The Genomes Project, A global reference for human genetic variation. *Nature* **526**, 68-74 (2015)

104. K. Prufer *et al.*, The complete genome sequence of a Neanderthal from the Altai Mountains. *Nature* **505**, 43-49 (2014).

105. M. Kirin *et al.*, Genomic Runs of Homozygosity Record Population History and Consanguinity. *Plos One* **5**, (2010)

106. C. Wang, X. Zhan, L. Liang, G. c. c. Abecasis, alo R, X. Lin, Improved ancestry estimation for both genotyping and sequencing data using projection procrustes analysis and genotype imputation. *American Journal of Human Genetics* **96**, 926-937 (2015).

107. C. Wang, X. Zhan, LASER: Locating Ancestry from SEquence Reads. http://csg.sph.umich.edu/chaolong/LASER/LASER\_Manual.pdf (2015)

108. G. Hellenthal *et al.*, A Genetic Atlas of Human Admixture History. *Science* **343**, 747-751 (2014)

109. S. Purcell *et al.*, PLINK: A tool set for whole-genome association and population-based linkage analyses. *Am J Hum Genet* **81**, 559-575 (2007)

110. C. C. Chang *et al.*, Second-generation PLINK: rising to the challenge of larger and richer datasets. *GigaSci* **4**, (2015)

111. pyliftover 0.3, https://github.com/konstantint/pyliftover (2014)

112. A. S. Hinrichs *et al.*, The UCSC Genome Browser Database: update 2006. *Nucleic Acids Res* **34**, D590-D598 (2006)

113. K. R. Veeramah *et al.*, An Early Divergence of KhoeSan Ancestors from Those of Other Modern Humans Is Supported by an ABC-Based Analysis of Autosomal Resequencing Data. *Molecular Biology and Evolution* **29**, 617-630 (2011)

114. R. R. Hudson, M. Slatkin, W. P. Maddison, Estimation of levels of gene flow from DNA sequence data. *Genetics* **132**, 583-589 (1992)

115. L. van Dorp *et al.*, Evidence for a Common Origin of Blacksmiths Cultivators in the Ethiopian Ari within the Last 4500 Years: Lessons for Clustering-Based Inference. *PLoS Genetics* **11**, e1005397 (2015)

116. M. Haber *et al.*, Genetic evidence for an origin of the Armenians from Bronze Age mixing of multiple populations. *European Journal of Human Genetics*, (2015).

117. O. Delaneau, J. Marchini, J. F. Zagury, A linear complexity phasing method for thousands of genomes. *Nat Methods* **9**, 179-181 (2012).

118. D. J. Lawson, G. Hellenthal, S. Myers, D. Falush, Inference of population structure using dense haplotype data. *PLoS Genet* **8**, e1002453 (2012)

119. D. Gamerman, *Markov Chain Monte Carlo: Stochastic simulation for Bayesian inference*. (Chapman Hall, 1997)

120. Nasidze *et al*., Genetic evidence for the Mongolian ancestry of Kalmyks. Am. J. Phys. Anthropol., **128**, 846–854 (2005)

121. J. K. Pickrell *et al.*, Ancient west Eurasian ancestry in southern eastern Africa. *Proceedings of the National Academy of Sciences* **111**, 2632-2637 (2014)

122. D. Reich *et al.*, Genetic history of an archaic hominin group from Denisova Cave in Siberia. *Nature* **468**, 1053-1060 (2010).

123. M. Meyer *et al.*, A High-Coverage Genome Sequence from an Archaic Denisovan Individual. *Science* **338**, 222-226 (2012).

124. B. Vernot *et al.*, Excavating Neandertal and Denisovan DNA from the genomes of Melanesian individuals. *Science*, aad9416 (2016).

125. M. Sikora *et al.*, Population Genomic Analysis of Ancient and Modern Genomes Yields New Insights into the Genetic Ancestry of the Tyrolean Iceman and the Genetic Structure of Europe. *Plos Genet* **10**, e1004353 (2014).

126. S. Walsh *et al.*, Developmental validation of the HIrisPlex system: DNA-based eye and hair colour prediction for forensic and anthropological usage. *Forensic Sci Int-Gen* **9**, 150-161 (2014).

127. K. L. Hart *et al.*, Improved eye- and skin-color prediction based on 8 SNPs. *Croat Med J* **54**, 248-256 (2013).

128. P. C. Sabeti *et al.*, Genome-wide detection and characterization of positive selection in human populations. *Nature* **449**, 913-U912 (2007).

129. R. L. Lamason *et al.*, SLC24A5, a Putative Cation Exchanger, Affects Pigmentation in Zebrafish and Humans. *Science* **310**, 1782-1786 (2005).

130. M. P. Donnelly *et al.*, A global view of the OCA2-HERC2 region and pigmentation. *Hum Genet* **131**, 683-696 (2012).

131. H. Eiberg *et al.*, Blue eye color in humans may be caused by a perfectly associated founder mutation in a regulatory element located within the HERC2 gene inhibiting OCA2 expression. *Hum Genet* **123**, 177-187 (2008).

132. V. A. Canfield *et al.*, Molecular Phylogeography of a Human Autosomal Skin Color Locus Under Natural Selection. *G3-Genes Genom Genet* **3**, 2059-2067 (2013).

133. S. Wilde *et al.*, Direct evidence for positive selection of skin, hair, and eye pigmentation in Europeans during the last 5,000 y. *P Natl Acad Sci USA* **111**, 4832-4837 (2014).

134. S. Beleza *et al.*, Genetic Architecture of Skin and Eye Color in an African-European Admixed Population. *Plos Genet* **9**, (2013).

135. S. Selinski *et al.*, Genotyping NAT2 with only two SNPs (rs1041983 and rs1801280) outperforms the tagging SNP rs1495741 and is equivalent to the conventional 7-SNP NAT2 genotype. *Pharmacogenet Genom* **21**, 673-678 (2011).

136. B. Patillon *et al.*, A Homogenizing Process of Selection Has Maintained an "Ultra-Slow" Acetylation NAT2 Variant in Humans. *Hum Biol* **86**, 185-214 (2014).

137. A. Sabbagh, P. Darlu, B. Crouau-Roy, E. S. Poloni, Arylamine N-Acetyltransferase 2 (NAT2) Genetic Diversity and Traditional Subsistence: A Worldwide Population Survey. *Plos One* **6**, e18507 (2011).

138. H. Magalon *et al.*, Population genetic diversity of the NAT2 gene supports a role of acetylation in human adaptation to farming in Central Asia. *Eur J Hum Genet* **16**, 243-251 (2008).

139. F. Luca *et al.*, Multiple Advantageous Amino Acid Variants in the NAT2 Gene in Human Populations. *Plos One* **3**, e3136 (2008).

140. I. B. Kuznetsov, M. McDuffie, R. Moslehi, A web server for inferring the human N-acetyltransferase-2 (NAT2) enzymatic phenotype from NAT2 genotype. *Bioinformatics* **25**, 1185-1186 (2009).

141. M. Garcia-Closas *et al.*, NAT2 slow acetylation, GSTM1 null genotype, and risk of bladder cancer: results from the Spanish Bladder Cancer Study and meta-analyses. *Lancet* **366**, 649-659 (2005).

142. R. K. Bains *et al.*, Molecular diversity and population structure at the Cytochrome P450 3A5 gene in Africa. *Bmc Genet* **14**, (2013).

143. M. Schirmer *et al.*, Genetic signature consistent with selection against the CYP3A4\*1B allele in non-African populations. *Pharmacogenet Genom* **16**, 59-71 (2006).

144. E. E. Thompson *et al.*, CYP3A variation and the evolution of salt-sensitivity variants. *Am J Hum Genet* **75**, 1059-1069 (2004).

145. H. Qiu *et al.*, CYP3 phylogenornics: evidence for positive selection of CYP3A4 and CYP3A7. *Pharmacogenet Genom* **18**, 53-66 (2008).

146. M. Bochud *et al.*, Association of CYP3A5 genotypes with blood pressure and renal function in African families. *J Hypertens* **24**, 923-929 (2006).

147. M. Bochud, P. Bovet, M. Burnier, C. B. Eap, CYP3A5 and ABCB1 genes and hypertension. *Pharmacogenomics* **10**, 477-487 (2009)

148. T. Nakajima *et al.*, Natural selection and population history in the human angiotensinogen gene (AGT): 736 complete AGT sequences in chromosomes from around the world. *Am J Hum Genet* **74**, 898-916 (2004)

149. J. H. Young *et al.*, Differential susceptibility to hypertension is due to selection during the out-of-Africa expansion. *Plos Genet* **1**, 730-738 (2005)

150. A. Helgason *et al.*, Refining the impact of TCF7L2 gene variants on type 2 diabetes and adaptive evolution. *Nat Genet* **39**, 218-225 (2007)

151. J. L. Vassy, M. F. Hivert, M. Dauriz, J. B. Meigs, Polygenic Type 2 Diabetes Prediction at the Limit of Common Variant Detection. *Diabetes* **63**, (2014)

152. G. O. Tadmouri *et al.*, Molecular and population genetic analyses of beta-thalassemia in Turkey. *Am J Hematol* **57**, 215-220 (1998)

153. A. Cao, R. Galanello, Beta-thalassemia. *Genet Med* **12**, 61-76 (2010)

154. T. Raj *et al.*, Common Risk Alleles for Inflammatory Diseases Are Targets of Recent Positive Selection. *Am J Hum Genet* **92**, 517-529 (2013)

155. C. D. Huff *et al.*, Crohn's Disease and Genetic Hitchhiking at IBD5. *Mol Biol Evol* **29**, 101-111 (2012)

156. V. D. Peltekova *et al.*, Functional variants of OCTN cation transporter genes are associated with Crohn disease. *Nat Genet* **36**, 471-475 (2004)

157. A. H. Freedman *et al.*, Genome Sequencing Highlights the Dynamic Early History of Dogs. *Plos Genet* **10**, e1004016 (2014)

158. K. Tamura, G. Stecher, D. Peterson, A. Filipski, S. Kumar, MEGA6: Molecular Evolutionary Genetics Analysis Version 6.0. *Mol Biol Evol* **30**, 2725-2729 (2013)

159. A. Hodgkinson, A. Eyre-Walker, Variation in the mutation rate across mammalian genomes. *Nat Rev Genet* **12**, 756-766 (2011)

160. G. Müldner, " Isotope Analysis of Animal Bone" in The Earliest Neolithic of Iran:

2008 Excavations at Sheikh-e Abad and Jani. R. Matthews, W. Matthews, Y.

Mohammadifar, Eds. (Oxbow Books, 2013)

161. H. Bocherens, M. Mashkour, D. Billiou, Palaeoenvironmental and Archaeological Implications of Isotopic Analyses (13C, 15N) from Neolithic to Present in Qazvin Plain (Iran). *Environmental Archaeology* **5**, 1-19 (2000).

162. A. P. Morris et al., Large-scale association analysis provides insights into the genetic architecture and pathophysiology of type 2 diabetes. Nat Genet 44, 981 (2012).

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**Fig 1: Map of prehistoric Neolithic and Iron Age Zagros genome locations.** Colors indicate isochrones with numbers giving approximate arrival times of the Neolithicculture in years BCE.

**Fig 2: PCA plot of Zagros, European, and Near and Middle Eastern ancient genomes. Comparing ancient and modern genomes,** Neolithic Zagros genomes form a distinct genetic cluster close tomodern Pakistani and Afghan genomes (Balochi, Brahui, Makrani) but distinct from European hunter-gatherersand Neolithic farmers. See Animation S1 for an interactive 3D version of the PCA including the third principal component.

**Fig 3: Level and structure of ancient genomic diversity.** (A) Total length of the genome in different ROH classes; shades indicate the range observed among modern samples from different populations and lines indicate the distributions for ancient samples. (B) The total length of short (<1.6Mb) vs long (≥1.6Mb) ROH. (C) Distribution of heterozygosity (𝜃) inferred in 1Mb windows along a portion of chromosome 3 showing the longest ROH segment in WC1. Solid lines represent the MLE estimate, shades indicate the 95% confidence intervals and dashed lines the genome-wide median for each sample. (D) Distribution of heterozygosity (𝜃) estimated in 1Mb windows across the autosomes for modern and ancient samples. (E) Similarity in the pattern of heterozygosity (𝜃) along the genome as obtained by a PCA on centered Spearman correlations. Ancient - Bich: Bichon, Upper Palaeolithic forager from Switzerland; KK1: Kotias, Mesolithic forager from Georgia; WC1: Wezmeh Cave, Early Neolithic farmer from Zagros; Mota: 4,500 year old individual from Ethiopia; BR2: Ludas-Varjú-dúló, Late Bronze Age individual from Hungary. Modern - YRI: Yoruban, W-Africa; TSI: Tuscans, Italy; PJL: Punjabi, Pakistan; GBR: British

**Fig 4: Modern-day peoples with affinity to WC1.** Modern groups with an increasingly higher (respectively lower) inferred proportion of haplotype sharing with the Iranian Neolithic Wezmeh Cave (WC1, 7,455-7,082 cal BCE, blue triangle) compared to the Anatolian Neolithic Barcın genome (Bar8; 6,212–6,030 cal BCE, red triangle) are depicted with an increasingly stronger blue color (respectively red color). Circle sizes illustrate the relative absolute proportion of this difference between WC1 versus Bar8. The key for the modern group labels is provided in Table S24.

**Supplementary Materials**

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Materials and Methods

Figs. S1 - S52

Tables S1 - S37

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Movie S1 (3D animation of PCA)