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Nasal floor variation among eastern Eurasian Pleistocene *Homo*

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Abstract A bi-level nasal floor, although present in most Pleistocene and recent human samples, reaches its highest frequency among the western Eurasian Neandertals and has been considered a feature distinctive of them. Early modern humans, in contrast, tend to feature a level (or sloping) nasal floor. Sufficiently intact maxillae are rare among eastern Eurasian Pleistocene humans, but several fossils provide nasal floor configurations. The available eastern Eurasian Late Pleistocene early modern humans have predominantly level nasal floors, similar to western early modern humans. Of the four observable eastern Eurasian archaic *Homo* maxillae (Sangiran 4, Chaoxian 1, Xujiayao 1, and Changyang 1), three have the bi-level pattern and the fourth is scored as bi-level/sloping. It therefore appears that bi-level nasal floors were common among Pleistocene archaic humans, and a high frequency of them is not distinctive of the Neandertals.

Key words: noses, maxilla, Asia, palate, Neandertal

Introduction

In his descriptions of the Shanidar Neandertal crania, Stewart (1958, 1961, 1977) noted that the floor of the internal nasal cavity was markedly lower than the inferior nasal aperture margin in Shanidar 1 and 2. This contrast in aperture and nasal floor levels provides a sinuous curve to the anterior nasal floor in lateral view, posterosuperiorly convex adjacent to the aperture margin and then concave in the region of the incisive canal, becoming level and parallel to the palate posteriorly. This morphological pattern (the bi-level nasal floor) has since been documented by Franciscus (2003) as the predominant pattern among western Eurasian late archaic humans (Neandertals) (cf. Trinkaus, 2006). Alternatively, Pleistocene and recent members of the genus *Homo* generally exhibit a flat nasal cavity floor that is largely parallel to the palate or one that is within one plane but slopes posteroinferiorly from the aperture margin.

Franciscus (1995, 2003) divided this nasal floor variation into the ordinal categories of level, sloped, or bi-level. His extensive analysis of the distributions of these character states, in western Old World samples of both Pleistocene *Homo* and recent humans, has documented a variable pattern in which all three patterns are present in most samples but vary markedly in frequencies. Among his recent European, southwest Asian and African samples, the first two patterns dominate with the bi-level configuration being present in ≤10% in all but a sub-Saharan African "Bantu" sample (Table 1). Additional data collected by one of us (S.D.M.) has documented a similar pattern among recent eastern Eurasian humans (Table 1). Among Pleistocene *Homo* remains, all of the configurations are present in all of the samples (Table 2 and Appendix 1). However, the level nasal floor pattern is the most common one in the pooled Early and Middle Pleistocene sample and the Late Pleistocene early modern human samples. In contrast, the later Middle Pleistocene and Late Pleistocene western Eurasian archaic humans (Neandertals *sensu lato*) predominantly exhibit the bi-level pattern.

However, these paleontological analyses consist entirely of Pleistocene remains from the western Old World, with the easternmost specimens deriving from Shanidar Cave at 44° E longitude. Sufficiently preserved Pleistocene *Homo* maxillae from eastern Eurasia are rare, but it is currently possible to assess the nasal floor configurations of four archaic *Homo* individuals from eastern Eurasia, as well as those of some early modern humans.

Materials and Methods

Nasal floor configurations

Following the definitions of Franciscus (2003), the nasal floor configurations of these Pleistocene and recent human maxillae are divided into ordinal categories of level, sloping, and bi-level, even though there is some degree of morphological continuity between them. Observed along the nasal floor lateral of the anterior nasal spine and the vomer attachment, and oriented relative to the alveolar plane and the

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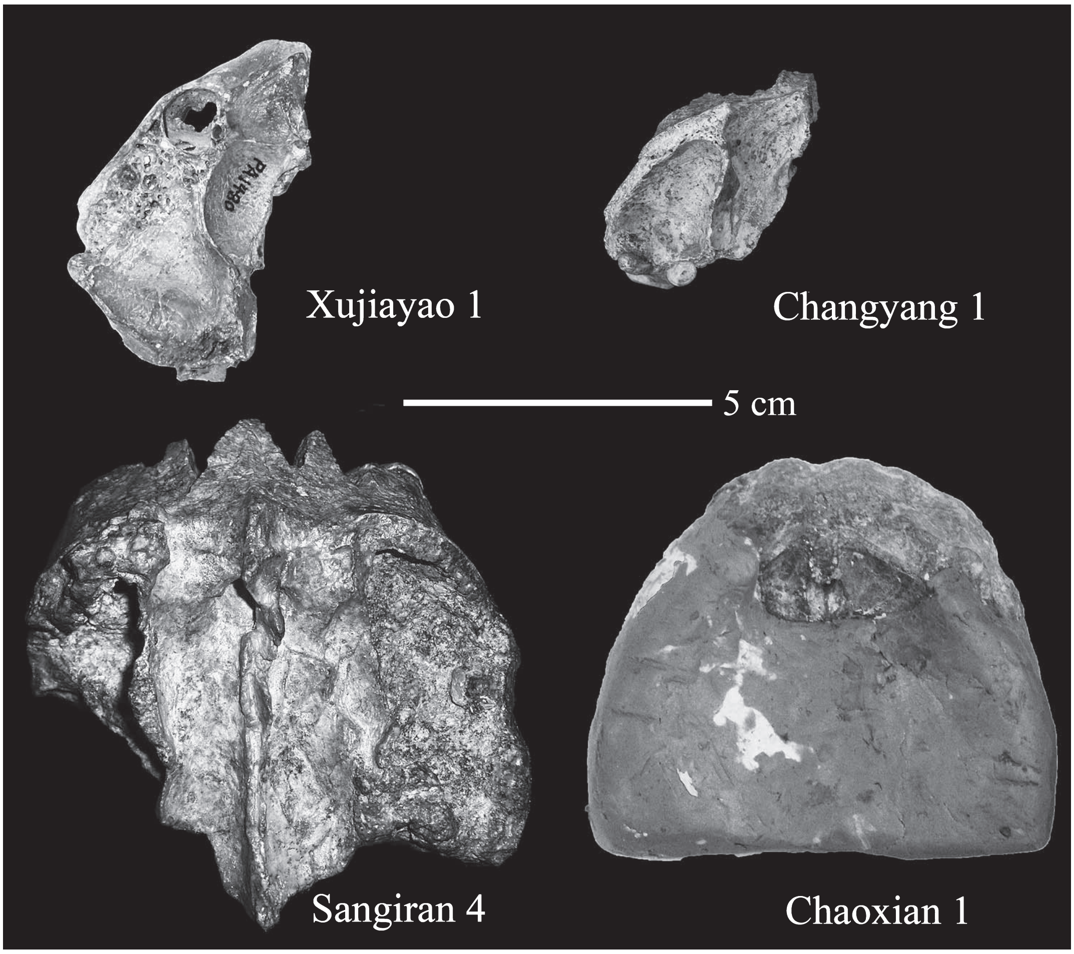

Figure 1. Superior views of the Sangiran 4, Chaoxian 1, Xujiayao 1, and Changyang 1 maxillae. All are oriented perpendicular to the midsagittal plane. Note than most of the Chaoxian 1 specimen has been reconstructed in plaster, based on the preserved palatal region. Scale: 5 cm.

posterior palate (as is needed for partial maxillae), these ordinal categories describe the degree to which, and manner in which, the nasal floor descends posterior of the anterior nasal sill. A "level" floor continues in the same plane as the sill and is anteroposteriorly straight. A 'sloping' floor is also straight but descends distinctly posteroinferiorly from the nasal sill. And a 'bi-level' floor, as originally noted by Stewart (1961), is posterosuperiorly convex in its anterior portion and descends posteroinferiorly rapidly behind the nasal sill, and then becomes horizontal and largely parallel to the palate as it extends more posteriorly.

Eastern Eurasian archaic *Homo* maxillae

Eastern Eurasian nasal floor configurations are discernible for one Early Pleistocene specimen (Sangiran 4) and for three late Middle/early Late Pleistocene archaic humans (Chaoxian 1, Xujiayao 1 (PA 1480), and Changyang 1 (PA 76)) (Weidenreich, 1945; Chia, 1957; Chia et al., 1979; Xu and Zhang, 1986; Chen and Yuan, 1988; Chen et al., 1994) (Figure 1). Other eastern Eurasian archaic human maxillae are known, but only the Jinniushan 1 maxillae appear to be sufficiently intact for assessment (Wu, 1988). Conversely, the Zhoukoudian Locality 1, Sangiran IX (Tjg 1993.05), and Sangiran Bpg 2001.04 maxillae are not sufficiently complete to discern their nasal floor configurations (Weidenreich, 1943; Kaifu et al. 2011; Zaim et al., 2011). Those from Lantian (Gongwangling) 1, Sangiran 17 and 27, and Dali 1 are too distorted or covered in matrix for accurate observation (Woo, 1965; Sartono, 1971; Wu, 1981; Indriati and Antón, 2008).

The Early Pleistocene Sangiran 4 left maxilla retains its inferior nasal margin and most of the nasal floor with little distortion. There is a post-mortem depression along the midline near the incisive foramen, but the lateral half of the floor appears undistorted. The right nasal floor sustained more damage, especially laterally along the maxillary sinus, but its form is close to that of the lateral left side.

The later Middle Pleistocene Chaoxian 1 maxilla retains all four incisor alveoli and the nasoalveolar clivus without distortion. The right nasal aperture margin is intact, as is the medial half of the left one. The nasal floor is then present on the right side and medial left side to posterior margin of the incisive foramen, joined by the anterior palate across the incisor alveoli and distally to the M^2 on the right side. Most of the nasal floor is therefore absent, but the anterior portion from the nasal sill to past the incisive foramen is present and sufficient to document its form.

The late Middle/early Late Pleistocene Xujiayao 1 left maxilla derives from a developmentally 7–9 year old juvenile (Jia et al., 1979), but Franciscus (1995, 2003) and Nicholas and Franciscus (2010) have shown that little change in nasal floor configuration occurs after the third year of postnatal development. The Xujiayao specimen preserves the intermaxillary suture from the nasoalveolar clivus anteriorly to the posterior side of the incisive foramen. The left nasal sill is intact to the lateral nasal aperture margin, and the nasal floor continues posterior along the maxillary sinus wall to the palatine foramen at the distal M^1. The nasal floor (and palate) is, however, broken off obliquely from the posterior incisive foramen to the palatine foramen. The nasal floor shape is nonetheless clear from the contour around the nasal sill and along the mid-left nasal floor to the level of the mesial M^1. The bone is undistorted.

The early Late Pleistocene Changyang 1 left maxilla has a preservation similar to that of Xujiayao 1, with the intermaxillary suture present (if abraded slightly), the lateral incisive foramen present, and then an oblique break of the palate/nasal floor from the posterior incisive foramen to the M^1. The nasal sill is present from the midline to the lateral nasal aperture margin, and the midline of the nasal floor is evident posterior of where the nasal floor and palate approach each other vertically. The bone is undistorted.

Therefore, although incomplete, these four specimens provide the midline of the nasal floor on at least one side, with the important anterior portion including the inferior nasal aperture margin and the anterior nasal floor to beyond the incisive foramen.

Eastern Eurasian early modern human maxillae

To provide Late Pleistocene modern human comparative data, nasal floor configurations were assessed for six Late Pleistocene (or probably Late Pleistocene) crania: Chilinshan 1 (PA 60), Liujiang 1 (PA 89), Minatogawa 4, Niah Cave 1, ZKD-Upper Cave 101 (AN 71), and Ziyang 1 (PA 58) (Wu, 1958, 1961; Chia and Wu, 1959; Woo, 1959; Brothwell, 1960; Suzuki, 1982; Shen et al., 2007). All of them have at least one largely complete nasal floor. Observations were made on the original specimens from Liujiang, Ziyang, and Chilinshan, on casts of the (lost) Upper Cave 101 and Minatogawa 4 specimens, and on a lateral radiograph of Niah 1. Data are currently unavailable for the Moh Khiew 1 and Late Pleistocene Australian maxillae.

Comparative samples

The nasal floor configurations of these Pleistocene eastern Eurasian humans are compared to samples of pan-Old World recent humans (Table 1) and western Old World Pleistocene humans (Table 2). Given the dearth of remains in both Africa and western Eurasia for the Early and Middle Pleistocene, the samples for those chronological periods are pooled within each region. The western Eurasian terminal Middle Pleistocene to mid-Late Pleistocene late archaic humans (Neandertals) are tabulated separately, but the data for pre-last glacial maximum early modern humans are pooled. The larger samples of terminal Late Pleistocene (post-last glacial maximum) modern humans are given separately for Europe and Africa. These data derive principally from Franciscus (2003) sorted by slightly different criteria and supplemented by additional observations.

Recent human variation is encompassed by western Old World data from Franciscus (2003) combined with eastern Old World data collected by S.D.M. (Table 1). Recent human males and females within samples do not differ significantly in their distributions for nasal floor configurations

Table 1. Distributions of nasal floor configurations in samples of recent (Late Holocene) humans*

	Level (%)	Sloped (%)	Bi-level (%)	*n*
Western Europe	48.6	41.4	9.9	111
Central Europe	39.4	51.4	9.2	109
Southeast Europe/southwest Asia	51.4	38.9	9.7	72
North Africa	69.1	22.1	8.8	68
Sub-Saharan Africa ‘Bantu’	22.7	58.0	19.3	119
Sub-Saharan Africa ‘Khoisan’	51.2	39.5	9.3	42
Australian	58.8	32.4	8.8	68
Northeast Asia	66.7	22.9	10.4	48

* Australian and eastern Asian data collected by S.D.M. Other frequencies from Franciscus (2003). Male and female data are pooled, given the non-significant differences between them (Franciscus, 2003).

Table 2. Summary counts for the three forms of nasal floor configuration in western Old World Pleistocene *Homo* samples (see Appendix 1 for pre-LGM (last glacial maximum) sample compositions, and Franciscus (2003) for the terminal Pleistocene ones)

	Level	Sloped	Bi-level
Terminal Pleistocene Europe	12	5	3
Terminal Pleistocene north Africa	45	14	2
Western Eurasia early modern humans	26	4.5	3.5
Western Eurasia late archaic humans	1	4	22
Western Eurasia Early/Middle Pleistocene	4	1	2
Africa Early/Middle Pleistocene	7	3	3

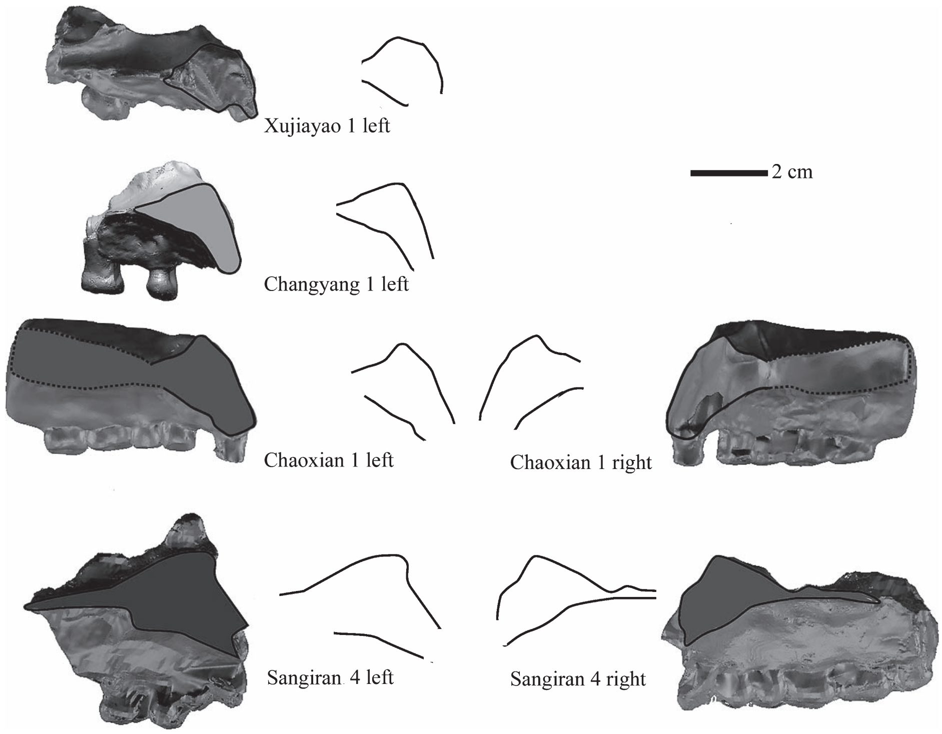

Figure 2. Nasal floor profiles for the four eastern Eurasian archaic *Homo* specimens, from laser scans of the specimens. Sangiran 4 is based on a cast; the others are from the original specimens. The dotted line on Chaoxian 1 indicates the portion restored in plaster.

(Franciscus, 2003), and the sexes are therefore pooled. The Changyang 1 and Lagar Velho 1 maxillae are ambiguously between sloping and bi-level; they are therefore scored as 0.5 for each category. The sample frequencies are compared using exact chi-square tests (Mehta and Patel, 1999).

Data collection

The nasal floor profiles for the most of available original specimens and casts (the latter including Sangiran 4, Minatogawa 4, and the lost Upper Cave 101 maxillae) were scanned using a NextEngine Model 2020i Desktop 3D Scanner and Rapidworks^{TM} software (NextEngine Inc.) to extract the parasagittal profiles through the incisor alveoli (Figure 2, Figure 3). The Liujiang cranium was scanned in coronal orientation by use of high-resolution industrial computed tomography (CT) scans (type: GY-1-450 XCT), housed in the Institute of High Energy Physics, Chinese Academy of Sciences.

Results

The four eastern Eurasian archaic *Homo* maxillae have a substantial difference in the level of the posterior nasal floor relative to anterior nasal aperture inferior margin (Figure 2, Appendix 2). The nasal floor of Sangiran 4 has been variably described in the literature (Franciscus and Trinkaus, 1988; Rightmire, 1998; McCollum, 2000); however, despite the bilateral asymmetry from minor fossilization distortion (Weidenreich, 1945; Rightmire, 1998; Figure 1), Sangiran 4 is best seen to exhibit a bi-level floor. It is difficult to describe it as level (contra Rightmire, 1998) given its evident bilateral profiles (Figure 2); the only reasonable alternative to bi-level might be sloping. The Chaoxian 1 and Xujiayao 1 maxillae are distinctly bi-level, even though the former preserves only the anterior portion of the nasal floor. The configuration of Changyang 1 is less apparent. It is either bi-level or sloping, depending on how one reconstructs the posterior extension of the nasal floor. Near the midline there is a bulge extending posteriorly from the anterior nasal spine over the superior incisive foramen, which is likely to have produced a bi-level floor. However, midline absence of the nasal floor posterior of the incisive foramen prevents confirmation of this. It is therefore classified here as bi-level/sloping.

In contrast, most of the early modern humans from eastern Eurasia exhibit level nasal floors, and the exception has a sloping floor (Figure 3, Appendix 2). The Upper Cave 101 floor has a slight undulation, but it is not sufficient for the maxilla to be considered bi-level. The Chilinshan 1 maxillae have a slight posterior slope, but insufficiently to be categorized as sloping. The Minatogawa 4 maxilla has a sloping floor.

The early modern eastern Asians, even with Chilinshan 1 (plus Minatogawa 4) scored as sloping, fall comfortably with the distributions of the recent human samples, the terminal Pleistocene European and north African samples, and the western Eurasian early modern humans (Table 1, Table 2). These three Pleistocene samples have a clear dominance of the level configuration, and the recent human samples are mostly dominated by either the level or the sloping pattern, with the bi-level configuration present in a minority of individuals.

The eastern Eurasian archaic humans (Figure 4), despite

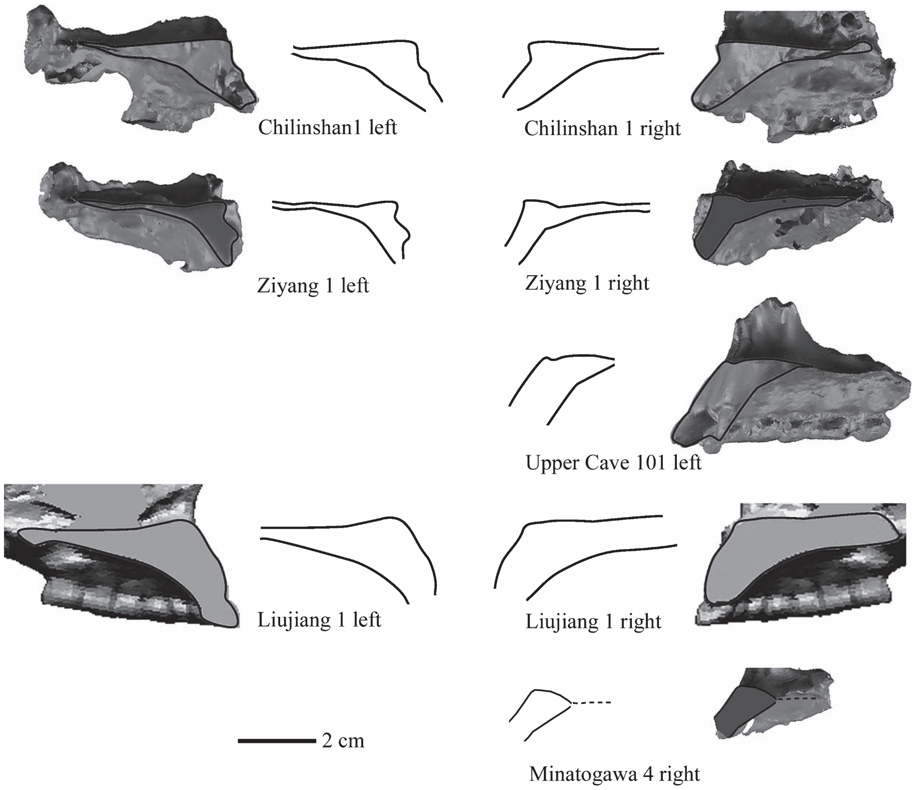

Figure 3. Nasal floor profiles for eastern Eurasian Late Pleistocene modern human specimens. Liujiang 1 is from a CT scan of the original specimen. Minatogawa 4 and Upper Cave 101 are from laser scans of casts. The others are from laser scans of the original specimens.

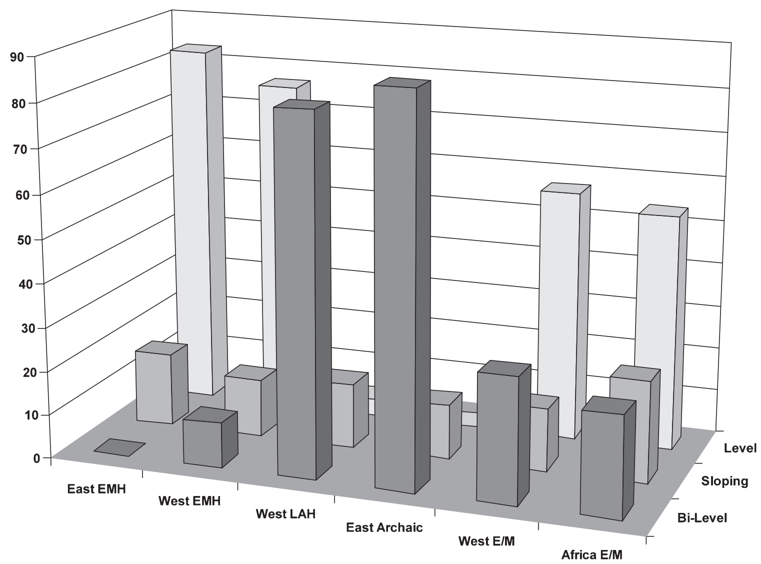

Figure 4. Frequencies of nasal floor configurations for pre-last glacial Pleistocene humans. EMH, early modern humans; LAH, late archaic humans; E/M, Early and Middle Pleistocene humans.

the small sample size, contrast with most of these modern human samples ($P = 0.007$ and 0.002 relative to the eastern and western Eurasian early modern human samples, respectively), and with most of the western Early and Middle Pleistocene humans ($P = 0.053$ and 0.032 relative to the western Eurasian and African samples, respectively). It is principally with the Neandertals, with their dominance of the bi-level configuration, that these eastern archaic specimens align ($P = 0.420$). This applies even if one only compares the Changyang, Chaoxian, and Xujiayao specimens to the penecontemporaneous late Middle and Late Pleistocene Neandertals ($P = 0.453$).

Discussion

The level, or near level, configurations of the eastern Eurasian early modern human nasal floors, from the earlier Liujiang and Niah specimens to the later Chilinshan and Minatogawa remains, conform well with the general pattern across early and recent modern humans. The dominance of bi-level and sloping nasal floors among the earlier, eastern Eurasian archaic human specimens could reflect unusual sampling of archaic populations possessing similar distributions of level and sloping configurations as seen in recent modern humans. However, the taphonomic probability of exclusively recovering specimens with inferiorly displaced nasal floors from populations characterized by a preponderance of level configurations is likely small. If these eastern Eurasian archaic specimens are in fact representative of populations principally characterized by depressed nasal floors, then the dominance of the bi-level (and sloping) nasal floors in eastern Eurasian archaic humans would parallel that present in the (much larger) sample of Neandertals.

The configurations of these eastern archaic maxillae, however, need not imply close affinities to the western Eurasian Neandertals. For example, several features of the nasomaxillary region have been shown to scale allometrically with overall facial size, both in recent humans and across *Homo* (Holton and Franciscus, 2008; Maddux and Franciscus, 2009; Maddux, 2011). Accordingly, the prevalence of depressed nasal floors in these two archaic Eurasian samples may simply be related to both populations possessing similarly sized (large) faces. Indeed, Franciscus (2003) has shown nasal floor morphology to be correlated with several measures of facial size across *Homo*, especially facial height and width. Although an allometric association between facial size and the nasal floor appears supported by the presence of bi-level nasal floors in other large faced archaic specimens from Europe and Africa (e.g. Petralona, Broken Hill, Bodo), such an inference is more difficult to test in the eastern Eurasian Pleistocene humans studied here, given their fragmentary nature. However, nasoalveolar clivus height, the distance between nasospinale and prosthion, can be measured on Choaxian 1 (28.4 mm), Sangiran 4 (28.1 mm), and Changyang 1 (24.5 mm). These archaic eastern Eurasian fossils thus possess clivus height measurements that are approximately 30–35% larger than the mean value of 16.9 mm for our recent East Asian modern human sample, but very similar to the Neandertal average of 24.2 mm (Maddux, unpublished data). Thus, it appears reasonable to suggest that the prevalence of bi-level nasal floors in archaic eastern Eurasian humans existed in conjunction with relatively large facial dimensions. Moreover, the Chinese Middle Pleistocene specimen from Jinnuishan, which was not available for inclusion in this study, possesses both a relatively intact midface and nasal floor (Wu, 1988). Thus, future evaluation of the nasal floor in this fossil specimen may shed further light on the relationship between nasal floor morphology and facial size.

These results also raise questions as to the anatomical bases of these alternative nasal floor configurations. Anatomically, these nasal floor configurations reflect the spatial relationships between three anatomical components: the nasoalveolar clivus, the anterior nasal floor, and the posterior nasal floor. Both the nasoalveolar clivus and the anterior nasal floor are developmentally derived from the premaxilla, while the posterior nasal floor is comprised of the palatine bones and palatine processes of the maxillae. In modern humans the premaxilla fuses to the maxilla within the first year of postnatal life (Barteczko and Jacob, 2004). However, Maureille and Bar (1999) found that synostosis of the premaxillary suture occurred as late as 6 years of age in Neandertals, and they argued that different premaxillary fusion schedules may account for many of the differences in adult Neandertal and modern human midfacial morphology. Given that the level, sloping, and bi-level nasal floor configurations contrast the spatial relationships between the anterior (premaxillary) and posterior (maxillary/palatine) aspects of the nasal floor, similar developmental timing of premaxillary suture fusion may provide an ontogenetic explanation for the prevalence of bi-level nasal floors in both Neandertals and eastern Eurasian archaic humans.

In addition to these considerations, the height of the nasoalveolar clivus is constrained by incisor root lengths, which vary among Pleistocene *Homo* and are generally longer among archaic than modern humans (Weidenreich, 1937; Vlček, 1969; Bailey, 2005; Trinkaus et al., 2012). Moreover, Nicholas and Franciscus (2010) have identified an ontogenetic link between nasal floor morphology and development of the permanent dentition, suggesting that the topography of the nasal floor may correspond to dentognathic demands. Accordingly, nasal floor morphology could reflect the need to maintain a functional distance between the nasal floor/palate relative to the dental occlusal plane and/or the superior portions of the internal nasal cavity (Björk and Skieller, 1976; Enlow and Hans, 1996). Thus, depressed nasal floors may serve to lower the palate relative to long dental roots in order to maintain a consistent distance between the palate and the occlusal surfaces of the dental crowns (i.e. palate height), while simultaneously increasing nasal cavity height. Alternatively, shorter root lengths may facilitate the maintenance of a functional palate height, not by lowering the palate, but by elevating the occlusal plane, thus permitting, or perhaps even necessitating, a nasal floor essentially level with the nasal margin (for a similar spatial argument related to palatal dimensions in earlier hominids, see McCollum, 1997).

Conclusions

An assessment of the nasal floor configurations of the available and sufficiently intact, if still incomplete, archaic *Homo* maxillae from eastern Eurasia shows them to have a prevalence of the bi-level pattern similar to that seen in the western Eurasian Neandertals. Conversely, early modern humans from eastern Eurasia mostly exhibit the level floor pattern predominant among early and recent modern human populations. The relationships between nasal floor morphology and other aspects of facial size and shape remain uncertain, and they are difficult to evaluate with the available and incomplete eastern Eurasian remains. However, these results are sufficient to question whether a high frequency of the bi-level pattern is a distinctive Neandertal feature and to query the phylogenetic and functional significance of this configuration.

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Appendix 1. Nasal floor configurations for samples of pre-last glacial maximum Pleistocene *Homo**

Level	Sloping	Bi-Level
Early/Mid Upper Paleolithic		
Arene Candide IP	Lagar Velho 1	
Cro-Magnon 1	Ohalo 2	Qafzeh 4
Cro-Magnon 2	Qafzeh 6	Skhul 4
Cro-Magnon 4	Qafzeh 10	Sunghir 1
Dolní Věstonice 3	Qafzeh 15	
Dolní Věstonice 13		
Dolní Věstonice 14		
Dolní Věstonice 15		
Dolní Věstonice 16		
Grotte des Enfants 4		
Grotte des Enfants 5		
Grotte des Enfants 6		
Loiyangalani 1		
Mladeč 8		
Muierii 1		
Nahal ’En-Gev 1		
Nazlet Khater 2		
Oase 2		
Paglicci 25		
Pataud 1		
Pavlov 1		
Qafzeh 9		
Qafzeh 11		
Sunghir 2		
Sunghir 3		
Sunghir 5		
Western Eurasia late archaic humans		
Krapina 48	Krapina 47	Amud 1
	Krapina 49	Arcy-Hyène 8
	Tabun 1	La Chapelle-aux-Saints 1
	Vindija 225	Devil’s Tower 1
		Engis 2
		La Ferrassie 1
		La Ferrassie 2
		Forbes’ Quarry 1
		Guattari 1
		Kůlna 1
		Montmaurin 4
		Palomas 96
		La Quina 5
		La Quina 18
		Roc de Marsal 1
		Saint Césaire 1
		Shanidar 1
		Shanidar 2
		Shanidar 5
		Subalyuk 2
		Tabun B1
		Vindija 259
Western Eurasia Early/Middle Pleistocene		
Arago 21	ATD6-69	ATD6-14
AT-SH Cr5		Petralona 1
AT-SH 1100 + 1111 + 1197 + 1198		
AT-SH 767 + 963		
Africa Early/Middle Pleistocene		
Broken Hill 2	Aliya 1	Bodo 1
Eliye Springs	Irhoud 1	Broken Hill 1
Florisbad	KNM-ER 3733	Rabat 1
KNM-WT 15000		
KRM AA43		
Ndutu 1		
Ngaloba (L.H. 18)		

* Data from Franciscus (2003) with the addition of Loiyangalani 1 (Muteti et al., 2010), Muierii 1 (Doboş et al., 2010), Oase 2 (Rougier et al., 2007), Palomas 96 (Walker et al., 2011), Qafzeh 10 and 15 (Tillier, 1999), Sunghir 1, 2, 3, and 5 (ET, personal observation), and Paglicci 25, ATD6-14 and ATD6-69 (SDM, personal observation).

Appendix 2. Nasal floor configuration in eastern Eurasian Pleistocene human remains

Level	Sloping	Bi-Level
Late Pleistocene modern humans		
Chilinshan 1	Minatogawa 4	
Liujiang 1		
Niah 1[a]		
Ziyang 1		
ZKD Upper Cave 101		
Late archaic humans		
	Changyang 1[b]	
		Chaoxian 1
		Xujiayao 1
Early Pleistocene human		
		Sangiran 4

[a] Niah 1 configuration determined from lateral maxillary radiograph in Kennedy (1977).
[b] The Changyang 1 nasal floor is scored as bi-level/sloping (see discussion in text).