



Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

Oblique human symphyseal angle is associated with an evolutionary rate-shift early in the hominin clade

James D. Pampush^{a, b, *}, Jill E. Scott^{c, d}, Chris A. Robinson^e, Lucas K. Delezenne^f

^a Department of Exercise Science, High Point University, High Point, NC, USA

^b Department of Physician Assistant Studies, High Point, NC, USA

^c Department of Anthropology, The University of Iowa, Iowa City, IA, USA

^d Department of Sociology and Anthropology, Metropolitan State University of Denver, CO, USA

^e Department of Biological Sciences, Bronx Community College, City University of New York, Bronx, NY, USA

^f Department of Anthropology, University of Arkansas, Fayetteville, AR, USA

ARTICLE INFO

Article history:

Received 9 March 2017

Accepted 21 June 2018

Available online xxx

Keywords:

Phylogenetic trend

'AUTEUR' (R package)

Preoral processing

Mandibular integration

Hypofunction hypothesis

Spandrel

ABSTRACT

The rate of change in primate mandibular symphyseal angles was modeled with particular aim of locating a rate-shift within the hominin clade. Prior work noted that the human symphyseal angle must have experienced a rapid rate of change in order to assume the modern human form, suggestive of the non-random work of natural selection. This study indicates that the rate of symphyseal evolution rose dramatically between *Australopithecus anamensis* and *Australopithecus afarensis* and continued throughout the diversification of the hominin clade. Noting the timing of this event, we speculate as to what ecological factors could have been at play in driving this rearrangement of the anterior mandible, contributing to the eventual appearance of the human chin.

© 2018 Elsevier Ltd. All rights reserved.

1. Introduction

The definition of the 'chin' remains slippery as there are disagreements over its essential characteristics (Pampush and Daegling, 2016a). Some argue that for a mandible to be in possession of a chin, there must be a raised 'falsum' ('⊥') produced through an interaction among tubercles, ridges, and depressions on the anterior surface of the symphysis (e.g., Schwartz and Tattersall, 2000). Others have opted for more simplistic definitions of chins as bony promontories on the anteroinferior mandible (e.g., Weidenreich, 1936; Daegling, 1993a), resulting in a anteriorly oriented symphysis. The bony projection (with and without a full falsum) contributes to the modern human mandible's unique shape, as it typically causes the lower border of the anterior symphysis to protrude beyond the anterior dentition. This unusual bony arrangement has captured the attention of biological anthropologists for over a century, and has been the focus of a considerable amount of research effort (for review, see Pampush and Daegling, 2016a). The reasons for this are threefold. First, as noted above,

there is substantial disagreement over what features constitute a 'chin,' therefore leading to debates over which taxa or specimens possess chins (cf. Wolpoff et al., 1981; Lam et al., 1996; Wolpoff, 1996; Schwartz and Tattersall, 2000). Second, apart from some claims that a few Neanderthal specimens possess chins (see above), there is general agreement that anatomically modern humans (*Homo sapiens*) are the only hominin species (living or extinct) to consistently exhibit 'true' chins (e.g., Robinson, 1914; DuBrul and Sicher, 1954; Daegling, 1993a; Dobson and Trinkaus, 2002; Pampush and Daegling, 2016a). Thus, there has been a persistent effort to understand this uniquely modern human feature, partly in anticipation of the insight it might provide into the evolution of our species (Daegling, 1993a; Pampush and Daegling, 2016a). The third reason for the high level of attention is that the cause underpinning the evolution of the chin has generally resisted identification, drawing additional scrutiny due to its enigmatic status (for review, see Daegling, 1993a; Schwartz and Tattersall, 2000, 2010; Pampush and Daegling, 2016a).

There have been numerous attempts to determine whether chins are adaptive, and therefore the product of natural selection. To date, there are three prominent adaptive hypotheses for the chin: (1) The 'masticatory stress hypothesis' proposes that chins defray mechanical forces concentrated at the symphysis during

* Corresponding author.

E-mail address: jpampush@highpoint.edu (J.D. Pampush).

mastication (Hylander, 1985; Daegling, 1993a; Gröning et al., 2011); (2) The ‘speech hypothesis’ posits that a chin is required as an anchor for the tongue during word-sound articulation (Robinson, 1914; Hooton, 1942; Coon, 1962; Ichim et al., 2006, 2007), or buffers the symphysis from minor stresses created during jaw opening (Daegling, 2012); (3) The ‘sexual selection hypothesis’ argues that chins are a sexual ornament used to judge mates (Hershkovitz, 1970; Thayer and Dobson, 2010). While each of these hypotheses has had some prior support and continues to have superficial and intuitive appeal, each has faltered on theoretical and/or empirical grounds (Pampush and Daegling, 2016a).

A second class of hypotheses has attempted to explain the chin as a non-adaptive byproduct of selection on other structures (i.e., a spandrel sensu Gould and Lewontin, 1979) of the mouth, face, or neck (e.g., DuBrul and Sicher, 1954; Krantz, 1980; Coquerelle et al., 2013a,b), incidentally producing chins as a residual consequence. Developing experiments and investigations examining this class of hypotheses has proven difficult for two reasons. First, as chins are frequently considered to be an evolutionary singularity (see review in Pampush and Daegling, 2016a), they do not lend themselves to examinations using the comparative approach, which is evolutionary biology’s dominant investigatory paradigm (Bock, 1980; Harvey and Pagel, 1991; Nunn, 2011; Nunn and Zhu, 2014). Second, this group of explanations classes the chin as an incidental byproduct, producing an epistemological asymmetry in that chance byproducts are resistant to confirmation or rejection, while this same problem does not apply to the non-random products of selection (Mayr, 1983). Three of the most prominent non-adaptive proposals for the human chin are: (1) ‘The hypofunction hypothesis,’ which posits that chins are the byproduct of dental and alveolar reduction (Gould, 1977; Gould and Lewontin, 1979; Cartmill and Smith, 2009); (2) The ‘self-domestication hypothesis,’ which proposes that chins are the products of a generalized facial shrinking brought about by selection for tameness in humans (Cieri et al., 2014); and finally, (3) the ‘airway impingement hypothesis’ posits that the lower border of the jaw is integrated with the need for space in the airway; impingement of the airway from short faces and bipedality is alleviated through drawing the tongue forward and producing a chin (DuBrul and Sicher, 1954; Coquerelle et al., 2013b, 2017).

The typical way the spandrel hypotheses have been approached is via developmental integration investigations and experiments. For example, Coquerelle et al. (2013a,b, 2017) in a series of investigations using fetal CT-scans showed developmental timing coordination between the pharyngeal space and anterior mandible. They interpreted these findings to mean that keeping the human pharynx open is done through pulling the origin of the genio-glossus forward. Others have conducted experiments on small mammals by feeding them soft diets in attempts to induce ‘hypofunction’ and produce a chin, but these experiments have been unsuccessful (Lieberman et al., 2004; Ravosa et al., 2007). In a set of more invasive experiments, Riesenfeld (1969) and Biggerstaff (1973) surgically extracted lower incisors and severed the muscles of mastication in developing rodents, inducing structures resembling chins. Despite coaxing chins out of rats and hamsters, most have regarded the invasive nature of the Riesenfeld (1969) and Biggerstaff (1973) studies as not accurately simulating the proposed evolutionary conditions invoked by the hypofunction hypothesis (Pampush and Daegling, 2016a).

An alternative approach to examining ontogenetic patterns, and one which more explicitly considers evolution apart from developmental plasticity, is to examine morphological relationships and trends (sensu McNamara, 1982; McShea, 1994, 2000) within the hominin lineage. While the ‘true’ chin (see Schwartz and Tattersall, 2000) is a complex feature involving a midsagittal ridge of bone

and two adjacent tubercles forming a raised ‘falsum’ (‘L’) on the anterior surface of the mandible, many of these discrete traits do not lend themselves well to examining phyletic trends. That said—while it is acknowledged that the chin is a complex feature—one important aspect of chin possession is the more obtuse angle formed between the symphyseal plane, and the alveolar plane (i.e., the symphyseal angle). Arguments can be made that an individual or specimen lacking sufficiently prominent mental tubercles, or conversely, incisura mandibulae anterior, may or may not have a chin; but very few would argue that an individual possessing a sub-90° symphyseal angle possesses a chin. Therefore, while not complete, the measure does a sufficient job of assessing ‘chin possession’ (Pampush, 2015), and ‘incipient’ chin conditions occur with symphyseal angles near 90° (e.g., Wolpoff, 1980; Smith, 1982; Schwartz and Tattersall, 2000). While abstract, this continuous trait allows for an examination of evolutionary trends related to the eventual appearance of human chins.

Functional investigations including the orientation of the symphysis (i.e., symphyseal angle) have linked it to countering ‘wish-boning’ loads in anthropoid jaws (Hylander, 1985; Ravosa, 1990; Daegling, 1993a,b, 2001; Ravosa, 1996, 2000; Daegling and McGraw, 2009); more acute angles are thought to provide a more optimal geometry for defraying masticatory stress at the symphysis. In more taxonomically focused investigations, symphyseal angle has been noted to be more obtuse (i.e., a profile more vertical and less mesiodistally long) in apes as compared to monkeys (e.g., Weidenreich, 1936; Andrews, 1971; White et al., 2000). White et al. (2000) questioned the utility of symphyseal angle for taxonomic analyses citing considerable intraspecific variation in the trait. However, when assessed for phylogenetic signal across the primate clade, Pampush (2015) showed there to be significant taxonomic trait clustering (i.e., high phylogenetic signal). This suggests that while symphyseal angle alone may not be useful for identifying a particular specimen to the species level, there is a high degree of correlation within lineages and between closely-related populations. The high level of interspecific heritability indicates that examinations of phylogenetic trends in symphyseal angle may be meaningful (even if the precise mechanisms producing this heritability are unknown; see Kamilar and Cooper, 2013).

The tendency towards a more vertical symphysis among apes is further developed within the hominin lineage (White, 1977; Skinner et al., 2006), initially appearing with the transition from *Australopithecus anamensis* to later forms like *Australopithecus afarensis* (Ward et al., 1999; Kimbel et al., 2006). Although *A. afarensis* is known to be variable in its symphyseal morphology (White and Johanson, 1982; Robinson, 2003), one of the diagnostic features distinguishing it from *A. anamensis* is a considerably derived snout and anterior mandible, both of which exhibit more vertical (orthognathic) profiles (Kimbel et al., 2004, 2006; Kimbel and Deleze, 2009). Among the hominin taxa currently dated to later than *A. afarensis*, the gross morphology of the hominin mandible—as compared to living great apes—is generally characterized as being shorter (mesiodistally), with a parabolic and broader (mediolaterally) dental arcade, possessing a more vertically oriented symphysis, smaller anterior dentition and attendant alveolus (Weidenreich, 1936; Hooton, 1942; DuBrul and Sicher, 1954; Coon, 1962; Daegling, 1989, 2001; Tattersall, 2000; Stelzer et al., 2017). These same features are further exaggerated in the transition from *Australopithecus* to *Homo* (Wolpoff, 1979; Dobson and Trinkaus, 2002). Daegling (1993a) had previously noted that, when considered in concert, these gross mandibular features are consistent with a reduction in masticatory stress concentration at the hominin symphysis. Therefore, observations on the general trends in symphyseal angle in hominin mandibular morphology may be consistent with some of the spandrel hypotheses. Thus,

Download English Version:

<https://daneshyari.com/en/article/8959446>

Download Persian Version:

<https://daneshyari.com/article/8959446>

[Daneshyari.com](https://daneshyari.com)