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Craniofacial modularity, character analysis, and the evolution of the premaxilla in early African hominins

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ABSTRACT

Phylogenetic analyses require evolutionarily independent characters, but there is no consensus, nor has there been a clear methodology presented on how to define character independence in a phylogenetic context, particularly within a complex morphological structure such as the skull. Following from studies of craniofacial development, we hypothesize that the premaxilla is an independent evolutionary module with two integrated characters that have traditionally been treated as independent. We test this hypothesis on a large sample of primate skulls and find evidence supporting the premaxilla as an independent module within the larger module of the palate. Additionally, our data indicate that the convexity of the nasoalveolar clivus and the contour of the alveolus are integrated within the premaxilla. We show that the palate itself is composed of two distinct modules: the FNP-derived premaxillae and the mxBA1-derived maxillae and palatines. Application of our data to early African hominin facial morphology suggests that at least three separate transitions contributed to robust facial morphology: 1) an increase in the size of the post-canine dentition housed within the maxillae and palatines, 2) modification of the premaxilla generating a concave clivus and reduced incisor alveolus, and 3) modification of the zygomatic, shifting the zygomatic root and lateral face anteriorly. These data lend support to the monophyly of *Paranthropus boisei* and *Paranthropus robustus*, and provide mounting evidence in favor of a *Paranthropus* clade. This study also highlights the utility of applying developmental evidence to studies of morphological evolution.

Introduction

Almost all comparative research in evolutionary biology, from broad studies of biogeography to detailed analyses of character adaptation, relies on having an accurate phylogeny. Although there has been debate over the reliability of parsimony-based phylogenetic analyses (Collard and Wood, 2000; Strait and Grine, 2004), parsimony analysis remains the most common method of inferring phylogeny from morphological data. One of the fundamental assumptions of the phylogenetic algorithm is that the characters used in the analysis are evolutionarily independent (Eldredge and Cracraft, 1980; De Queiroz, 1993; Shubin and Wake, 1996; Emerson and Hastings, 1998; Abouheif, 1999; McCollum, 1999; O'Keefe and Wagner, 2001; Schwenk, 2001; Strait, 2001). However, simply because characters have been identified as anatomically distinct does not mean that they are developmentally or evolutionarily independent, as distinct anatomical characters could be under pleiotropic control. In such a case, phylogenetic analyses would be biased towards identifying a group of characters as synapomorphies when they are actually not independent, and towards resolving the phylogeny in favor of a monophyletic relationship for the taxa that shared those characters. Although identifying character independence is a significant potential problem for phylogenetic analysis, there is currently no accepted method for identifying instances of the problem, or in addressing its potential influence on the results of phylogenetic analysis.

In this study we specifically address the issue of evaluating character independence for phylogenetic analyses by applying a developmental framework to generate a priori hypotheses of

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integration and modularity in the skull and then use geometric morphometric data to test these hypotheses. Specifically, we evaluate modularity of the premaxilla within the cranium and we test for integration of two characters on the premaxilla that have been treated as independent evolutionary characters: the nasoalveolar clivus and the anterior alveolar arcade. Finally, we apply our findings of modularity and integration to character independence in the mid-face of early African hominins.

Early hominin facial anatomy

Early hominin facial evolution is characterized by two general patterns that are thought to reflect differences in dietary adaptations (Broom and Robinson, 1950a, 1952; Robinson, 1954; Tobias, 1967; Rak, 1983, 1985; Kimbel et al., 1988) (Fig. 1). Great apes and humans, as well as *Australopithecus afarensis* and *Homo habilis*, share similar midfacial morphology, with the nasoalveolar clivus and palate forming a broad, convex radius (Fig. 1A; Rak, 1983). In contrast, several other species of early hominin, including *Paranthropus robustus* from southern Africa and *Paranthropus boisei* of eastern Africa, have robust midfacial morphology, manifested by a concave or flat nasoalveolar clivus and a posteriorly shifted neurocranium that is modified by postorbital constriction from massive temporalis muscles (Fig. 1A–B). Additionally, robust early hominins have extremely large molars, far beyond the range of any extant primate, which are associated with a modified palate that is shortened anteriorly and retracted towards the neurocranium relative to the rest of the face (Fig. 1B–C). These craniodental features have supported the inference of a specialized diet emphasizing foods that require significant mastication (Broom and Robinson, 1950a,b; Broom and Robinson, 1952; Tobias, 1967; Rak, 1983, 1985; Kimbel et al., 1988).

While there is general agreement about the craniodental distinctiveness of robust species, there remains significant debate whether this distinctiveness is synapomorphic or homoplastic. Resolution of this issue depends largely on uniting disparate interpretations of the independence of traits functionally related to mastication. In this regard, two competing hypotheses have generally been proposed to explain the evolution of the facial anatomy of robust hominins. Based on a functional analysis of the faces of early hominins, Rak (1983, 1985) characterized two distinct anatomical shifts that he argued were responsible for robust facial morphology. He posited that characters such as 1) the position of the zygomatic root relative to the tooth row, 2) the topography of the inferior nasal entrance, and 3) the relatively concave central face around the nasal aperture (facial dishing), were all part of a coordinated change in facial structure towards advancement of the peripheral face. This was distinct from the retraction of the palate, which was responsible for subnasal orthognathism and the concave nasoalveolar clivus (although he thought that both shifts were adaptations to the same function). Rak further argued that these traits represented multiple, independent evolutionary changes, and were synapomorphies uniting *P. robustus* and *P. boisei* in a robust clade.

In contrast, McCollum (1999) argued that the complex of traits seen in robust East and South African hominins might have resulted from selection for large post-canine dentition and relatively small anterior dentition. She hypothesized that, due to constraints on palate size and the position of the vomer, “all of the skeletal traits identified as synapomorphies of a *Paranthropus* clade are merely developmental by-products of dental size and proportions” (McCollum, 1999:304). In other words, she argued that, as a consequence of morphological integration, evolution of relatively large post-canine dentition caused coordinated changes to multiple facial characters of robust species. This argument led her to suggest the possibility that separate eastern and southern African robust clades might share robust facial features as a result of convergence on a similar dietary adaptation requiring relatively large post-canine dentition.

Modularity and integration

The two hypotheses about the evolution of robust morphology mentioned above have distinct implications for the phylogeny of

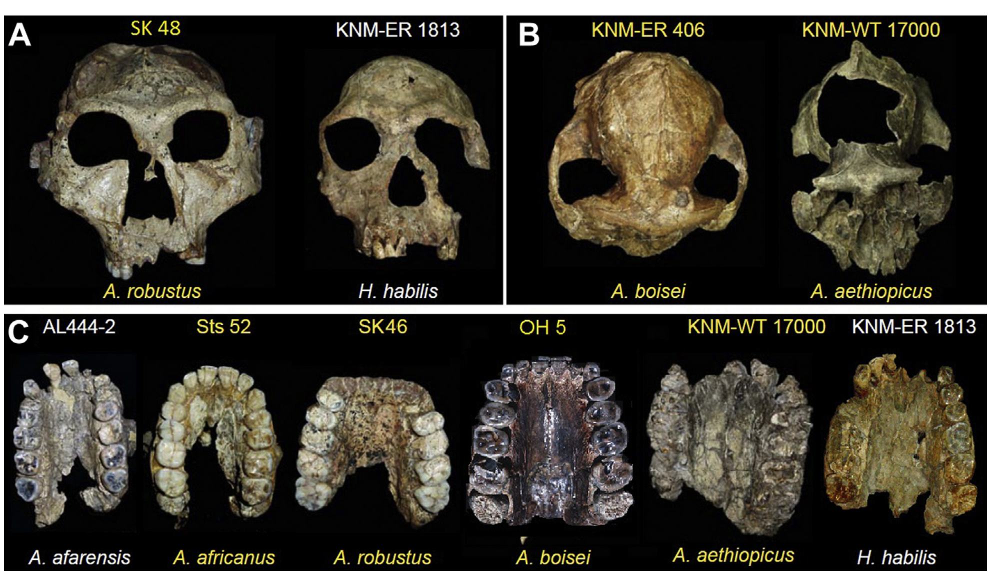

Figure 1. Diversity in early hominin midfacial and palate morphology. (**A**) Frontal cranial views of SK 48 (*Paranthropus robustus*, left) and KNM-ER 1813 (*Homo habilis*, right). (**B**) Dorsal cranial views of KNM-ER 406 (*P. boisei*, left) and KNM-WT 17000 (*P. aethiopicus*, right). Note the dramatic reduction in the size of the premaxilla in the orthognathic face of *P. boisei*, relative to its putative ancestor, *P. aethiopicus*. (**C**) Ventral views of palates of early hominin species. From left to right, *A. afarensis*, *A. africanus*, *P. robustus*, *P. boisei*, *P. aethiopicus*, and *H. habilis*. Note the difference in relative molar size as well as the size and shape of the premaxillary region. See text for details. Robust species are identified in yellow, gracile species in white. Note that in order to capture as much resolution as possible, specimens are not reproduced to scale. OH 5 image courtesy of Don Johanson. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)