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TITLE:

The most recent common ancestor of modern humans was born in Eurasia.

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ABSTRACT:

Ancient DNA has given a new vision to the recent history of human evolution. However, by always relying on the information provided by whole genome sequencing, some relevant relationships between modern humans and its archaic relatives have been misinterpreted by hybridization and recombination causes. In contrast, the congruent phylogeny, obtained from non-recombinant uniparental markers, indicates that humans and Neanderthals are sister subspecies, and that the most recent common ancestor of modern humans was not of African origin but Eurasian.

Keywords: Human, ancientDNA, Phylogeny

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Ancient DNA, coupled with whole genome analysis, is revealing the real complexity of the recent human history, far from the straightforward vision drawn by previous genetic analysis. The intricate relationships of European and other Eurasian populations in the past is a paradigmatic example (Raghavan et al. 2014; Fu et al. 2016). Farther back in time ancient DNA has also allowed the direct comparison of autosomes and the non-recombining mitochondrial DNA and Y-chromosome markers between archaic and modern humans (Meyer et al. 2012, 2016; Prüfer et al. 2014; Mendez et al. 2016). The surprise was that the hominin phylogenies obtained using uniparental markers or autosomal sequences were discordant. MtDNA and Y-chromosome phylogenies showed that Neanderthals and modern humans were sister subspecies whereas genome-wide data joints Denisovans and Neanderthals as the closest pair leaving modern humans as an out-group. Based on the assumption that mtDNA and Y-chromosomes are transmitted as single genes and do not necessarily reflect the true relationships between individuals and populations as the whole autosomes do, several hypotheses have been proposed to explain the discrepancies observed (Posth et al. 2017; Petr et al. 2020). In summary, they propose the existence of hybridization between Denisovans and a genetically very divergent archaic hominin which could have introgressed its mtDNA and Y-

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chromosome lineages that later were fixed into the Denisovan population, phylogenetically distancing it from its next relatives the Neanderthals or, alternatively, an ancestor of modern humans could have introgressed their uniparental lineages into Neanderthals which, upon fixation in this group, would bring them closer to modern humans and away from their closest relatives the Denisovans, but, as the own proponents recognize, these hypotheses face severe drawbacks. Under neutral theory conditions, the average number of generations elapsed between the introgression and fixation of a haploid lineage is 2Ne, being Ne the effective population size (Kimura and Ohta 1969). Assuming Ne = 5,000 and a mean generation time of 25 years, a fixation event would last about 10,000 generations or around 250,000 years, but this would occur only as long as the lineage is transmitted each time to the next generation and that has a 1/Ne probability. Thus, the chance of a lineage to be lost in the process is very high. In addition, this unlikely event has to occur twice, once for the mitochondrial and once for the Y-chromosome. Furthermore, in hybridization events, it usually happens that the male heterogametic offspring is totally or partially infertile (Forejt 1996). There are clues that this type of incompatibility occurred in crosses between Neanderthals and Denisovans with humans (Jégou et al. 2017), so that, the probability

 doi:10.20944/preprints202012.0470.v1

of fixation for the Y-chromosome is even lower. As if this were not enough, it must be remembered that these haploid lineages are introgressed as whole gametes that also introduce specific autosomal variants from the putative super-archaic hominin into the Denisovan genome, or specific autosomal human variants into the Neanderthal genome. These variants have to be also eliminated in order to keep the inferred autosomal phylogenetic relationships.

However, what is the case if we trust on mtDNA and Y-chromosome as more efficient tools than autosomes to recover relatively deep population phylogenies and accept the uniparental phylogenetic alternative?

First, we must admit that the genomic relationships found are due to non-uniform interspecific gene flow. That is, more gene flow occurred between Denisovan and Neanderthals than between the later and modern humans. This could be true because, as deduced by their respective geographic ranges, Denisovans and Neanderthals were in partial sympatry more time than any of them with modern humans. Although, in a first analysis only a small amount of gene flow from Neanderthals into Denisovans was detected (Prüfer et al. 2014), a later finding of a F1 hybrid descendant of a cross between a Neanderthal female and a

 doi:10.20944/preprints202012.0470.v1

Denisovan male, the later with traces of Neanderthal admixture in their ancestors (Slon et al. 2018), suggests that these interbreeding events could be frequent. However, more samples and analyses are necessary to confirm this supposition.

The second requirement necessary to justify our hypothesis is to explain why, if the interspecific gene-flow was relatively frequent to leave a significant signal in the autosomes, no uniparental Neanderthal markers have been detected in the Denisovan gene pool or vice versa? As we commented previously, under neutrality conditions the loss, in the next generation, of a haploid marker introduced in a population is an event with a high probability of success ((No-1)/No). However, under the same conditions, the simultaneous introduction of a whole genome has a different destiny since, from the first meiosis, it will recombine with the receptor genome, giving rise to hybrid chromosomes and will continue recombining in successive generations, giving smaller fragments dispersed into more chromosomes following a slow dilution process. In addition, the Y-chromosome could be lost by male hybrid sterility. Furthermore, if the interbreeding events were male biased, and females rise their hybrid offspring in their own population, their

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mtDNAs would not pass to the population of the external fertilizing male.

To emphasize the important changes that this hypothesis introduces in human evolution, we reconstructed the hominin mtDNA phylogeny using the Neighbor-Joining method (Saitou and Nei 1987), taking as representative of modern humans a sub-Saharan African individual belonging to haplogroup L1c (Accession code: MF621129), the Mezmaiskaya 1 specimen (Accession code: FM865411) as representative of Neanderthals, the Denisovan 3 specimen (Accession code: NC013993) as representative of Denisovans, and the Sima de los Huesos specimen (Accession code: NC023100) as representative of the Middle Pleistocene hominins found in Atapuerca (Spain). The tree has a 100% bootstrap support for all the nodes (Figure 1). Branch shortening between Denisova and Atapuerca is as expected by the different age of death of both specimens. Resting the specific number of substitutions in their respective terminal branches gives a difference of 89 mutations between them that, transformed in time using the chosen mutation rate, gives a difference of about 360,000 years between the death of these two lineages. Assuming an approximate age of 50,000 years old for Denisova 3 (Reich et al. 2010), the age of the Atapuerca

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specimen would be around 410,000 years old which is similar to its age dated by archaeological methods (430,000 years old) (Arsuaga et al. 2014). However, applying the same calculations to the modern human-Neanderthal pair they resulted in a difference age, between these two specimens, of 227,000 years which is more than three times the age calculated for the Mezmaiskaya remains by archaeological methods (Skinner et al. 2005). We suggest that this difference could be attributed to the marked acceleration of the human mutation rate in recent times (Henn et al. 2009). Coalescence between Neanderthal and modern humans occurred 540,370 years ago (95% CI: 494,782 to 585,958 ya). And that of the Atapuerca-Denisova 3 pair 482,780 ya (95% CI: 439,705 to 565,855 ya). The most recent common ancestor (TMRCA) between Atapuerca and the Neanderthal-modern human pair is approximately 671,822 years old, and that of the later pair and Denisovan is approximately 815,585 years old. As expected by the respective age of the specimens compared, the split age between Denisovan and modern humans (876,357; 95%CI: 818,314 to 934,400 ya) is older that the split age of Denisovan and Neanderthals (754,814; 95% CI: 700,957 to 808,671 ya). These relationships and the ages when branches split are within the range found by other authors for the same groups of hominins (Green et

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al. 2008; Krause et al. 2010; Meyer et al. 2014; Sawyer et al. 2015). The analysis of Y-chromosome sequences for the same hominin groups (excluding Atapuerca) reflects the same tree topology as that obtained with mtDNA (Mendez et al. 2016; Petr et al. 2020). However, TMRCA of Denisovan and modern human Y-chromosome was estimated around 700 thousand years ago (kya) (Petr et al. 2020) that is younger than the one obtained for the same pair using mtDNA. Similarly, The Neanderthal and modern human Y-chromosome divergence around 370 kya (Petr et al. 2020) is significantly more recent than the ones estimated with the maternal marker. For the later pair, the mtDNA divergence is more in agreement with the Y-chromosome split age, around 588 kya, estimated by other authors (Mendez et al. 2016).

Regardless of the minor differences in split ages estimated with mtDNA or Y-chromosome markers, the acceptance of the identical phylogenetic relationships between the different hominin groups, found by the use of uniparental markers, has important implications for the history of modern human geographic origin. The first, and most important, is the fact that modern humans and Neanderthals are sister subspecies and that their common ancestor is related to a hominin group, the Denisovans, with Eurasian, not African roots.

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Hence it follows that, contrary to all previous hypotheses, the most recent common ancestor of modern humans was born in Eurasia. Denisovans are a mysterious hominin group that until recently lacked of any morphological identification. Its surprisingly genetic discovery at the Denisovan Cave was facilitated by successful ancient DNA extractions from undetermined remains (Meyer et al. 2012). More recently, it has been detected in the Tibet from a Late Middle Pleistocene mandible and from coetaneous sediments (Chen et al. 2019; Zhang et al. 2020), which provided evidence that some fossil remains, described as archaic hominins in different regions of China, could also belong to Denisovan related groups (Ao et al. 2017; Li et al. 2017). It deserves mention that many of the morphological characteristic attributable to Denisovan anatomy were foreseen from DNA methylation patterns (Gokhman et al. 2019). Other possible localization of Denisovan populations in Asia were inferred by the presence of Denisovan introgressed DNA in the genome of fossil or present-day modern human genomes, sampled from regions as distant as Mongolia, South east Asia or Melanesia (Reich et al. 2011; Sankararaman et al. 2016; Vernot et al. 2016; Browning et al. 2018; Skov et al. 2018; Jacobs et al. 2019; Massilani et al. 2020). All this evidence points to Denisovans as a species with a geographic continental range.

 doi:10.20944/preprints202012.0470.v1

The second implication is to suppose that some geographic barrier must have existed to interrupt gene flow between the ancestors or Neanderthals and modern humans in order to facilitate its genetic divergence. It is well known from the archaeological record, also contrasted by ancient DNA studies, that Neanderthal groups moved across Europe reaching Central Asia and the Middle East well before of 100 kya (Orlando et al. 2006; Krause et al. 2007; Briggs et al. 2009; Pomeroy et al. 2017). In contrast, the direct ancestors of modern humans have not been detected in Europe at that time. Our guess is that they crossed the Strait of Gibraltar very early, perhaps about 400 kya, and settled in northwestern Africa, in the region now known as the Maghreb, in which fossil remains and Middle Stone Age artefacts of an early or recent anatomically modern human have been excavated at Jebel Irhoud site (Morocco), and dated around 300 kya (Hublin et al. 2017; Richter et al. 2017). Thus, the cradle of the human evolution in Africa began in northwestern Africa and, from there, spread to the rest of the continent. From here, it follows that any hominin African lineage assumed to be direct ancestor of modern humans has to be derived of the Jebel Irhoud population.

 doi:10.20944/preprints202012.0470.v1

Finally, around 150 kya a group of not fully evolved modern humans left Africa for Eurasia where they met, again, its sister relatives, the Neanderthals and Denisovans (Kuhlwilm et al. 2016).

AO H., LIU C.-R., ROBERTS A. P., ZHANG P., XU X., 2017 An updated age for the Xujiayao hominin from the Nihewan Basin, North China: Implications for Middle Pleistocene human evolution in East Asia. Journal of human evolution **106**: 54–65.

ARSUAGA J. L., MARTÍNEZ I., ARNOLD L. J., ARANBURU A., GRACIA-TÉLLEZ A., SHARP W. D., QUAM R. M., FALGUÈRES C., PANTOJA-PÉREZ A., BISCHOFF J., POZA-REY E., PARÉS J. M., CARRETERO J. M., DEMURO M., LORENZO C., SALA N., MARTINÓN-TORRES M., GARCÍA N., ALCÁZAR DE VELASCO A., CUENCA-BESCÓS G., GÓMEZ-OLIVENCIA A., MORENO D., PABLOS A., SHEN C.-C., RODRÍGUEZ L., ORTEGA A. I., GARCÍA R., BONMATÍ A., BERMÚDEZ DE CASTRO J. M., CARBONELL E., 2014 Neandertal roots: Cranial and chronological evidence from Sima de los Huesos. Science **344**: 1358–63.

BRIGGS A. W., GOOD J. M., GREEN R. E., KRAUSE J., MARICIC T., STENZEL U., LALUEZA-FOX C., RUDAN P., BRAJKOVI'C D., KU'CAN \vZeljko, OTHERS, 2009 Targeted retrieval and analysis of five Neandertal mtDNA genomes. Science **325**: 318–321.

BROWNING S. R., BROWNING B. L., ZHOU Y., TUCCI S., AKEY J. M., 2018 Analysis of human sequence data reveals two pulses of archaic Denisovan admixture. Cell **173**: 53–61.

CHEN F., WELKER F., SHEN C.-C., BAILEY S. E., BERGMANN I., DAVIS S., XIA H., WANG H., FISCHER R., FREIDLINE S. E., OTHERS, 2019 A late middle pleistocene denisovan mandible from the tibetan plateau. Nature **569**: 409–412.

FOREJT J., 1996 Hybrid sterility in the mouse. Trends in genetics **12**: 412–417.

FU Q., POSTH C., HAJDINJAK M., PETR M., MALLICK S., FERNANDES D., FURTWÄNGLER A., HAAK W., MEYER M., MITTNIK A., OTHERS, 2016 The genetic history of ice age Europe. Nature **534**: 200–205.

GOKHMAN D., MISHOL N., MANUEL M. DE, JUAN D. DE, SHUQRUN J., MESHORER E., MARQUES-BONET T., RAK Y., CARMEL L., 2019 Reconstructing Denisovan anatomy using DNA methylation maps. Cell **179**: 180–192.

GREEN R. E., MALASPINAS A.-S., KRAUSE J., BRIGGS A. W., JOHNSON P. L. F., UHLER C., MEYER M., GOOD J. M., MARICIC T., STENZEL U., PRÜFER K., SIEBAUER M., BURBANO H. A., RONAN M., ROTHBERG J. M., EGHOLM M., RUDAN P., BRAJKOVIĆ D., KUĆAN Z., GUSIĆ I., WIKSTRÖM M., LAAKKONEN L., KELSO J., SLATKIN M., PÄÄBO S., 2008 A complete Neandertal mitochondrial genome sequence determined by high-throughput sequencing. Cell **134**: 416–26.

HENN B. M., GIGNOUX C. R., FELDMAN M. W., MOUNTAIN J. L., 2009 Characterizing the time dependency of human mitochondrial DNA mutation rate estimates. Molecular Biology and Evolution **26**: 217–230.

HUBLIN J.-J., BEN-NCER A., BAILEY S. E., FREIDLINE S. E., NEUBAUER S., SKINNER M. M., BERGMANN I., CABEC A. LE, BENAZZI S., HARVATI K., GUNZ P., 2017 New fossils from Jebel Irhoud, Morocco and the pan-African origin of Homo sapiens. Nature **546**: 289–292.

JACOBS G. S., HUDJASHOV G., SAAG L., KUSUMA P., DARUSALLAM C. C., LAWSON D. J., MONDAL M., PAGANI L., RICAUT F.-X., STONEKING M., OTHERS, 2019 Multiple deeply divergent Denisovan ancestries in Papuans. Cell **177**: 1010–1021.

 doi:10.20944/preprints202012.0470.v1

JÉGOU B., SANKARARAMAN S., ROLLAND A. D., REICH D., CHALMEL F., 2017 Meiotic genes are enriched in regions of reduced archaic ancestry. Molecular biology and evolution **34**: 1974–1980.

KIMURA M., OHTA T., 1969 The Average Number of Generations until Fixation of a Mutant Gene in a Finite Population. Genetics **61**: 763–71.

KRAUSE J., FU Q., GOOD J. M., VIOLA B., SHUNKOV M. V., DEREVIANKO A. P., PÄÄBO S., 2010 The complete mitochondrial DNA genome of an unknown hominin from southern Siberia. Nature **464**: 894–897.

KRAUSE J., ORLANDO L., SERRE D., VIOLA B., PRÜFER K., RICHARDS M. P., HUBLIN J.-J., HÄNNI C., DEREVIANKO A. P., PÄÄBO S., 2007 Neanderthals in central Asia and Siberia. Nature **449**: 902–904.

KUHLWILM M., GRONAU I., HUBISZ M. J., FILIPPO C. DE, PRADO-MARTINEZ J., KIRCHER M., FU Q., BURBANO H. A., LALUEZA-FOX C., RASILLA M. DE LA, ROSAS A., RUDAN P., BRAJKOVIC D., KUCAN Ž., GUŠIC I., MARQUES-BONET T., ANDRÉS A. M., VIOLA B., PÄÄBO S., MEYER M., SIEPEL A., CASTELLANO S., 2016 Ancient gene flow from early modern humans into Eastern Neanderthals. Nature **530**: 429–33.

LI Z.-Y., WU X.-J., ZHOU L.-P., LIU W., GAO X., NIAN X.-M., TRINKAUS E., 2017 Late Pleistocene archaic human crania from Xuchang, China. Science **355**: 969–972.

MASSILANI D., SKOV L., HAJDINJAK M., GUNCHINSUREN B., TSEVEENDORJ D., YI S., LEE J., NAGEL S., NICKEL B., DEVIÈSE T., HIGHAM T., MEYER M., KELSO J., PETER B. M., PÄÄBO S., 2020 Denisovan ancestry and population history of early East Asians. Science (New York, N.Y.) **370**: 579—583.

MENDEZ F. L., POZNIK G. D., CASTELLANO S., BUSTAMANTE C. D., 2016 The divergence of Neandertal and modern human Y chromosomes. The American Journal of Human Genetics **98**: 728–734.

MEYER M., ARSUAGA J.-L., FILIPPO C. DE, NAGEL S., AXIMU-PETRI A., NICKEL B., MART'\INEZ I., GRACIA A., CASTRO J. M. B. DE, CARBONELL E., OTHERS, 2016 Nuclear DNA sequences from the Middle Pleistocene Sima de los Huesos hominins. Nature **531**: 504–507.

MEYER M., FU Q., AXIMU-PETRI A., GLOCKE I., NICKEL B., ARSUAGA J.-L., MART'\INEZ I., GRACIA A., CASTRO J. M. B. DE, CARBONELL E., OTHERS, 2014 A mitochondrial genome sequence of a hominin from Sima de los Huesos. Nature **505**: 403–406.

MEYER M., KIRCHER M., GANSAUGE M.-T., LI H., RACIMO F., MALLICK S., SCHRAIBER J. G., JAY F., PRÜFER K., FILIPPO C. DE, OTHERS, 2012 A high-coverage genome sequence from an archaic Denisovan individual. Science **338**: 222–226.

ORLANDO L., DARLU P., TOUSSAINT M., BONJEAN D., OTTE M., HÄNNI C., 2006 Revisiting Neandertal diversity with a 100,000 year old mtDNA sequence. Current Biology **16**: R400–R402.

PETR M., HAJDINJAK M., FU Q., ESSEL E., ROUGIER H., CREVECOEUR I., SEMAL P., GOLOVANOVA L. V., DORONICHEV V. B., LALUEZA-FOX C., RASILLA M. DE LA, ROSAS A., SHUNKOV M. V., KOZLIKIN M. B., DEREVIANKO A. P., VERNOT B., MEYER M., KELSO J., 2020 The evolutionary history of Neanderthal and Denisovan Y chromosomes. **369**: 1653–1656.

POMEROY E., LAHR M. M., CRIVELLARO F., FARR L., REYNOLDS T., HUNT C. O., BARKER G., 2017 Newly discovered Neanderthal remains from Shanidar Cave, Iraqi Kurdistan, and their attribution to Shanidar 5. Journal of Human Evolution **111**: 102–118.

POSTH C., WIßING C., KITAGAWA K., PAGANI L., HOLSTEIN L. VAN, RACIMO F., WEHRBERGER K., CONARD N. J., KIND C. J., BOCHERENS H., OTHERS, 2017 Deeply divergent archaic mitochondrial genome provides lower time boundary for African gene flow into Neanderthals. Nature communications **8**: 1–9.

PRÜFER K., RACIMO F., PATTERSON N., JAY F., SANKARARAMAN S., SAWYER S., HEINZE A., RENAUD G., SUDMANT P. H., FILIPPO C. DE, OTHERS, 2014 The complete genome sequence of a Neanderthal from the Altai Mountains. Nature **505**: 43–49.

RAGHAVAN M., SKOGLUND P., GRAF K. E., METSPALU M., ALBRECHTSEN A., MOLTKE I., RASMUSSEN S., STAFFORD JR T. W., ORLANDO L., METSPALU E., OTHERS, 2014 Upper Palaeolithic Siberian genome reveals dual ancestry of Native Americans. Nature **505**: 87–91.

REICH D., GREEN R. E., KIRCHER M., KRAUSE J., PATTERSON N., DURAND E. Y., VIOLA B., BRIGGS A. W., STENZEL U., JOHNSON P. L. F., MARICIC T., GOOD J. M., MARQUES-BONET T., ALKAN C., FU Q., MALLICK S., LI H., MEYER M., EICHLER E. E., STONEKING M., RICHARDS M., TALAMO S., SHUNKOV M. V., DEREVIANKO A. P., HUBLIN J.-J., KELSO J., SLATKIN M., PÄÄBO S., 2010 Genetic history of an archaic hominin group from Denisova Cave in Siberia. Nature **468**: 1053–60.

REICH D., PATTERSON N., KIRCHER M., DELFIN F., NANDINENI M. R., PUGACH I., KO A. M.-S., KO Y.-C., JINAM T. A., PHIPPS M. E., OTHERS, 2011 Denisova admixture and the first modern human dispersals into Southeast Asia and Oceania. The American Journal of Human Genetics **89**: 516–528.

RICHTER D., GRÜN R., JOANNES-BOYAU R., STEELE T. E., AMANI F., RUÉ M., FERNANDES P., RAYNAL J.-P., GERAADS D., BEN-NCER A., HUBLIN J.-J., MCPHERRON S. P., 2017 The age of the hominin fossils from Jebel Irhoud, Morocco, and the origins of the Middle

Stone Age. Nature **546**: 293–296.

SAITOU N., NEI M., 1987 The neighbor-joining method: a new method for reconstructing phylogenetic trees. Molecular biology and evolution **4**: 406–425.

SANKARARAMAN S., MALLICK S., PATTERSON N., REICH D., 2016 The combined landscape of Denisovan and Neanderthal ancestry in present-day humans. Current Biology **26**: 1241–1247.

SAWYER S., RENAUD G., VIOLA B., HUBLIN J.-J., GANSAUGE M.-T., SHUNKOV M. V., DEREVIANKO A. P., PRÜFER K., KELSO J., PÄÄBO S., 2015 Nuclear and mitochondrial DNA sequences from two Denisovan individuals. Proceedings of the National Academy of Sciences **112**: 15696–15700.

SKINNER A. R., BLACKWELL B. A. B., MARTIN S., ORTEGA A., BLICKSTEIN J. I. B., GOLOVANOVA L. V., DORONICHEV V. B., 2005 ESR dating at Mezmaiskaya Cave, Russia. Appl Radiat Isot **62**: 219–24.

SKOV L., HUI R., SHCHUR V., HOBOLTH A., SCALLY A., SCHIERUP M. H., DURBIN R., 2018 Detecting archaic introgression using an unadmixed outgroup. PLoS Genetics **14**: e1007641.

SLON V., MAFESSONI F., VERNOT B., FILIPPO C. DE, GROTE S., VIOLA B., HAJDINJAK M., PEYRÉGNE S., NAGEL S., BROWN S., OTHERS, 2018 The genome of the offspring of a Neanderthal mother and a Denisovan father. Nature **561**: 113–116.

VERNOT B., TUCCI S., KELSO J., SCHRAIBER J. G., WOLF A. B., GITTELMAN R. M., DANNEMANN M., GROTE S., MCCOY R. C., NORTON H., OTHERS, 2016 Excavating Neandertal and Denisovan DNA from the genomes of Melanesian individuals. Science **352**: 235–239.

 doi:10.20944/preprints202012.0470.v1

ZHANG D., XIA H., CHEN F., LI B., SLON V., CHENG T., YANG R., JACOBS Z., DAI Q., MASSILANI D., OTHERS, 2020 Denisovan DNA in Late Pleistocene sediments from Baishiya Karst Cave on the Tibetan Plateau. Science **370**: 584–587.

Figure 1 Legend:

Phylogenetic relationships among archaic and modern humans based on mitochondrial DNA whole sequences. All branch splits are supported by 100% bootstrap iterations. Age estimations in years, are represented at the basal nodes.

 doi:10.20944/preprints202012.0470.v1