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Denny and the relatives. Holding a finger to a groundbreaking discovery

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Abstract

The discovery of a distinctive fossil human genome at Denisova cave in Siberia has revolutionized the world of paleoanthropology during the last ten years. The Denisovan genome was later found in modern day people from Tibet, East Asia and Oceania, and from a few additional remains at Denisova cave. Among the latter, the 13 years old (Denisova 11) female individual nicknamed Denny stands out as exceptional. Denny had a Denisovan father with some Neanderthal ancestry in his blood, and a Neanderthal mother, suggesting mating between the two hominin groups was common in the Denisova area. As of today, although Denisovans are treated as a full-fledged species in everyday practice and several spectacularly preserved skull specimens found in China are suspected to represent true Denisovans, this human lineage has no formal definition, no type material, no established area of origin, and a dim origin tracing back to an archaic hominin migrating out of Africa around 1 million years ago.

Keywords: Denisova, Neanderthals, Paleogenomics, Inbreeding, *Homo*, Paleoanthropology

Riassunto

La scoperta del genoma di una specie umana sconosciuta in un resto fossile a Denisova in Siberia ha rivoluzionato il mondo della paleoantropologia negli ultimi dieci anni. Il genoma Denisoviano è stato successivamente trovato nei Tibetani, negli Asiatici e negli abitanti dell'Oceania moderni, oltre che in altri fossili di Denisova. Tra questi, un individuo femminile morto a soli 13 anni e colloquialmente nota come Denny spicca per aver avuto il padre denisoviano con lontani parenti Neanderthal, e la madre Neanderthaliana, dando prova dell'unione diretta fra due diverse linee filetiche umane. Sebbene i Denisoviani siano trattati come un'autentica specie nella pratica antropologica, e diversi esemplari fossili ritrovati in Cina siano stati proposti essere veri Denisoviani, questo lignaggio umano estinto non ha una definizione formale, nessun materiale tipo, nessuna area di origine stabilita e una debole traccia genetica che risale a un ominide arcaico migrato dall'Africa circa 1 milione di anni fa.

Parole chiave: Denisova, Neanderthals, paleogenomica, inbreeding, Homo, paleoantropologia

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Across the myriad of available, often feebly defended, and ill-applied concepts of species, Kitcher's (Kitcher 1984) *Cynical Species Concept* or "whatever a competent taxonomist chooses to call a species" (Wells et al. 2022) is probably the closest to everyday scientific practice. The cynical species bears the unvaluable advantage of holding beauty in the eye of the beholder, meaning that for the concept to apply, practitioners must just call a species whatever they think a species is, period. In the field of paleoanthropology, taxonomy is no less vicious than cynical. The paucity of human remains is in stark contrasts with the flood of names used to refer to them, and many among the *Homo rudolfensis*, *H. heidelbergensis*, *H. bodoensis*, *H. longi* and maybe even *H. ergaster* or *H. erectus* names are probably doomed to succumb in the wake of the unpredictable twists of fate new

discoveries and trends in taxonomy will bring about. We have no solution to offer to any intricate paleoanthropological naming dilemma, and did not go beyond practical solutions in our own research (Timmermann et al. 2022; Raia et al. 2020). And yet, we and our fellow paleoanthropologists are now facing one of the most challenging species concepts ever, a species which has no name, has no shape, and has no area of origin, the Denisovans. When Svante Pääbo's team retrieved an uniquely diverse archaic hominin genome from a fossil finger bone found in Denisova cave in the Altai Mountains, Siberia (Reich et al. 2010), the field of paleoanthropology was about to change forever, and yet the shockwaves were just begun. Although genetic evidence leaves no doubt about the proximity between Denisovans and Neanderthals (Sawyer et al. 2015; Mafessoni et al. 2020;

Brown et al. 2022), there is similarly undisputed evidence that Denisovan DNA is present in our own blood. Proof of introgression of Denisovan genome into *Homo sapiens* is manifest in modern day people from Tibet, New Guinea and the Philippines at the very least (Jacobs et al. 2019; Larena et al. 2021), with Ayta people in Luzon (Philippines) carrying the highest amount of Denisovan genetic signature in the world (Larena et al. 2021). Some of the Denisovan-acquired genes have positive effects on modern-day people fitness. For example, an allelic variant of the *EPAS1* gene derived from Denisovan genome confers adaptation to high-altitude environments protecting from hypoxia in Tibetans (Huerta-Sánchez et al. 2014; X. Zhang et al. 2021).

Whereas light has been shed on Denisovan introgression events with contemporary hominins (Schaefer, Shapiro, and Green 2021; Wohns et al. 2022), the Denisovan morphology remains elusive. The material from Denisova cave itself is very fragmentary, so that we have very little idea about how Altai Denisovans must have looked alike, and most of what we know about this lost cousin of ours is limited to a manifold of fossils, two robust mandibles and a bunch of (rather large) molars. Besides Denisova cave finds, protein analyses implied Denisovan allegiance for a jawbone found at Baishiya Cave, Gansu, China (Chen et al. 2019; D. Zhang et al. 2020), which in turn suggests a molar found in Cobra cave in Laos (Demeter et al. 2022) and possibly a mandible dragged by a fisherman off the coast of Penghu, Taiwan (Chen et al. 2019) are Denisovans as well. Contrasting to this paucity of remains, a rather impressive list of fossils were tentatively attributed to Denisovans, still based on morphological

proximity (Bergström et al. 2021). This extensive collection of Denisovan candidates includes the skulls from Harbin (Ni et al. 2021), Jinniushan (Rosenberg, Zuné, and Ruff 2006), Dali (Athreya and Wu 2017), Xujiayao (Ao et al. 2017), Xuchang (Li et al. 2017) and Hualongdong (Wu et al. 2019) in China. Ni et al. (2021) conducted a cladistic analysis of Harbin 'dragon man', finding it is closely allied to Xiahe (Baishiya) mandible, within a distinctive group of hominin remains further including Jinniushan and Dali fossils (which were traditionally considered to be Asian representatives of *Homo heidelbergensis*, Rightmire 2004). Hence, the attribution of Harbin to Denisova is at least feasible and has been in fact supported by a several paleoanthropologists (Gibbons 2021). As a matter of fact, the facial skeleton of Dali, Jinniushan, and Hualongdong hardly reconciles with any other extinct (and named) hominin (Bergström et al. 2021). Although absence of evidence is not evidence per se, the Asian *H. heidelbergensis* finds and several unnamed Chinese skulls and partial cranial material like Xuchang, Hualongdong and Xujiayao make it feasible that we have indeed good knowledge of Denisovan cranial variability. On the taxonomic side, though, since there is no formal definition and type material for Denisovans, until any of these exceptional skulls is confirmed to be Denisovan based on DNA analysis or paleoproteomics, there is no opportunity to erect a new species name gathering them all under a single heading. Hence, depending on whether Ni et al.'s results (Ni et al. 2021) and the taxonomic opinion of several scholars are trusted (Gibbons 2017; Bergström et al. 2021), and whether we accept phylogenetic proximity (as per Ni and colleagues' cladistic analysis)

is equivalent to taxonomic uniformity, either we know a lot about Denisovan morphology, or almost nothing other than the shape of their jawbone and molars. The matter is further complicated by the fact that most late Pleistocene hominins seems to have interbred with each other quite often. Although finding Denisovan or Neanderthal genome in modern day humans has no bearing on the correct recognition of our extinct relatives' appearance, the emerging evidence that morphology reflects genetic admixture in fossil *Homo* to some extent (Harvati and Ackermann 2022; Churchill, Keys, and Ross 2022; Gunz et al. 2019) must be carefully taken into account.

Contrary to the several instances of Neanderthal admixture with *H. sapiens* (e.g. Oase-1 and Ust'-ishim, Fu et al. 2014; 2015), evidence for Denisovan admixture with other-species extinct hominins is very rare in the fossil record (Zavala et al. 2021). Though, in 2018 Vivianne Slon and colleagues sequenced DNA fragments retrieved from a 90,000 years old long bone fragment named Denisova 11 (Slon 2018), which is now commonly referred to as Denny. This unfortunate 13 years old girl happened to have had a Denisovan dad and a Neanderthal mom, making Denny the only known fossil individual ever found to have parents belonging to two distinct human lineages. Denny is in good company at Denisova cave, where at least another individual (Denisova 3) and her own father, bear signs of genetic admixture between Denisovan and Neanderthals. Yet, outside Denisova, the evidence of Denisovans to Neanderthals mating is quite rare. Intriguingly, Denny's mom ancestry traces to Western Eurasian rather than to Siberian Neanderthals. This, together with the

evidence that Denisovans (and Neanderthals) exchanged genes with an unknown archaic hominin around some 600,000 years ago (Rogers, Harris, and Achenbach 2020), and with the enigmatic finding of Denisovan genetic signature in Sima de los Huesos (Atapuerca, Spain, Meyer et al. 2016) suggest that long distance dispersal might have taken place for both Neanderthals and the Denisovans, hence this latter's ancestry could be found much more westward than the Altai Mountains.

With no name, no shape, no place of origin and yet abundant evidence left behind, Denny and her relatives truly represent the most interesting, yet the most challenging discovery of a fossil non-species ever made. Whether or not resolving this deep-rooted mystery stands buried somewhere or written in a yet to be sequenced paleo-genome, the world of paleoanthropology is on the alert. For sure, the best is yet to come.

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