COMMENTARY

The labyrinth of human variation

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Morphological analyses of the human temporal labyrinth (cochlea and especially the semicircular canals) have progressed (along with advances in tomography) from using the labyrinth to orient crania (1), to document the earlier hominin ancestral pattern (2), to document an apparently derived "Neandertal" configuration (3), to establish Neandertal persistence into the Upper Paleolithic (4), and to infer Late Pleistocene populational interconnections across Eurasia (5, 6). Through these mostly paleontological analyses, it has been assumed that recent (and early modern) humans had a consistent labyrinthine pattern, albeit with individual variation. Global assessments have been absent, and the recent human sample has been dominated by western Eurasian specimens.

The analysis of Ponce de León et al. (7) of global recent human variation in labyrinthine proportions is therefore a welcome addition to our understanding of human variation. It is especially welcome because labyrinthine proportions are established prenatally and are subject to little or no developmental plasticity (8). The analysis therefore has the potential to provide both core data on variation of this morphological feature and the basis for human populational inferences in space and by extension in time. However, recent human labyrinthine variation has implications beyond its global patterns.

Recent Human Variation

The analysis of Ponce de León et al. (7) is important in documenting that the variation of labyrinthine proportions is principally within their regional samples and that only a small proportion of the variation is between their regions. Moreover, the variation closely fits an isolation-by-distance model of human variation, whether it is a remnant of the Late Pleistocene modern human dispersal from Africa or a product of isolation-by-distance once modern humans were established both across Africa and Eurasia and into greater Australia and the Americas.

Since the classic study of Lewontin (9), almost half a century ago, it has been repeatedly documented that the overwhelming majority of human genetic variation is within populations or regional clusters of human populations (e.g., refs. 10–12). In these apparently neutral or near-neutral genetic markers, there is very little differentiation across subsets of the living human species. The features that are commonly employed to distinguish regional groups of humans are either secondary dermal features (literally only skin deep) or can be related to long-term (cumulative and low level) selective environmental pressures [e.g., solar radiation on skin pigmentation (13) and temperature plus humidity on body proportions and nasal morphology (14, 15)]. Two phenotypic complexes that have been quantitatively analyzed on a global scale, cranial morphometrics (16) and dental discrete traits (17), exhibit levels of within versus between region variation in line with neutral genetic variation. Dental discrete variation should be a direct reflection of the underlying genotype, but cranial variation has a component of developmental plasticity (16); their relative distributions of variation nonetheless remain well within the range of values obtained from genetic markers.

In this context, the analysis here of recent human labyrinthine proportions provides more solid evidence of what should have been evident from basic comparative human anatomy more than a century ago; we are all basically the same, at a populational level, under the skin. This message was clearly stated by Lewontin (9), and it needs to be continuously repeated given the current "racialized" state of the world, both developed and developing.

Issues of Genetic Sampling

Ponce de León et al. (7) make a strong statement that the wholesale sampling of temporal petrous portions from human crania for the purposes of ancient DNA (aDNA) analyses is a destruction of irreplaceable data. The authors imply that it is permissible if the temporal bones have been CT-scanned at high resolution (μCT levels; 20–40 μm), but that assumes the durability of digital media, that all relevant information can be extracted from those digital data, and little or no chemical

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diagenesis from the radiation. I would argue that the current level of extraction of petrous portions (if not whole temporal bones) for aDNA analyses is simply unjustified. These crania are an irreplaceable documentation of past human biology, both population relationships and especially paleobiology. Native groups globally are increasingly (and justifiably) demanding at least ethical treatment of these remains, if not their repatriation and reburial. aDNA preservation is generally poor for all except in the Arctic, leading to many (already damaged) specimens yielding little or no usable DNA sequence data, and many of the others providing very limited reliable aDNA for comparative analyses.

In other words, such material damage is unacceptable if the long-term harm or loss exceeds the short-term gain. This is a routine consideration in laboratory animal and clinical studies, and it should be applied to irreplaceable past human remains. This has become especially critical in human paleontology. There are several human fossils that currently exist only as images and DNA sequences (e.g., refs. 18 and 19), having been entirely consumed by aDNA extraction. The (formerly) most complete nonmodern human humerus, from the original 1856 Neandertal fossil, is now partial and in pieces, having been sawed and drilled for DNA (20). Less invasive but often paleobiologically ill-informed damage to human fossils is now ubiquitous, given the current preoccupation (driven by high-profile publishing) with attempting to extract aDNA from these truly irreplaceable documents of remote humans. I would argue that the plea of Ponce de León et al. (7) is but a first step to stop the destruction, whether of Medieval cemetery samples or Late Pleistocene humans.

It should also be emphasized that, given the scarcity of specimens for aDNA extraction (especially for Pleistocene remains), independent analyses of the specimens almost never occur. Given the high level of nonreproducibility of laboratory results (e.g., refs. 21 and 22), what is the level of confidence in these aDNA sequences?

To these preservation-related concerns can be added the question of what is being gained from these extractions and destructions of past human remains. They are overwhelmingly focused on population relationships, population dispersals, and hence the drawing of arrows on maps (usually without consideration of geographical features and past ecozonal movements). Historical linguists in the 19th century were very good at drawing these maps based on language affinities, and many of their conclusions, with refinements, form the basis of our understanding of Holocene human dispersals. The current large-scale extraction of Holocene aDNA is therefore damaging specimens found mostly in the 20th century, analyzing them with 21st century technology, to answer 19th century questions. Have we not progressed beyond these ethnocentrically and racially motivated questions?

Much the same applies to the primary question for which Late Pleistocene aDNA has been extracted: inferring the population processes (or who was having sex with whom) involved in modern human emergence. Despite the high-profile nature of the Neandertal and early modern human aDNA analyses, they have provided little insight beyond what was previously known from human fossil morphology. Late Middle Pleistocene modern human emergence in east Africa was documented by the late 1960s (23, 24); further work there (25, 26) has only refined the data. The Interpleniglacial dispersal of modern humans has long been known from their remains (27), and Late Pleistocene body proportions reinforced their African ancestry (28). The high probability of a modest level admixture with modern human dispersal has been inferred from early modern human morphology, which exhibits variations beyond what would be expected from a simple dispersal from Africa (29, 30; see also ref. 31). It took more than a decade of aDNA extraction, and moving beyond haploid genetic markers, to rediscover what was already known. And the fossils suffered in the meantime.

Conclusion

The detailed and thorough analysis of Ponce de León et al. (7) is therefore a welcome addition to our understanding of global patterns of human phenotypic variation, and further documentation that human variation is principally within regional populations and patterns geographically. And their concern with the wholesale destruction of human temporal bones for DNA extraction is but a first attempt to stop the irreparable damage being done to human remains, from the Pleistocene to the near present, to obtain DNA sequences of questionable import.

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