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Allometric scaling of infraorbital surface topography in *Homo*

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ABSTRACT

Infraorbital morphology is often included in phylogenetic and functional analyses of *Homo*. The inclusion of distinct infraorbital configurations, such as the "canine fossa" in *Homo sapiens* or the "inflated" maxilla in Neandertals, is generally based on either descriptive or qualitative assessments of this morphology, or simple linear chord and subtense measurements. However, the complex curvilinear surface of the infraorbital region has proven difficult to quantify through these traditional methods. In this study, we assess infraorbital shape and its potential allometric scaling in fossil *Homo* ($n = 18$) and recent humans ($n = 110$) with a geometric morphometric method well-suited for quantifying complex surface topographies. Our results indicate that important aspects of infraorbital shape are correlated with overall infraorbital size across *Homo*. Specifically, individuals with larger infraorbital areas tend to exhibit relatively flatter infraorbital surface topographies, taller and narrower infraorbital areas, sloped inferior orbital rims, anteroinferiorly oriented maxillary body facies, posteroinferiorly oriented maxillary processes of the zygomatic, and non-everted lateral nasal margins. In contrast, individuals with smaller infraorbital regions generally exhibit relatively depressed surface topographies, shorter and wider infraorbital areas, projecting inferior orbital rims, posteroinferiorly oriented maxillary body facies, anteroinferiorly oriented maxillary processes, and everted lateral nasal margins. These contrasts form a continuum and only appear dichotomized at the ends of the infraorbital size spectrum. In light of these results, we question the utility of incorporating traditionally polarized infraorbital morphologies in phylogenetic and functional analyses without due consideration of continuous infraorbital and facial size variation in *Homo*. We conclude that the essentially flat infraorbital surface topography of Neandertals is not unique and can be explained, in part, as a function of possessing large infraorbital regions, the ancestral condition for *Homo.* Furthermore, it appears likely that the diminutive infraorbital region of anatomically modern *Homo sapiens* is a primary derived trait, with related features such as depressed infraorbital surface topography expressed as correlated secondary characters.

Introduction

The infraorbital region has long played a prominent role in the determination of systematic relationships and functional interpretation in *Homo*. This is particularly evident in the case of Neandertals and anatomically modern *Homo sapiens* (AMHS), each of which has been argued to possess derived infraorbital anatomy. The AMHS infraorbital region is generally characterized as distinctly depressed or exhibiting a "canine fossa"[1](Stringer et al., 1984; Stringer, 1985; Maureille, 1994; Lahr and Wright, 1996; Arsuaga et al., 1997, 1999; Bermúdez de Castro et al., 1997; Lieberman, 1998; Lieberman et al., 2002; Trinkaus, 2006). Conversely, the infraorbital region of Neandertals is often described as lacking a depression, and instead possessing a "puffy," inflated, or expanded infraorbital

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[1] For a detailed discussion of the problematic use of the term "canine fossa" see Maureille (1994). We employ the term here as defined by Arsuaga et al. (1999): "…an extended infraorbital depression that affects most, if not the entire zygomatic process of the maxilla. We thus distinguish the canine fossa from other depressions, such as a vertical groove inferior to the infraorbital foramen (this furrow-like sulcus, which would lie lateral to the canine jugum, was called the 'sulcus maxillaris' by Weidenreich, 1943). Our definition of canine fossa is coincident with the infraorbital depression *sensu* Maureille (1994) which produces an horizontal incurvation as well as an incurvation of the zygomaticoalveolar crest."

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morphology (Mann and Trinkaus, 1974; Heim, 1976; Smith, 1983; Stringer et al., 1984; Rak, 1986; Trinkaus, 1987, 2006; Minugh-Purvis, 1993; Maureille, 1994; Arsuaga et al., 1997, 1999; Wolpoff, 1999; Ponce de León and Zollikofer, 2001; Harvati, 2007).

The distinction between the Neandertal and the AMHS infraorbital region dates as far back as 1868, when Thomas Huxley called attention to the unusual convex configuration of the Gibraltar 1 infraorbital region in comparison to the typically concave infraorbital region of AMHS (Broca, 1869, 1878; Sollas, 1908). Huxley thus began a long standing convention of treating the convex "inflated" infraorbital region of Neandertals and the concave "canine fossa" of AMHS as dichotomized characterizations of infraorbital surface topography. However, since most researchers now accept AMHS and Neandertals as separate evolutionary lineages, it becomes important to assess whether the infraorbital morphologies of both Neandertals and AMHS are each separately derived from the morphologies present in the ancestral population from which each lineage arose from which each lineage arose (i.e. Middle Pleistocene *Homo*). This is particularly necessary as incipient expression of these distinct infraorbital features is commonly employed to infer systematic relationships within the genus *Homo*. For example, the widely accepted relationship between European *Homo heidelbergensis* and later Neandertals is based, in part, on a temporal morphocline in infraorbital flatness (Arsuaga et al., 1993, 1997; Rightmire, 1998; Bermúdez de Castro et al., 2003). Similarly, the proposed ancestral position of *Homo antecessor* to AMHS centers primarily on the presence of a canine fossa in the ATD6-69 specimen (Bermúdez de Castro et al., 1997, 1999a,b, 2003; Arsuaga et al., 1999).

An important issue in studies of infraorbital morphology has been the difficulty of assessing topographical contours across the entire infraorbital region. Sergi (1947) implemented a qualitative approach that involved visually assessing infraorbital curvature in three planes: sagittal (*incurvatio sagittalis*), coronal (*incurvatio horizontalis*), and transverse (*incurvatio inframalaris*). In his approach, specimens exhibiting curvature in all three planes (i.e., AMHS) were deemed "flexion" types, while specimens lacking curvature (i.e., Neandertals) were labeled "extension" types. Later, researchers such as Hrdlička (1952), Montagu (1960), De Villiers (1968), and Thorne (1976) implemented qualitative approaches for assessing infraorbital surface topography by sorting specimens into discrete shape categories. A number of additional infraorbital features have also been qualitatively coded (Table 1), including inferior orbital rim morphology, zygomaxillary sutural ridge prominence, zygomaticoalveolar crest curvature, malar orientation, and malar shape (Weidenreich, 1943; Sergi, 1947; De Villiers, 1968; Lahr, 1994; Lieberman, 1995; Lahr and Wright, 1996). When applied to the fossil record, these qualitative methodologies have generally supported an infraorbital dichotomy between Neandertals and AMHS, but have struggled to reach a consensus regarding the nature of the infraorbital morphologies present in Middle and Early Pleistocene *Homo* (e.g., Rak, 1986 vs. Sohn and Wolpoff, 1993). Moreover, while often informative and easily implemented, the subjective nature and proclivity for high inter- and intra-observer error in qualitative coding is widely acknowledged (Landis and Koch, 1977; Molto, 1979; De Stefano, 1983; Rösing, 1984; De Stefano et al., 1984; Espeland and Handelman, 1989).

In contrast, most metric methodologies attempting to assess size and shape of the infraorbital region have focused on measuring the maximum depth of infraorbital depression (Table 2). Many of these, such as those of Rideau (1968), Larnach and Macintosh (1970), and Lieberman et al. (2002, 2004) have involved the use of chord and subtense measures. These methods generally involve striking a chord from the landmark alare to a parallel point (relative to the Frankfurt Horizontal plane) on the zygomaxillary suture, and measuring the maximum subtense from this chord to the infraorbital surface. Alternatively, Maureille and Houët (1997a) measured the degree of the angle formed at the junction of a chord from alare to the middle of the infraorbital region (the exact midpoint between alare and the parallel point on the zygomaxillary suture) and a chord from the midpoint to the point on the zygomaxillary suture. In their analysis, AMHS generally possessed infraorbital angles of approximately 155°, while Neandertals possessed angles near or slightly greater than 180°. While these metric techniques provide a less subjective approach to assessing infraorbital depression than discrete methods, they are still considerably restricted as they assess curvature of the infraorbital region exclusively in a single transverse plane. Thus, these methods fail to

Table 1
Principal qualitative studies of infraorbital region morphology.

Terminology	Coding	Author
Canine fossa	Present/absent	Lieberman et al. (2002)
Rounding of infero-lateral margin of the orbit (RO)	Present/absent	Lahr and Wright (1996)
Infraorbital margin Malar orientation Malar shape Zygomaxillary suture ridge *Incisura malaris*	Rolled/steep Lateral/anterior Round/square Present/absent Present/absent	Lieberman (1995)
Canine fossette	Four categories of depth (absent, weak, average, strong)	Maureille (1994)
Canine fossa	Present/absent	Stringer et al. (1984)
Infraorbital fossa	Five categories of depth (absent, slight, medium, deep, very deep)	Thorne (1976)
Infraorbital excavation	Four categories of curvature in three planes: (inflated, slight moderate, marked)	De Villiers (1968)
Suborbital fossa	Three categories of depth (none, slight, marked)	Montagu (1960)
Suborbital fossa	Three categories of depth (slight, medium, pronounced)	Hrdlička (1952)
Incurvatio sagittalis *Incurvatio horizontalis* *Incurvatio inframalaris*	Present/absent	Sergi (1947)
Sulcus maxillaris	Present/absent	Weidenreich (1943)

Table 2
Principal quantitative studies assessing infraorbital region morphology.

Terminology	Measurement	Author
Canine fossa depth	Maximum subtense to the infraorbital surface from a chord between zygomaxillare and alare	Lieberman et al. (2002, 2004)
Infraorbital angle	Angle created by the vertices from alare to infra-orbitaire, and from zygomaxillaire anterior to infra-orbitaire	Maureille and Houët (1997a)
Infraorbtial fossa depth	Maximum subtense to the infraorbital surface from a chord between the midpoint of the zygomaxillary suture and a point on the lateral nasal margin "…almost at the level of the nasal floor"	Larnach & Macintosh (1970)
Suborbital fossa depth	Maximum subtense to the infraorbital surface from a chord between alare and a parallel point on zygomaxillary suture	Rideau (1968)
Suborbital fossa depth	Chord 1: basion to alare Chord 2: basion to "lateral point" (anteriormost point on zygomatic) Chord 3: basion to "medial point" (posteriormost point on infraorbital surface) Depth = ([ba-ala] + [ba-lat]/2) − (ba-med)	Birkby (1963)