CT-Based Descriptions of the Paranasal Complex of Sungir-1, an Upper Paleolithic European

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ABSTRACT

Although the intricacies of the underlying processes of paranasal sinus development are still unknown, the documentation of sinus morphology is necessary to fully comprehend the evolutionary history of these structures, and for understanding the complex ontogenetic and phylogenetic processes shaping hominin diversity. As such, the purpose of this study is to present, for the first time, detailed descriptions for internal paranasal structures of the Sungir-1 specimen. The Sungir-1 specimen was scanned via computed tomography (CT) in Moscow, Russia. Using these CT scans, the maxillary and frontal sinuses were semi-automatically segmented and digitally rendered into three-dimensional (3D) models; volumetric data were obtained from these models. Sinus volumes were also obtained from CT scans of another Upper Paleolithic specimen, Mladeč-1, and three morphologically distinct modern human samples (Late Holocene)—West Africans, Mongolians, and Croatians. Volumetric-data was cursorily compared to previously published reports for additional Middle and Upper Paleolithic fossils, as well as additional Late Holocene modern human specimens. Overall, Sungir-1 exhibits relatively large maxillary sinuses occupying most of the maxillary body (volumes: right, 24.63cm^3; left, 26.18cm^3). Initial observations indicate that Sungir's tall, wide maxillary sinuses are smaller than those of Neanderthals, and likely most similar to those of Mongolians and other Central Asian samples previously described in the literature. Sungir-1's frontal sinuses are relatively small and simple (volumes: right, 1.51cm^3; left, 2.23cm^3; combined, 3.74cm^3)—adding to the complexity of frontal sinus variation already evident in the fossil and modern human record. Studies incorporating shape analyses of these internal structures are currently underway to better understand the position of Sungir-1 relative to diverse modern human groups, as well as any environmental effects.

INTRODUCTION

The Sungir-1 adult male cranium is representative of an Upper Paleolithic *Homo sapiens* individual from the Sungir site (56°10′30″N, 40°30′30″E), which is located 192km northeast of Moscow, Russia (Bader 1978). This site originally revealed archeological material in 1955, during initial excavations by A.F. Nacharav (Trinkaus et al. 2014: Ch. 3). In the following decades, several graves were excavated by O.N. Bader, ultimately revealing human remains of several individuals (identified as Sungir-1 to Sungir-9). Sungir-1 was specifically unearthed in June 1964 as an almost complete skeleton from Grave-1 along with grave goods including ivory beads, ochre, and other adornments (Bader 1998). The date of occupation—around the interstadial, marine isotope stage 3 (MIS 3; ~28,000 ^{14}C years BP)—as well as the abundance of archaeological material with well-preserved human remains, makes this a particularly rich Upper Paleolithic site (see Trinkaus et al. 2014: Ch. 2 for discussion on dating and climatic implications; also see Sikora et al. 2017 for evidence of more recent date ranges for Sungir-6). Additionally, as most Upper Paleolithic sites are found in Western and Central Europe, Sungir is relatively unique in that it represents one of the few Eastern European sites. This makes Sungir central in interpretations of how early modern humans may have adapted biologically and culturally to the harsher climates found in more northern latitudes (see Holt and Formicola 2008 for general, related discussions of Upper Paleolithic assemblages).

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As such, several studies have assessed how the morphology of the Sungir specimens compares to other periglacial hominins, and whether morphological changes indicative of climatic adaptation are evident (e.g., Bader et al. 2000; Bunak 1980; Evteev et al. 2017; Mednikova 2005; Trinkaus et al. 2014). Bunak (1980) found that Sungir-1 is morphologically most similar to early central Europeans, including Předmostí 3 and specimens similar to those from the Cro-Magnon site. In a more recent study, Evteev et al. (2017) also found close similarities between Sungir-1 and Late Holocene modern Europeans. These interpretations are slightly different from genetic evidence, which aligns Sungir-1 with West Eurasian (not central European) populations (Sikora et al. 2017). Further, previous morphological studies may be considered limited in that they focus on external cranial features, without including internal features such as the nasal cavity and paranasal sinuses, which are arguably more strongly correlated with climatic conditions (see Maddux et al. 2017 for functional reviews of internal nasal morphology and climate). These studies suggest that cold-adapted populations possess relatively taller, narrower nasal cavities (e.g., Holton et al. 2013; Maddux et al. 2017; Noback et al. 2011) with concomitantly larger, particularly taller and wider, maxillary sinuses (Butaric 2015; Butaric and Maddux 2016; Maddux and Butaric 2017; Noback et al. 2016). As such, if Sungir-1 was adapted to a colder, harsher environment, one may expect them to possess similar patterns of nasal-sinus variation; however, descriptions and analyses of the internal structures for Sungir are lacking.

Relatively recently, Trinkaus and colleagues (2014) published an extensive book, *The People of Sunghir: Burials, Bodies, and Behavior in the Earlier Upper Paleolithic,* describing the historical context, archaeological material, and skeletal morphology of the Sungir specimens in great detail. However, while traditional radiographs were obtained for the fossil crania, revealing some of the internal structures, full descriptions of these structures are still lacking—particularly for Sungir-1. This lack of detail is likely due to known limitations associated with traditional radiographs, such as issues of superimposition that preclude detailed views of the paranasal sinuses.

To partially fill in this gap of knowledge, this study uses a recently obtained computed tomographic (CT) scan of the Sungir-1 cranium to access and describe the patterns of pneumatization— i.e., the degree of paranasal sinus development and/or the presence of air-filled cavities—of this specimen. While the primary purpose of this paper is to provide qualitative descriptions of the paranasal sinus complex of Sungir-1, we also provide a cursory comparison of sinus volume to other modern human populations (Late Holocene) and several Paleolithic *Homo* specimens. These descriptions serve as the first part in a two-part study on the internal morphology of Sungir-1. A second study is underway to incorporate shape analyses of the internal nasal cavity and maxillary sinus structures to better understand the position of Sungir-1 relative to diverse modern human groups.

MATERIALS AND METHODS

The Sungir-1 CT scan was obtained by one of the authors (SV) via a Brilliance-64 (Philips, Netherlands) in Moscow, Russia; resulting scans have voxel heights and widths of 0.51mm x 0.51mm, with a slice thickness of 0.3mm. Scans were imported in Amira 5.6 (Stalling et al. 2005) for viewing and post-processing by the first author (LNB). Initial inspection of the scans indicated the presence of foreign materials, including matrix in the nasal cavity, ethmoidal air spaces, and the frontal and maxillary sinuses. Additionally, CT scans revealed that the wax placed in the orbits and nasal cavity of the fossil had also permeated into the ethmoidal and maxillary spaces. Still, both the wax and sedimentary matrix were clearly distinguishable from the bone in most regions, and were segmented out via standard semi-automated and manual techniques (see Prossinger et al. 2003; Prossinger and Teschler-Nicola 2006; Weber and Bookstein 2011 for reviews on working with fossil specimens). However, taphonomic processes damaged the fragile ethmoidal air spaces—as such these were not isolated or described here. Of further note is that the neurocranium of Sungir-1 is distorted with destruction to the cranial base (see Bunak 1980 for details); this destruction is too severe to allow visualization or reconstruction of the sphenoidal sinus. Owing to this, the authors made no attempt to virtually reconstruct the neurocranium of this specimen. Thus, the primary focus in this paper will be a discussion of the remaining maxillary sinuses and frontal sinuses of Sungir-1.

During post-segmentation of the sinuses, 3D models of the cranium, as well as the frontal and maxillary sinuses, were digitally rendered. Note that the posterior-inferior region of the right maxilla is broken; thus, this region of the right maxillary sinus was reconstructed based on the contours of the remaining walls and visual similarity to the left maxillary sinus. However, it should be noted that the dimensions and volumetric measures of this reconstructed sinus may be slightly smaller than actuality (see Table 1 below). Post-processing of the models, including smoothing techniques and removal of artifacts and manifold triangles, was conducted in Geomagic Studio 2014.10 (3D Systems, Inc.). These models assist in the visualization of the structures further detailed below. Volumes were also obtained from each sinus model for comparative purposes (see Table 1 and the discussion below.) A composite of the models comprising Sungir-1's internal facial skeleton is provided in Figure 1 below, with pertinent CT-slices provided in Figures 2 and 3 below. Further descriptions are detailed below.

Maxillary sinus and frontal sinus volumes were also calculated from another Upper Paleolithic specimen, Mladeč-1. The Mladeč-1 CT scan was obtained via the Digital Archive of Fossil Hominoids (http://www.virtual-anthropology.com/3d-data/data-webshop); this specimen was originally scanned in 1996 with a Phillips, Mx8000IDT CT scanner in Vienna, Austria, with voxel height and widths of 0.47mm x 0.47mm, and slice thickness of 0.75mm. Maxillary sinus volumes for Mladeč-1 were obtained by similar methods discussed above, using semi-automatic and manual techniques to remove foreign materials (i.e., gypsum, sinter, etc; see Prossinger and Teschler-Nicola 2006). Note that the frontal sinus of Mladeč was not segmented for this study; while some scholars indicate that this sinus is present (see Wolpoff et al. 2006: 282, 293), this area of the frontal bone is filled with material that closely resembles the pattern of trabecular bone. Whether this "filament-like structure" (as described by Dr. H. Prossinger, see Wolpoff et al. 2006: 282) is deposited or indeed trabecular bone (indicating aplasia of the frontal sinus) is difficult to determine with a medical-grade CT scanner. However, even if the frontal sinus was present and subsequently filled with secondary matrix, the boundaries of the space are too obscure for accurately outlining this sinus.

Additionally, maxillary and frontal sinus volumes were obtained from three morphologically distinct modern human (Late Holocene) samples—West Africans, Mongolians, and Croatians. Maxillary sinus volumes were obtained from a previous study (Butaric 2015), while frontal sinus volumes were obtained specifically for this project using semi-automatic techniques in Amira 5.6. For size-standardization processes, upper facial width was also collected. This distance was measured across the right and left frontomalare temporale, based on landmarks collected from previous studies (Butaric and Maddux 2016; Maddux and Butaric 2017). While composite measures are preferable to single linear distances for size-standardization purposes (see Jungers et al. 1995), the use of upper facial width allows the inclusion of more hominin specimens and comparisons using previously-published hominin data (following previous studies, Noback et al. 2016; Rae et al. 2011). Scaled volumes were obtained by dividing the cubed-root of the sinus volume by the individual's upper facial breadth.

RESULTS

Overall, Sungir-1 exhibits relatively large maxillary sinuses that occupy most of the maxillary body (Figure 1 and 2): right maxillary sinus (reconstructed) volume, 24.63cm^3; left maxillary sinus, 26.18cm^3. Initial inspection indicates that the right and left side are relatively similar in dimensions and shape, but note that depth and possibly height of the right sinus are likely to be slightly affected by the damaged right posterior maxilla described above.

Each maxillary sinus extends toward the alveolar region, inferiorly passing the nasal floor. A thin layer of bone separates the left posterior tooth roots from the floor of the left sinus, while the molar roots on the right side seem to protrude into the sinus cavity; however, this protrusion of the right side is likely due to the broken nature of this region (see CT slices in Figure 2d). Aside from this, the floor of each sinus is relatively level in that they lack molar-root penetration. As is best seen on the left side, the floor of the maxillary sinus slopes such that the posterior region is more superiorly placed when the specimen is in Frankfort horizontal (see Figure 2c).

Both maxillary sinuses extend laterally to pneumatize toward the zygomaticofacial suture and may even extend into the zygoma itself (see Figure 2b, blue arrow)—although this is difficult to confirm in hospital-grade CT scans. Superiorly, a thin orbital wall bounds the sinus roof, but they do not extend far into the frontal processes of the maxilla and do not swell into the orbit itself, as described in some Neanderthal crania (see Schwartz and Tattersall 2002). Posteriorly, the left sinus pneumatizes extensively within a maxillary body that extends past the third maxillary molar (see Figure 2c, blue arrow). This appearance of a convex posterior maxilla wall has been previously described in other hominins as the "development of a posterior 'balloon'" (Schwartz and Tattersall 2002: 236), which is likely exaggerated in Sungir-1 by the degree of dental wear and alveolar remodeling (as suggested by an anonymous reviewer; also see Trinkaus et al. 2014: 136–138 for detailed maxillary alveolar and dental descriptions). A similar situation likely occurred on the right side, based on visual inspection in the area that remains (see Figure 2d). Concomitant expansion is not noted anteriorly, and the anterior walls of both maxillary sinuses border around the level of the first and second maxillary premolars.

Overall, Sungir-1 possesses relatively small frontal sinuses; this, in combination with Sungir-1's relatively thickened glabellar region, may be why these structures could not be visualized in traditional radiographs (Trinkaus et al. 2014: 121). As can be seen in Figures 1 and 3, the left sinus is slightly larger and more complex than the right, with the left frontal sinus volume measuring 2.23cm^3 and right 1.51cm^3. Indeed, a calculated asymmetric index of 67.71 (smaller sinus/larger sinus x 100) indicates moderate asymmetry (see Yoshino et al. 1987 for categories of frontal sinus asymmetry). Although both sinuses extend superiorly above the superior orbital rim, they are still relatively small and unimpressive in nature. The left sinus appears to be slightly taller, pneumatizing further superiorly into the frontal bone. The superior outline of the left sinus is also more complex and is scalloped with three distinct arcades. In anterior view, the superior outline of the right sinus is relatively simple, with a single arcade. However, in the lateral view, the right sinus does exhibit a secondary compartment that extends posteriorly (see Figures 1 and 3). Neither sinus extends laterally past the supraorbital foramen/notch or pneumatizes well into the frontal squama. Nor does either sinus fully pneumatize the available anterior-posterior glabellar space, leaving a relatively thick layer of bone anterior to the sinus; this feature can be seen in the sagittal CT slices (see Figure 3c).

COMPARISONS WITH OTHER SPECIMENS

Table 1 provides the absolute and relative volumes for the maxillary and frontal sinuses and upper facial breadth for the samples studied here; previously published averages are also provided for several modern human samples. Figure 4 provides a visual representation of frontal and maxillary sinus volumes versus upper facial breadth for several fossil hominins and modern humans (Croatians, Mongolians, West Africans) of focus in the current study.

In terms of absolute size, Sungir-1 is above the average

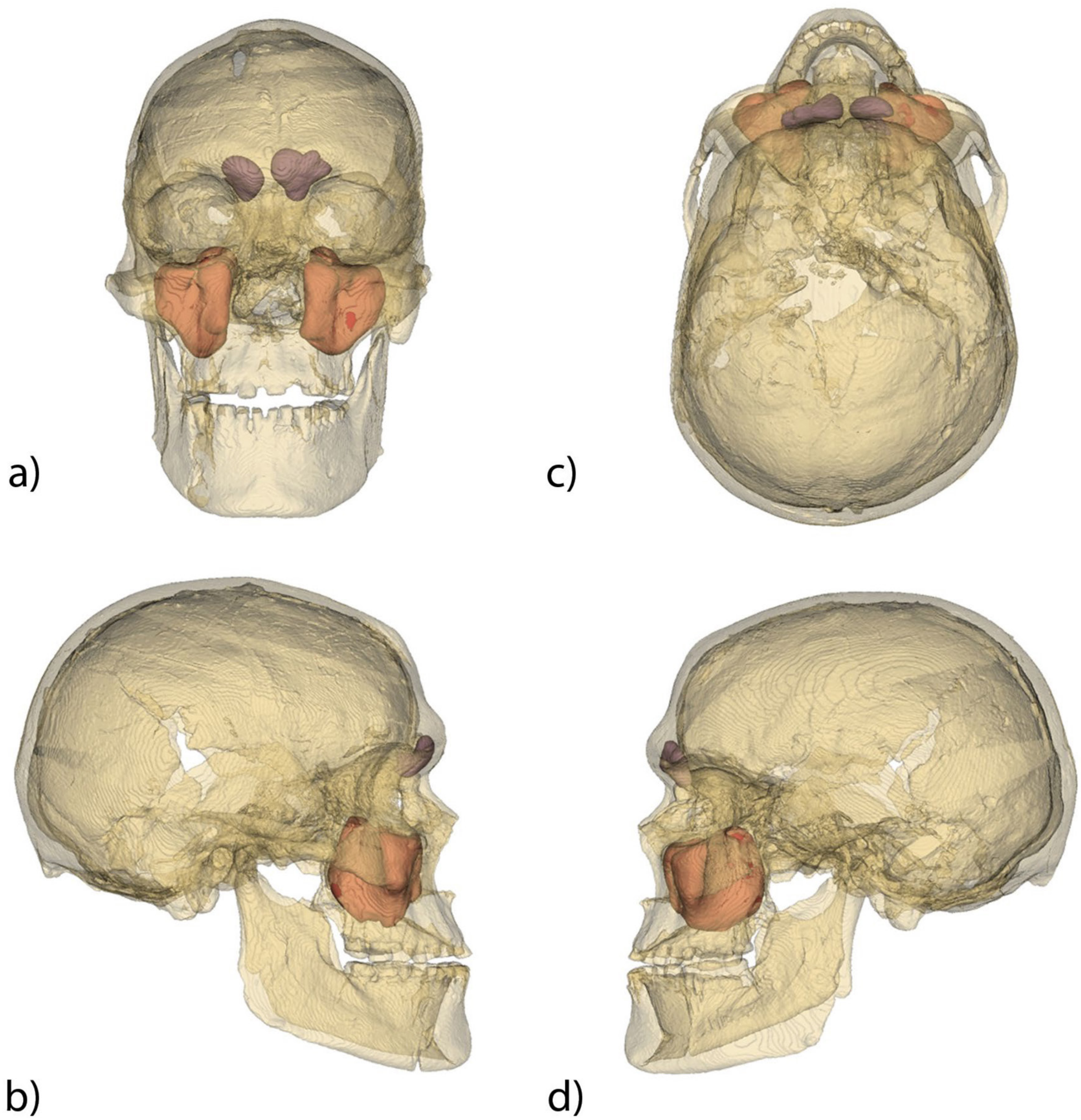

Figure 1. 3D digitally rendered model of Sungir-1 illustrating the frontal (purple) and maxillary (red) sinuses in (a) anterior view; (b) lateral right-side view; (c) superior view; and, (d) lateral left-side view.

maxillary sinus volumes presented for several globally-diverse modern humans (see Table 1) but is not quite as large as Broken Hill and Guattari-1. Here it should be noted that despite these excessively large absolute volumes, previous studies indicate most fossil specimens fit within modern human ranges once adjusted for overall body size (Rae et al. 2011). This can be seen in Figure 4, in which most of the hominin fossils plotted fall within the range of both maxillary and frontal sinus volumes; the exception here being Guattari, which plots far above the modern humans. Note that in terms of maxillary sinus volume, Sungir plots at the upper limits of the modern human range.

Based on initial visual observations of maxillary sinus shape, Sungir possesses tall and wide maxillary sinuses, which are likely most similar to those of Northern and Central Asian samples previously described (e.g., Buriats and Mongolians, see Butaric and Maddux 2016; Maddux and Butaric 2017); however, the advanced 3D shape analyses (currently underway) will need to be conducted to support—or negate—that assertion. Still, relatively tall and wide maxillary sinuses would fit well within the tall, wide maxillary body previously described in this specimen (Trinkaus et al. 2014), following the general patterns found between the external maxillary body and internal sinus among modern humans from colder climates (see Maddux and Butaric 2017). While taller, wider, and overall larger maxillary sinuses (at least in absolute terms) are often found among Middle and Upper Paleolithic *Homo*, Sungir-1 does not exhibit excessive anterior pneumatization. This is in contrast to conditions seen in Neanderthal crania whereby "hyperpneumatized" specimens were previously described as exhibiting "puffy" or "inflated" faces

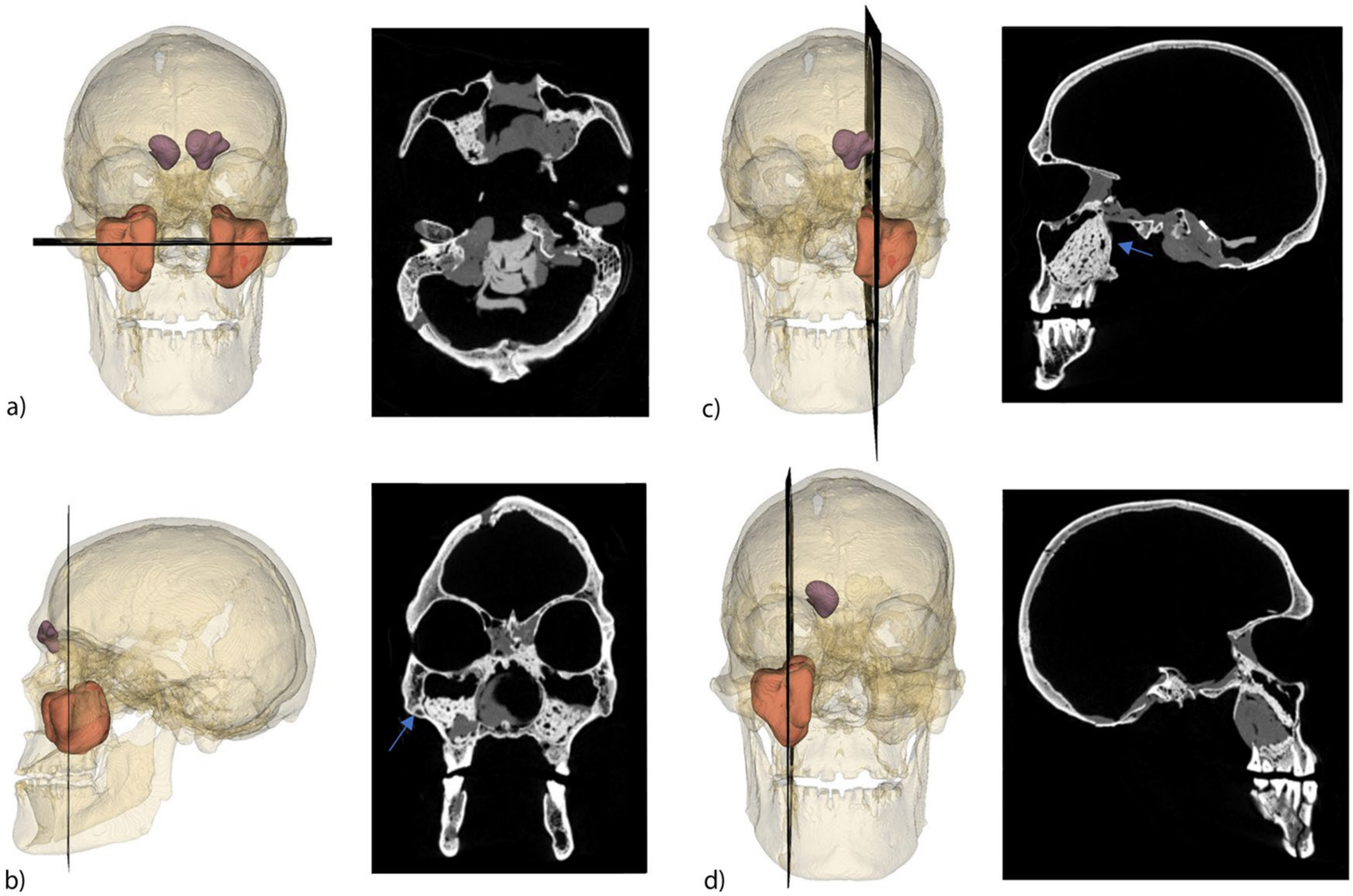

Figure 2. Detailed CT-slices illustrating various views of the maxillary sinus: (a) axial slice for maximum breadth; (b) coronal slice for maximum breadth, note encroachment to zygomaxillary suture (blue arrow, see text); (c) sagittal slice for maximum area of left sinus, note posterior pneumatization (blue arrow, see text); and, (d) sagittal slice for maximum area of right sinus, note broken posterior wall (see text).

(Coon 1962; Heim 1974, 1994; but see Maddux and Franciscus, 2009; Rae et al. 2011; Vlček 1967; Zollikofer et al. 2008). However, this is not surprising given the previously described, concave nature of Sungir's infraorbital region, typical of early modern humans (Trinkaus et al. 2014: 132).

In terms of frontal-sinus size and complexity, the Sungir-1 frontal sinuses are relatively small and simple compared to most archaic *Homo* and some modern human samples (see Table 1 for volumetric averages). This is particularly true when compared to the extensive frontal sinus complexes found among specimens such as Broken Hill (Prossinger 2008; Spoor and Zonneveld 1999; Zollikofer et al. 2008), Steinheim (Prossinger 2008; Prossinger et al. 2003), Petralona (Seidler et al. 1997), and even some more contemporary modern human specimens (see Figure 2D in Zollikofer et al. 2008 for an extreme example). However, frontal sinus size and shape is highly variable among archaic *Homo* and modern human individuals—so much so that this structure is often used as "fingerprints" for positive identifications in a forensic setting (Besana and Rogers 2010; Christensen 2005; Yoshino et al. 1987). As such, asymmetry in frontal sinus size—such as that found here in Sungir-1—is relatively frequent among modern humans and hominin specimens (also see Zollikofer et al. 2008). Further, relatively large specimens such as Forbes' Quarry, Saccopastore-2, and Ceprano (Bruner and Manzi 2005; Manzi et al. 2001; Rae et al. 2011; Zollikofer et al. 2008) also possess relatively unimpressive frontal sinuses, despite well-developed supraorbital regions.

DISCUSSION

Although the exact underlying processes of paranasal sinus pneumatization (and their repercussions, if any) are still being investigated, the documentation of sinus morphology is necessary to fully comprehend the evolutionary history of these structures, and for understanding the complex ontogenetic and phylogenetic processes shaping hominin diversity (Zollikofer et al. 2008). As such, the purpose of the current study was to present, for the first time, a detailed description of the internal paranasal structures in the Sungir-1 specimen. Overall, Sungir-1 exhibits large maxillary sinuses, but is still within the upper ranges compared to modern human groups from diverse ecogeographic locations; however, these structures are not as large in terms of absolute size compared to other hominin fossils, particularly Neanderthals (see Zollikofer et al. 2008).

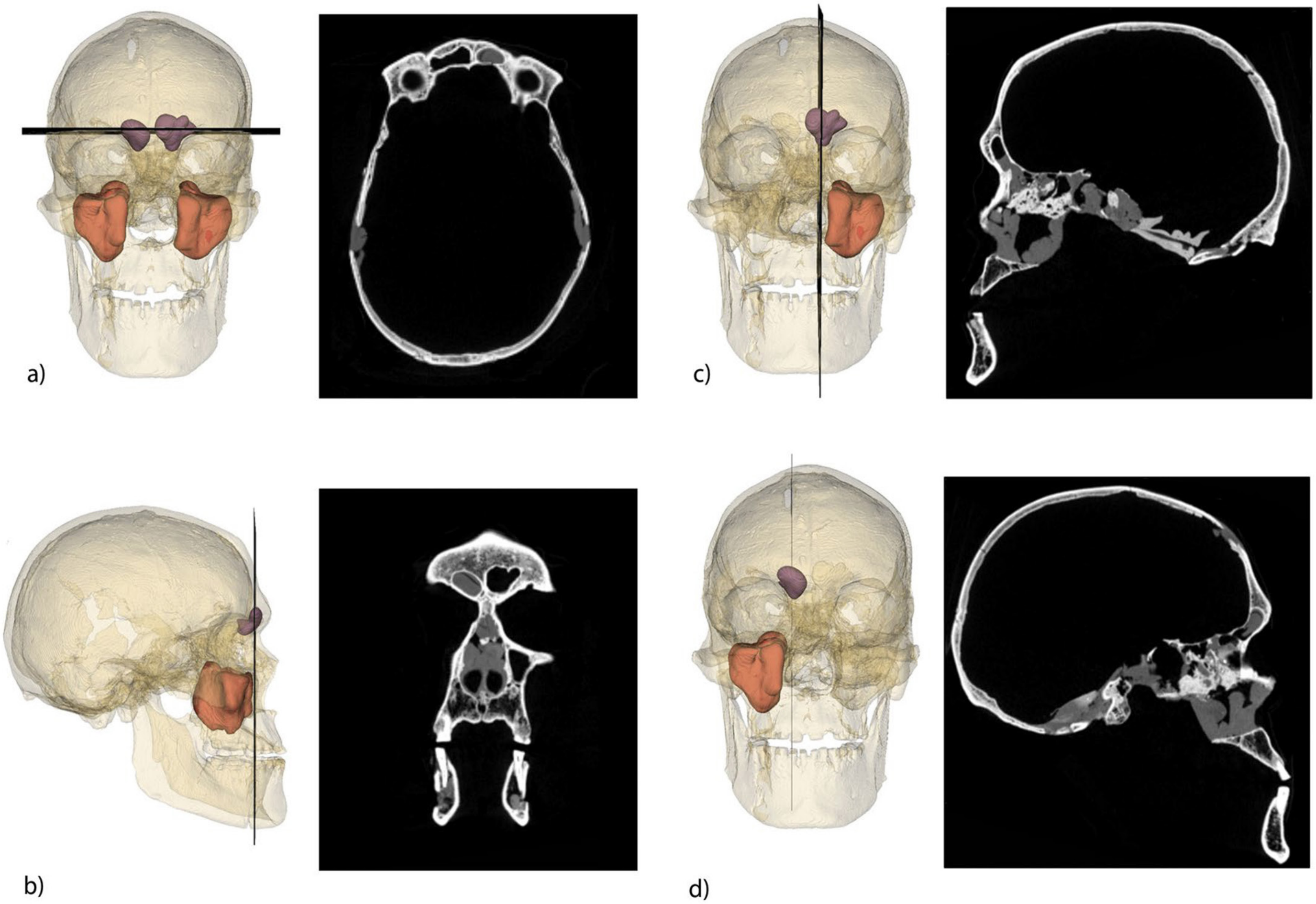

Figure 3. Detailed CT-slices illustrating various views of the frontal sinus: (a) axial slice for maximum breadth; (b) coronal slice for maximum area; (c) sagittal slice for maximum anterior-posterior depth of left sinus; and, (d) sagittal slice for maximum anterior-posterior depth of right sinus. Notice asymmetry of right versus left frontal sinus (see text).

Several studies hypothesize that the maxillary sinus is simply a byproduct of nasal cavity size, such that larger, particularly wider, nasal cavities result in concomitantly smaller maxillary sinuses and vice versa. As such, while it has been argued that while nasal cavity size directly reflects climatic pressures, the maxillary sinus indirectly correlates with climate (e.g., Shea 1977; Rae et al. 2003). Several studies (Holton et al. 2013; Maddux et al. 2017; Noback et al. 2011) indicate that individuals from cold-dry climates possess relatively taller and narrower nasal cavities. This functionally-relevant morphology serves to increase both surface area of the respiratory system and adds turbulence to inspired air, both of which aid in warming and humidifying inspired air to protect lung tissues from desiccation (see Maddux et al. 2017). The maxillary sinuses, thus, have been hypothesized to act as zones of accommodation, "allowing" these phylogenetic and ontogenetic changes in nasal form that would otherwise be difficult if the surrounding areas were filled with trabecular bone (see Holton et al. 2013; Maddux and Butaric 2017). While previous studies indicate a correlation between climate, nasal form, and maxillary sinus volume among some modern human populations (Butaric 2015; Holton et al. 2013; Shea 1977), more recent studies suggest a stronger signal particularly between climate, nasal form, maxillary sinus *shape,* and an expanded maxillary-zygomatic region (Butaric and Maddux 2016; Maddux and Butaric 2017); further, these recent studies suggest that maxillary sinus shape likely reflects a role in accommodating multiple areas of the face, not just nasal cavity form alone.

With this in mind, the large, visually taller and wider, maxillary sinuses of Sungir-1 may relate to an adaptation to the colder-harsher environments of Eastern Europe during the Upper Paleolithic. However, it should be noted that it is maxillary sinus *shape*—or how that volume is distributed—that would reflect climatic adaptations (see Butaric 2015; Ito et al. 2015; Maddux and Butaric 2017; Noback et al. 2016), which likely explains the lack of differentiation of sinus volume among the modern human groups in Figure 4. Thus, more detailed studies incorporating more advanced 3D geometric shape analyses of the maxillary sinuses are needed (and currently underway) to fully understand the position of Sungir-1 relative other *Homo* specimens and the potential influence of climate.

TABLE 1. MAXILLARY AND FRONTAL SINUS VOLUMES AND UPPER FACIAL BREADTH FOR SEVERAL UPPER PALEOLITHIC (UP) AND MIDDLE PLEISTOCENE (MP) *HOMO* SPECIMENS AND MODERN HUMAN SAMPLES FROM THE LATE HOLOCENE (LH) WITH PUBLISHED DATA.*

	Geographic Region	Time Period	Maxillary Sinus Volume cm³ (scaled)			Frontal Sinus Volume cm³ (scaled)			Upper Facial Breadth cm	References
			n	Averaged	Range	*n*	Combined	Range		
Fossils										
Sungir-1	Europe/Eurasia	UP	-	25.41 (0.26)	-	-	3.74 (0.13)	-	11.50	this study
Mladeč-1	Europe	UP	-	18.78 (0.24)	-	-	-	-	11.00	this study
Guattari-1	Europe	MP	-	40.87 (0.31)	-	-	7.77 (0.18)	-	11.10	Rae et al. 2011
Forbes' Quarry-1	Europe	MP	-	22.93 (0.26)	-	-	7.34 (0.18)	-	10.80	Rae et al. 2011
Broken Hill	South Africa	MP	-	28.24[a] (0.23)	-	-	25.63 (0.22)	-	13.30	Spoor & Zonneveld 1999
Tabun	West Asia	MP	-	-	-	-	4.64 (0.16)	-	10.7	Rae et al. 2011
Krapina 3	Europe	MP	-	-	-	-	9.55 (0.19)	-	11.1	Rae et al. 2011
Modern Humans (this study)										
Croatians	Europe	LH	*20*	14.32 (0.24)	7.46–21.03 (0.19–0.29)	*20*	5.22[b] (0.14)[b]	0–21.39 (0–0.26)	10.32	Butaric 2015; this study
West Africans	West Africa	LH	*20*	13.26 (0.23)	8.44–25.64 (0.20–0.28)	*21*	6.07 (0.17)	0.57–13.46 (0.08–0.23)	10.47	Butaric 2015; this study
Mongolians	Central Asia	LH	*19*	15.93 (0.24)	11.35–25.22 (0.21–0.27)	*19*	4.11 (0.14)	0.24–10.85 (0.06–0.20)	10.53	Butaric 2015; this study
Modern Humans (previous publications)										
Lithuanians	Europe	LH	*26*	-	9.13–35.46	*26*	-	0.39–23.21	8.7–10.45	Rae et al. 2011
European-derived	Europe	LH	*26*	16.4	9.91–27.52	-	-	-	-	Fernandes 2004
European-derived	Europe	LH	*20*	17.68	11.96–30.94	-	-	-	-	Holton et al. 2013
Nigerians	West Africa	LH	*24*	13.29	-	*24*	7.79	-	-	Amusa et al. 2011
African-derived	West Africa	LH	*20*	11.34	3.29–23.00	-	-	-	-	Holton et al. 2013
Nubians	North Africa	LH	*20*	13.98[c]	-	*35*	2.74[c]	-	9.94	Noback et al. 2016
Egyptians	North Africa	LH	*19*	14.57	9.59–20.62	-	-	-	-	Butaric 2015
Zulu	South Africa	LH	*17*	11.04	4.68–20.56	-	-	-	-	Fernandes 2004
Khoi San	South Africa	LH	*17*	11.33	5.71–17.37	-	-	-	-	Butaric 2015
Malays	Southeast Asia	LH	*19*	15.29	8.24–21.58	-	-	-	-	Butaric 2015
Iranians	West Asia	LH	*17*	14.26	8.82–19.94	-	-	-	-	Butaric 2015
Buriats	Central Asia	LH	*20*	18.52	9.52–29.09	-	-	-	-	Butaric 2015
Greenlanders	Arctic	LH	*17*	15.35[c]	-	*32*	0.66[c]	-	10.08	Noback et al. 2016
Alaskans	Arctic	LH	*20*	15.16	7.69–22.19	-	-	-	-	Butaric 2015

*Unless indicated, maxillary sinus volumes are averaged right and left sides, while frontal sinus volumes are combined right and left sides. For this study, hominins and modern human groups present with absolute and size-corrected volumes scaled by upper facial breadth (located below absolute values in parentheses); see text for scaling process.

[a]Taken as half of the combined right and left maxillary sinus (56.47cm³), as presented in Spoor and Zonneveld (1999).

[b]Two Croatians did not exhibit a frontal sinus; 0 values were not factored into the calculated averages.

[c]Unclear from original publication whether these values are averaged or combined right and left side.

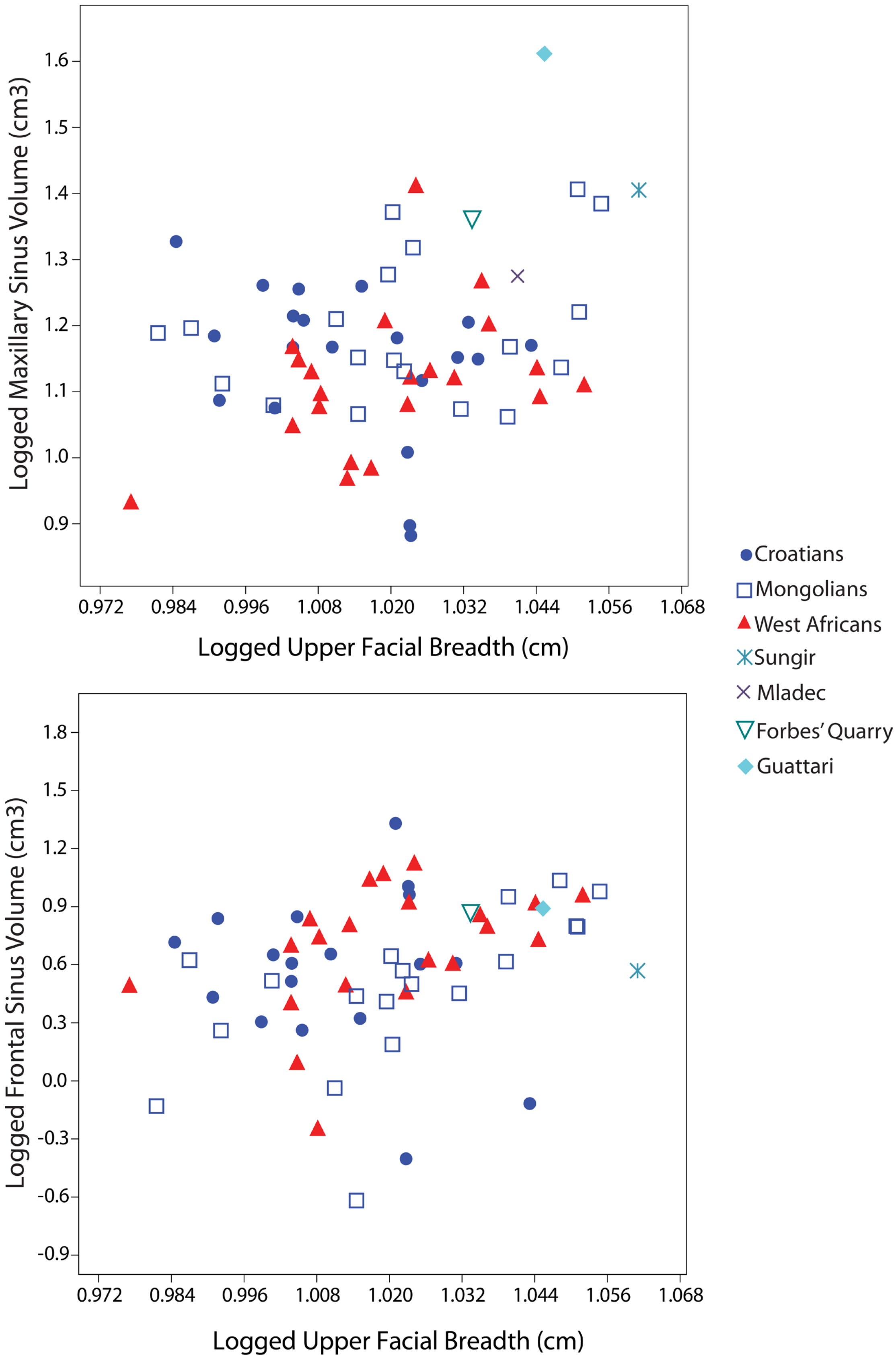

Figure 4. Bivariate plots of logged maxillary sinus (top) and frontal sinus (bottom) volumes versus upper facial breadth for several fossil hominins and modern humans. Note, Broken Hill was an extreme outlier in terms of upper facial breadth, and was removed from both graphs for better visualization of the remaining groups.

In terms of frontal sinus morphology, despite a well-developed supraorbital region Sungir-1 possesses relatively simplified frontal sinuses that fall well within the range of several modern human samples. In attempting to explain frontal sinus morphology, early studies also suggested a climatic pattern, such that populations in extreme cold possess small, often absent, frontal sinuses to protect the brain and surrounding organs from cold air (Hanson and Owsley 1980; Koertvelyessy 1972). In conjunction with the smaller frontal sinuses of Sungir-1, such an assertion may initially seem to suggest evidence of cold-adaptation among these specimens. However, as previous studies largely focused on radiographs, which do not reveal small sinuses and cannot delineate the inferior aspects of the frontal sinus, true incidences of frontal sinus aplasia are largely unknown as are the underlying reasons for these developmental anomalies (but see Noback et al. 2016). Alternatively, Zollikofer et al. (2008: 1513) posit that frontal sinus morphology simply relates to the differential growth processes of surrounding regions, such that superior growth relates to the spatial relationship between the orbits and frontal squama while anterior growth relates to spatial relationships of the neurocranium, face, and browridge. However, robust studies analyzing ontogenetic processes of either the frontal and maxillary sinuses in relation to the growing external architecture among globally diverse samples of modern humans (and fossil crania) are largely lacking in the literature; as such, the hypotheses above remain untested. Additionally, this does not necessarily explain the pattern of variation whereby frontal sinus size does not follow supraorbital size in many specimens—individuals with extremely large browridges still house small, or even absent, frontal sinuses. Several studies (e.g., Witmer 1997; Zollikofer and Weissmann 2008) argue that paranasal sinuses are "opportunistic pneumatizers"—invading neighboring bone whenever possible. However, neither theoretical reasoning nor empirical testing has provided support into why sinuses do not always behave in this way. For example, why do the sinuses of some individuals remain smaller, failing to take the "opportunity" to pneumatize as much bone as possible?

Indeed, despite centuries of research, the underlying reasons for population variation in terms of paranasal sinus patterning (in terms of absence/presence and in size and shape), both in relation to climate and in general, remain heavily debated in the literature (see Blanton and Biggs 1969; Keir 2009; Rae and Koppe 2004 for reviews). This is partially due to the variability found among maxillary sinus and, particularly, frontal sinus morphology, which has made it difficult to support or negate structural and functional hypotheses attributed to paranasal pneumatization. Further, while it is generally suggested that the sinuses only play a passive role in facial development, there is some indication that they may possess a developmental potential of their own (Koppe et al. 1994, 1996; Libersa et al. 1981). A large portion of the problem in interpreting paranasal sinus variation is that most researchers (current first author included) investigating paranasal sinus form among diverse populations have focused on the adult-state (e.g., Butaric 2015; Butaric and Maddux 2016; Fernandes 2004; Holton et al. 2013; Koertvelyessy 1972; Maddux and Butaric 2017; Noback et al. 2011; Rae et al. 2011; Shea 1977; Zollikofer et al. 2008). Additional studies focusing on paranasal sinus variation among sub-adults from diverse modern human samples and fossil specimens are needed to further our understanding of how internal facial structures may (or may not) play a role in the ontogenetic and phylogenetic processes shaping current patterns of modern human craniofacial variation.

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