

# Temporal labyrinths of eastern Eurasian Pleistocene humans

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One of the morphological features that has been identified as uniquely derived for the western Eurasian Neandertals concerns the relative sizes and positions of their semicircular canals. In particular, they exhibit a relatively small anterior canal, a relatively larger lateral one, and a more inferior position of the posterior one relative to the lateral one. These discussions have not included full paleontological data on eastern Eurasian Pleistocene human temporal labyrinths, which have the potential to provide a broader context for assessing Pleistocene *Homo* trait polarities. We present the temporal labyrinths of four eastern Eurasian Pleistocene *Homo*, one each of Early (Lantian 1), Middle (Hexian 1), and Late (Xujiayao 15) Pleistocene archaic humans and one early modern human (Liujiang 1). The labyrinths of the two earlier specimens and the most recent one conform to the proportions seen among western early and recent modern humans, reinforcing the modern human pattern as generally ancestral for the genus *Homo*. The labyrinth of Xujiayao 15 is in the middle of the Neandertal variation and separate from the other samples. This eastern Eurasian labyrinthine dichotomy occurs in the context of none of the distinctive Neandertal external temporal or other cranial features. As such, it raises questions regarding possible cranial and postcranial morphological correlates of *Homo* labyrinthine variation, the use of individual "Neandertal" features for documenting population affinities, and the nature of late archaic human variation across Eurasia.

cranium | China | petrous | cochlea

One of the morphological features, which has been used to distinguish the Neandertals from early and recent modern humans, as well as earlier Pleistocene *Homo*, is the arrangement of their semicircular canals (or labyrinthine morphology) (1–3). Given its prenatal formation, developmental stability, and minimal side or sex differences (4–6), labyrinthine morphology should provide a direct reflection of one aspect of genetic variation across these samples. It is also frequently preserved paleontologically within the petrous portion of the temporal bone. In their labyrinths, Neandertals have been shown to have a suite of features involving absolute dimensions, proportions, and angulations, most which appear to be related to their relatively small anterior semicircular canals, comparatively larger lateral semicircular canals, and a more inferior position of the posterior semicircular canal relative to the lateral one (1). This pattern is present in almost all of the known Neandertal labyrinths; it has not been documented among other Pleistocene members of the genus *Homo*; and it is rare among recent humans. However, with the exception of partial data on the labyrinths of three Early Pleistocene *Homo* crania (4, 7) that primarily serve to document the ancestral *Homo* configuration, the Pleistocene comparisons have been limited to western Old World archaic humans (mostly Neandertal lineage) and modern humans (1, 2, 8–12), plus one central Asian late archaic human (13). Given that East Asian archaic *Homo* remains are distinctly non-Neandertal in their overall configurations (14), it is of interest to assess the labyrinthine morphology of the available East Asian Pleistocene

humans relative to other Pleistocene *Homo* (SI Appendix, Table S1). These sufficiently preserved and available eastern Asian human remains include the Early Pleistocene Lantian (Gongwangling) 1, the Middle Pleistocene Hexian 1, the Late Pleistocene archaic Xujiayao 15, and the Late Pleistocene modern Liujiang 1.

## Results

Three of these East Asian Pleistocene *Homo* temporal labyrinths (Fig. 1) provide configurations that appear generally similar to those of recent humans (and the apparent ancestral *Homo* pattern), those from Lantian, Hexian, and Liujiang. In particular, in lateral view their lateral canals largely bisect the posterior ones. In contrast, the lateral canal of Xujiayao 15 is positioned in the superior portion of its posterior canal. This proportion is reflected in their sagittal labyrinthine indices (SLIs) of 41.4, 53.5, and 45.5 for the first three, respectively, but one of 61.4 for Xujiayao 15. In this feature (Fig. 2), the first three are well within recent and early modern human variation and only Hexian 1 overlaps the limits of the Neandertal variation (Spy 1). Xujiayao 15 is among the Neandertals (who are significantly different from the other samples:  $P < 0.0001$ ), similar to a small minority of the recent humans (7.2% with  $SLI \geq 61$ ,  $n = 180$ ), one Middle Paleolithic modern human (Qafzeh 15), and one Middle Pleistocene European specimen (Reilingen 1) (Fig. 2). Two of the Early Pleistocene specimens are within recent human variation, although Sangiran 4 has a high value for this feature (4).

The Neandertals have also been noted to have relatively small anterior and large lateral canal radii, and the percent that each

## Significance

The assessment of the paleobiology and morphological affinities of the Neandertals and other Late Pleistocene archaic humans is central to resolving issues regarding the emergence and establishment of modern human morphology and diversity. One feature, which has been used as a distinctive Neandertal feature in this context, is the apparently derived shape of their temporal labyrinths (especially semicircular canals). Analysis of East Asian labyrinths documents the "Neandertal" pattern in the Xujiayao 15 temporal bone, although none of the Xujiayao human remains exhibits other distinctly Neandertal features. It therefore raises questions regarding possible biological correlates of labyrinthine morphology, distinctive Neandertal features, and the nature of late archaic human variation across Eurasia.

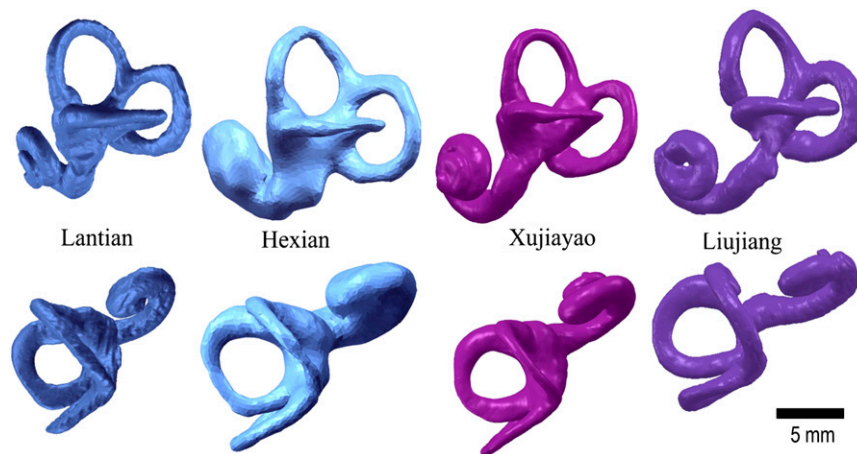
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**Fig. 1.** Reconstructed temporal labyrinths of East Asian Pleistocene humans from Lantian 1 (reversed), Hexian 1, Xujiayao 15, and Liujiang 1 (reversed), in lateral (*Upper*) and superior (*Lower*) views.

radius makes up of the three summed radii is significantly different across the fossil samples for the anterior and lateral ones ( $P < 0.0001$ ) but not the posterior canal ( $P = 0.053$ ) (*SI Appendix, Table S2*). A comparison of anterior to lateral radii (Fig. 2) confirms the separation of most of the Neandertals from the other samples (including the Early Pleistocene specimens from Lantian and especially from Sangiran and Olduvai). Xujiayao 15 is among the Neandertals with the lowest indices, outside of the ranges of the other comparative samples. Liujiang 1 and two of the European Middle Pleistocene specimens (Reilingen 1 and Steinheim 1) overlap the Neandertal range in this feature.

In these two features together, the only Pleistocene specimen other than Xujiayao 15 that falls within the Neandertal range of variation is Reilingen 1, which is poorly dated within the Middle to early Late Pleistocene (15). Hexian 1 overlaps the Neandertal range of variation in each of these proportions, but it lies along

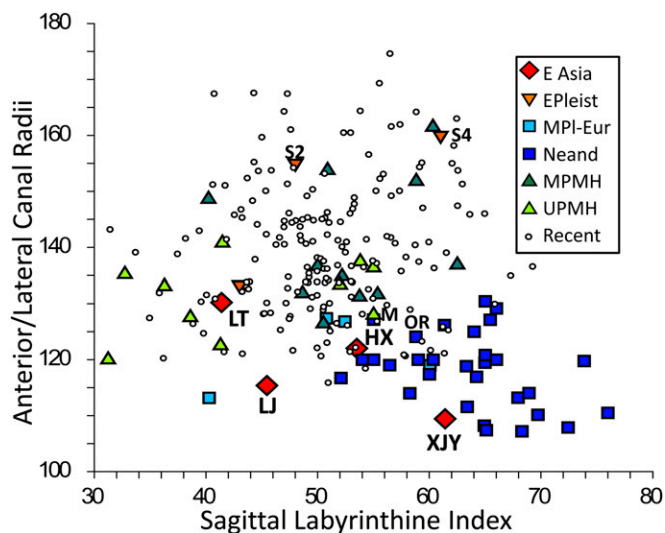
the margin of that Neandertal distribution and remains within the recent human distribution.

Therefore, despite some overlap between the Neandertals and the other comparative samples in the separate indices (Fig. 2), in combination, these two indices separate 56.7% ( $n = 30$ ) of the Neandertals completely from the distribution of the other samples. All but one Neandertal (Le Moustier 1) are at or beyond the limits of those other samples (96.7%). Xujiayao 15 is with the majority of the Neandertals in being well outside of the bivariate variation of the other Pleistocene and recent *Homo* labyrinths. This proportional similarity of Xujiayao 15 to the Neandertals is also expressed by the relative proportions of their anterior, posterior, and lateral canals (*SI Appendix, Fig. S1*).

The cochlear dimensions and proportions of the Chinese human fossils are all within the ranges of the comparative group variations (*SI Appendix, Table S4*). Regarding the torsion of the anterior (ASCtor), posterior (PSCtor), and lateral (LSCtor) semicircular canals, the Xujiayao 15 and other Chinese fossil specimens show less torsion in ASCtor compared with the Middle Paleolithic modern humans and the Neandertals (*SI Appendix, Table S3*).

With respect to the shape of the labyrinth, Xujiayao 15 is separate from the three other East Asian specimens in exhibiting the hyperrotated morphology apparently derived for the Neandertals (1). Compared with recent humans, the ampullar line (APA), the facial nerve canal (FC3), and the posterior petrosal surface (PPp) are positioned more vertically in relation to the arc of the lateral semicircular canal (LSCm) in the sagittal plane. This conformation is correlated with the low position of the posterior semicircular canal, expressed by SLIs (*SI Appendix, Table S3*). The angle between the lateral canal plane and the posterior petrosal surface ( $LSCm < PPp$ ) of Hexian 1 is close to the Neandertal mean, and the position of the facial nerve canal is also more vertical than the modern human variation. However, this conformation is not associated with a hyperrotated morphology in the Hexian 1 labyrinth (i.e., SLI and  $LSCm < APA$  are outside or near the limits of Neandertal variation). Finally Xujiayao 15 is separate from the comparative samples regarding the position of its cochlea reflected in the angle between the sagittal plane basal turn of the cochlea (COs) and the LSCm, which is oriented more superiorly and whose angle ( $LSCm < COs$ ) lies close to the upper limits of all of the comparative groups.

As previously noted (1), the ranges of variation of many of these individual labyrinthine measurements overlap across Pleistocene and recent human samples, but in combination they largely separate the Neandertals (and to a lesser extent European Middle



**Fig. 2.** Plot of the index of the anterior to lateral semicircular canal radii versus the sagittal labyrinthine index for Pleistocene and recent humans. E Pleist, Early Pleistocene remains from Sangiran (S2 and S4) and Olduvai; HX, Hexian 1; LJ, Liujiang 1; LT, Lantian 1; M, Le Moustier 1; MPI-Eur, Middle Pleistocene specimens from Europe; MPMH, Middle Paleolithic modern humans; Neand, western and central Eurasian Neandertals; OR, Obi-Rakhmat 1; Recent, global sample of recent modern humans; UPMH, western Old World Upper Paleolithic modern humans; and XJY, Xujiayao 15.

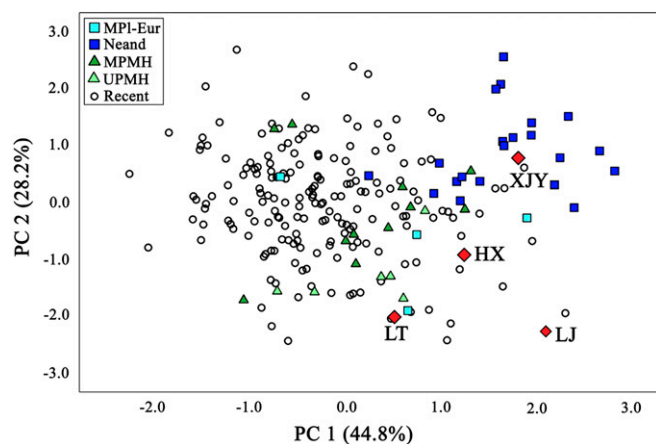
Pleistocene remains) from non-Neandertal human samples. Therefore, a principal component analysis was performed on six variables of the bony labyrinth (*SI Appendix, Table S5*), the two first principal component (PC) axes (PC 1 and PC 2) represent 73% of the total sample variance. PC 1 reflects the relative proportions of the posterior and lateral semicircular canals, whereas PC 2 accounts for the sagittal shape of the labyrinth. Fig. 3 illustrates the distribution of the individuals following the first two principal components. Xujiayao 15 falls in the middle of the Neandertal distribution and at the edge of the recent human one, whereas Lantian 1, Hexian 1, and Liujiang 1 are separate from the Neandertals, especially with respect to PC 2. Again, Le Moustier 1 plots with the recent humans.

A more comprehensive assessment of the affinities of the eastern Eurasian labyrinths is provided by a discriminant function analysis with cross-validation on 25 variables (*SI Appendix, Table S6*). The number of variables was maximized and included in a step-by-step analysis (ending with 14 active variables). The analysis provides an overall success rate of 77.6% across five samples (not including the Early Pleistocene one), but if the two Neandertal lineage samples are combined and the three modern human samples are pooled, the success rate rises to 94.5%. Only one Neandertal lineage labyrinth (Le Moustier 1) is aligned with modern humans, for a 94.7% success rate ( $n = 23$ ), and the remaining misclassified Neandertal lineage vs. modern human specimens are all recent humans. In this context, Lantian 1 and Hexian 1 group with the Middle Paleolithic modern humans ( $P = 0.985$  and  $0.999$ ), and Liujiang 1 is with the three modern human samples ( $P = 0.326$ ,  $0.389$ , and  $0.283$ , for a total of  $0.998$ ). Xujiayao 15 groups with the Neandertals ( $P = 0.948$ ).

These individual proportions and overall morphometrics therefore align the Lantian, Hexian, and Liujiang labyrinths with early and recent modern humans, and by extension with Early Pleistocene *Homo* (given limited data on the last). Xujiayao 15, in contrast, falls entirely with the Late Pleistocene Neandertals, distinct from the early and recent modern humans and from the Early and Middle Pleistocene *Homo*.

## Discussion

These data and comparisons confirm what has been documented for the western Old World, that there is a general similarity in temporal labyrinthine proportions through most of the genus



**Fig. 3.** Scatter plot of the first two principal components (PC 1 and PC 2) based on six variables in the principal components analysis [the posterior (PSC-R) and lateral (LSC-R) semicircular canal radii, the posterior (PSC-%R) and lateral (LSC-%R) radial proportions, the sagittal labyrinthine index (SLI), and the lateral semicircular canal arc versus ampullar line angle (LSCm < APA)]. The Neandertal in the middle of the recent human distribution is Le Moustier 1. HX, Hexian 1; LJ, Liujiang 1; LT, Lantian 1; and XJY, Xujiayao 15.

*Homo* (1, 7). The exception is the western and central Eurasian Neandertals (1–3), almost all of whom exhibit a derived morphology of their labyrinths. As with many individual features, for which the Neandertals are overwhelmingly separate from modern humans but for which their distributions overlap given sufficient sample sizes (16), the ranges of variation of these samples overlap in their labyrinthine aspects. This minimal distributional overlap is evident in the positions of the Le Moustier 1 labyrinth and those of a few recent humans.

In eastern Asia, the Early and Middle Pleistocene Lantian 1 and Hexian 1 crania follow the general *Homo* pattern, and they join Sangiran 2 and 4 in establishing this labyrinthine morphology as ancestral for *Homo* across Eurasia. The Late Pleistocene Liujiang 1 has an equally modern labyrinthine configuration, in agreement with its overall modern human morphology (17). In this context, the labyrinthine morphology of the Xujiayao 15 temporal bone conforms to the derived Neandertal pattern, the first documentation of this pattern among Pleistocene *Homo* outside of the Neandertal geographical range.

Despite the similarity of the Xujiayao 15 labyrinth to those of the Neandertals, its external temporal morphology (Fig. 4 and *SI Appendix, Fig. S2*) bears little affinity to that of the Neandertals (18, 19). It shares ancestral *Homo* features with the Neandertals, including a large juxtastoid eminence and an inferomedially sloping lateral mastoid process. It differs in its other aspects. The squamous portion is high and rounded. The zygomatic arch extends posteriorly above the auditory porus, continuing into a supramastoid crest that is horizontal and ends temporally at the parietal notch. The porus is ovoid, but its long axis is vertical. The laterally rugose mastoid process lacks an anterior mastoid tubercle. The parietomastoid suture slopes inferiorly to asterion, and the transverse sinus crossed to the temporal bone across the posterior parietomastoid suture. Some of these aspects of Xujiayao 15 can be found on individual Neandertal specimens, but the constellation of discrete traits of the bone is outside of the well-documented range of variation in Neandertal temporal bone external morphology.

The same morphological consideration applies to the Xujiayao human remains generally (*SI Appendix, Table S7*). A couple of their features are common among the Neandertals but not unique to them (the Xujiayao 1 bilevel nasal floor and strongly shoveled maxillary central incisor ( $I^1$ ) and canine ( $C^1$ ), and the Xujiayao 14 enlarged superior medial pterygoid tubercle) (20–22), but the overall configurations of the Xujiayao remains are unlike those of most Neandertals (20–25). The Xujiayao 1 inferior nasal margin is broad and rounded, and its  $M^1$  has marked cingular development and peripherally placed cusps. The Xujiayao 1 and 13 maxillary first molars ( $M^1$ s) possess subrectangular contours. The Xujiayao 6 and 12 occipital bones are angled at the nuchal torus and lack suprainiac fossae. The Xujiayao 14 mandibular ramus is wide and gonially everted, and it has an open mandibular foramen and a laterally placed mandibular notch crest. The same pattern holds for other, late Middle and early Late Pleistocene archaic human remains from eastern Asia (14, 26–28). What emerges from these East Asian later Pleistocene archaic humans, therefore, is a complex mix of features, many of them generally ancestral for *Homo* and a few features that occur frequently in the Neandertals but need not be diagnostic of them. The Xujiayao 15 labyrinth therefore provides the first secure evidence of a distinctly derived Neandertal configuration in eastern Asia.

The geographically closest presence of a similar labyrinthine configuration is the fragmentary Obi-Rakhmat 1 cranium from Uzbekistan (13), a specimen assigned to the Neandertals on the basis of its dental morphology (29) despite an apparent mix of morphological features in other aspects of the remains (13). The next geographically closest, morphologically “Neandertal”



**Fig. 4.** Lateral views of the Xujiayao 15 left temporal bone (*Upper*) and the La Quina 27 Neandertal right temporal bone (reversed, *Lower*).

labyrinths are from the eastern Mediterranean littoral (Dederiyeh 1 and Tabun 1).

The broader implications of the finding, a “Neandertal” labyrinthine morphology in an otherwise distinctly “non-Neandertal” sample of late archaic humans from eastern Eurasia, remain unclear. It is tempting to use it as evidence of population contact (gene flow) between central and western Eurasian Neandertals and these eastern archaic humans. Indeed, this labyrinthine morphology has been used repeatedly as a taxonomic marker of the Neandertals (1, 3, 11–13). However, there have also been suggestions (1) that labyrinth shape may be related to other aspects of Neandertal biology, albeit with reservations, and only secondarily a consequence of their phylogenetic history.

Spoor et al. (1) suggested a series of Neandertal postcranial features that might account for at least the dimensions of their anterior and posterior semicircular canals, as related to overall agility in locomotion (3, 30). None of these postcranial features is known for the Xujiayao humans, but they can be assessed for the Neandertals. However, for them to be relevant to the Neandertal (and Xujiayao 15) labyrinthine proportions, they need to be features that distinguish the Neandertals from both modern humans and the earlier Pleistocene, non-Neandertal, humans who lack this unusual labyrinthine configuration.

There is a series of Neandertal features that may be related to issues of balance and agility (1). Neandertals have relatively abbreviated limbs (31), yet similarly proportioned modern arctic humans do not appear to differ from other modern humans in their labyrinths (1). Neandertals have robust necks, especially

with respect to cervical spinous processes (19, 32), but their occipital nuchal areas are modest in size for Pleistocene *Homo* (19, 33, 34). Moreover, their necks were not particularly short (19, 32, 35). Their clavicles are moderately long, but they scale to body mass in the same manner as other humans (36). Some, but not all, Neandertals have broad pelvises (37), but so apparently do all archaic *Homo* (38–40). Neandertal (and earlier *Homo*) femoral diaphyseal shape has suggested more mediolateral and less anteroposterior loading during locomotion; however, properly scaled, there is no difference through Pleistocene *Homo* in anteroposterior femoral strength, only mediolateral variation apparently related to pelvic breadth (41, 42). Related are issues of head balance and momentum in running with a prognathic and platycephalic cranium (43); however, the Neandertals had shorter faces than their Pleistocene *Homo* predecessors (44, 45), and their relative neurocranial heights are similar to all earlier *Homo* and overlap the variation of early modern humans (46). Given the contrast in labyrinth morphology between earlier Pleistocene *Homo* and the Neandertals, it is therefore difficult to account for the latter’s (and Xujiayao 15’s) labyrinth configuration from postcranial and overall cranial proportions.

It has also been suggested that labyrinthine variation may be influenced by cranial base configuration, especially as related to posterior cranial fossa proportions (1), and this interpretation has been supported by some covariation with cranial base proportions among recent humans (47). Neandertals have relatively small posterior cranial fossae, yet the same proportions are in at least one early modern human with a modern labyrinth configuration (Cro-Magnon 1) (48). It is possible that other neurocranial considerations, related to cerebral expansion on an archaic *Homo* cranial base (49), given similar endocranial capacity and encephalization across all Late Pleistocene humans (50), are related to the labyrinthine morphology, but that remains to be evaluated. The endocranial capacity of Xujiayao 15 is unknown, but another individual from the same sample (Xujiayao 6) has an estimated cranial capacity  $\sim 1,700$  cc, among the larger Late Pleistocene crania; the earlier East Asian crania providing labyrinthine details have substantially smaller neurocrania (Hexian 1: 1,025 cc and Lantian 1:  $\sim 780$  cc) (51, 52), making it unlikely that the petrous angular similarities between Xujiayao 15 and Hexian 1 are due to brain size.

It is therefore unclear whether the Neandertal labyrinthine configuration, and by extension that of Xujiayao 15, can be attributed to other aspects of their biology. Moreover, the overall cranial morphology of the Xujiayao sample is incompletely known and their postcrania are unknown.

These considerations of the Xujiayao 15 labyrinth also raise questions regarding the use of individual features (whether morphological or molecular), in the absence of relatively complete paleontological remains, to identify the presence of Neandertals in regions outside of their well-documented core area of western Eurasia (west of  $\sim 45^\circ$  E, versus  $\sim 70^\circ$  E for Obi-Rakhmat and  $\sim 114^\circ$  E for Xujiayao). Indeed, many of the features so used are generally ancestral for later *Homo* (if poorly documented other than among the Neandertals), of unknown phylogenetic polarity, of uncertain primacy in morphological integration, and/or isolated features in otherwise non-Neandertal remains. The Xujiayao 15 labyrinthine morphology, and other features documented for eastern Eurasian and the earlier Pleistocene *Homo* (e.g., 16, 19, 20, 28, 36, 39, 42, 53), suggest that many of the purported “Neandertal” features were widespread during the Pleistocene, albeit often occurring in higher frequencies among the Neandertals.

Regardless of the ultimate populational and morphofunctional implications of the Xujiayao 15 and the other East Asian labyrinthine configurations, they serve to further confirm the general modern human pattern as the ancestral *Homo* one and to document that the apparently derived Neandertal configuration was not

unique to western Eurasia. Given its presence in Europe, southwest Asia, central Asia, and now eastern Asia, it may well have been present across Eurasia during the later Pleistocene among archaic humans. As such, whether a discrete feature in itself or a secondary consequence of other aspects of morphological variation, it becomes less of a “Neandertal” marker and of broader relevance to the paleobiology of later Pleistocene *Homo*.

## Materials and Methods

The petrous portions of the Lantian, Xujiayao, and Liujiang fossils and 26 recent Chinese temporal bones were  $\mu$ -computed tomography (CT) scanned using an industrial CT scanner (225 kV  $\mu$ CT, made by the Institute of High Energy Physics, Chinese Academy of Sciences) in the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) (tube voltage: 150 kV; tube current: 110  $\mu$ A; pixel size: 44  $\mu$ m for Xujiayao and Lantian, 56  $\mu$ m for Liujiang, and 48  $\mu$ m for the recent Chinese). Hexian 1 was scanned with a high-resolution industrial CT scanner (450 kV) in the IVPP (tube voltage: 450 kV, tube current: 1.5 mA, pixel size: 0.2 mm), given that it is a full neurocranium and is minerally dense. All specimens were therefore scanned at resolutions more than adequate to extract and measure their temporal labyrinths (Fig. 1). The labyrinthine structures were extracted and measured using Mimics 15.1

(Leuven; Materialise NV). The measurement specifications (SI Appendix, Tables S2–S4) are from Spoor et al. and Spoor (1, 4).

The comparative sample data were compiled from personal research and the literature (SI Appendix, Table S1). Note that the complete set of labyrinthine variables (1, 4) is not available for all of the fossil and recent human specimens, due to preservation in some fossils and completeness of measurement collection in others. This has resulted in different sample sizes in the various comparisons used. The principal component analysis (PCA) was conducted on the six variables (PSC-%R, PSC-R, LSC-R, LSC-%R, SLI, LSCM <APA) that were used in Bouchneb and Crevecoeur (2). Multivariate analysis used stepwise discriminant analysis (ending with active variables) using cross-validation for the comparative samples and the East Asian fossils as separate specimens. The comparative group classification was computed in “equal size” to avoid larger groups (such as the recent human sample) being given more weight in computing the posterior probabilities. Analyses were done using SPSS v.15.0

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