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Phylogenetic signal in molar dental shape of extant and fossil catarrhine primates

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ABSTRACT

Morphology has been widely used for inferring the phylogenies of numerous taxonomic groups. Recent molecular studies performed on extant non-human primates, however, have cast doubt on the reliability of cranial and postcranial characters for characterizing evolutionary affinities. Because molecular evidence is often not available for fossil specimens, detecting phylogenetic signals in anatomical features is of great relevance. Here we have analyzed molar (M_1 and M_2) crown shape by means of geometric morphometrics in a large sample of both extant and fossil Miocene catarrhine primates to detect the phylogenetic signal in molar morphometry. Results support that molar shape carries a strong phylogenetic signal, mostly at the superfamily level but also to some extent at the family level. Dietary factors, however, appear to have less influence, especially for M_2. The Miocene Pliopithecoidea, Cercopithecoidea, and Hominoidea superfamilies clearly grouped according to the expected taxonomic affinities with the extant groups, although some discrepancies were found depending on the tooth considered. Our findings suggest that although molar crown shape can be used as a reliable proxy for establishing taxonomic affinities of catarrhine fossil primates with extant groups, a significant amount of interspecific variation exists, indicative of derived adaptations at the genus or species level.

1. Introduction

Morphological analyses of anatomical structures have been widely used for inferring the phylogenies of taxonomic groups, including primates (Delson and Andrews, 1975; Lockwood et al., 2004; Macholán, 2006; Astúa, 2009; Ivanović et al., 2009). Phylogenetic signal has been defined as the degree to which phylogenetic relatedness among taxa is associated with phenotypic similarity (Klingenberg and Gidaszewski, 2010). If the signal is strong, the shapes of anatomical structures of closely related species are expected to be more similar to each other than to those of more distantly related species (Macholán, 2006; Klingenberg and Gidaszewski, 2010). However, modern approaches for phylogenetic reconstructions in molecular biology have presented incongruences between morphological and molecular phylogenies, and doubt has arisen concerning the phylogenetic signal underlying the shape of anatomical structures (e.g., Disotell, 1996, 2000; Collard and Wood, 2000; Pilbeam, 2000). Although various studies based on shape variation have reported a positive phylogenetic signal in their respective target structures (Polly, 2001, 2003; Macholán, 2006; Cardini and Elton, 2008; Astúa, 2009; Ivanović et al., 2009), others have not (Nicola et al., 2003; Monteiro and Dos Reis, 2005). Moreover, the inclusion of fossil taxa in the analyses contributes to more consistent interpretations, in congruence with living molecular phylogenies (Stewart and Disotell, 1998; Santini and Tyler, 2004; Strait and Grine, 2004) and phylogenetic relationships, once phylogenetic signals of anatomical traits are confirmed (Pilbeam, 1997).

Teeth constitute the fossil evidence most widely used in paleontological research for interpreting the biology of extinct species. On account of their durability (Polly, 2001; Bailey, 2004; Hillson, 2005; Macholán, 2006), teeth are abundant in the fossil record.

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More important, teeth remain unchanged after mineralization (Hillson, 2005), and thus serve as a permanent record for discerning morphological information on between-population variability and overall phylogenetic consistency (Polly, 2001). Thus, the teeth of various mammal groups have been used in morphometric studies to test ecological, taxonomic, or phylogenetic hypotheses (Renaud et al., 1996; Renaud, 1999; Polly, 2001, 2003; Caumul and Polly, 2005; Macholán, 2006), including non-human primates and fossil hominins (Bailey, 2004; Pan et al., 2004; Olejniczak et al., 2004, 2007; Martinón-Torres et al., 2006; Pilbrow, 2006; Gómez-Robles et al., 2007, 2011; Skinner et al., 2009; Gamarra et al., 2009, 2011; White, 2009; Liu et al., 2010; Singleton et al., 2011). Despite these efforts, only few studies have focused on extant or past morphological traits of a wide selection of catarrhine species to characterize dental shape variation and taxonomic relationships (Delson and Andrews, 1975; Buck et al., 2010). Although early reports (Bennett and Goswami, 2012) analyzed a large primate sample, including catarrhines and platyrrhines as well as strepsirrhines, a comprehensive study of molar crown shape of a broad range of extant catarrhine species along with fossil taxa is lacking.

Extant Cercopithecoidea (Colobinae and Cercopithecinae) share specialized slicing molar teeth (bilophodont), sexual dimorphism in canine size, and postcranial adaptations for pronograde locomotion (Fleagle, 1999; Delson, 2000), whereas the Hominoidea (Hylobatidae and Hominidae) have retained primitive dental traits, such as five short and rounded cusps on molar teeth (bunodont) for grinding, a Y-shape cusp pattern, broad incisors, and reduced size difference between premolars (Fleagle, 1999; Delson et al., 2000; Begun, 2007). Despite the distinct anatomical traits in both groups, the classification of extinct catarrhines has been extensively debated (Fleagle, 1999; Begun, 2002, 2010; Harrison, 2002; Rasmussen, 2002; Casanovas-Vilar et al., 2011). In this context, phylogenetic relationships for the Eurasian Miocene hominoids have been a long standing topic of debate (Moyà-Solà and Köhler, 1995; Begun et al., 1997, 2012; Cameron, 1997; Stewart and Disotell, 1998; Andrews and Bernor, 1999; Begun and Nargolwalla, 2004; Moyà-Solà et al., 2004, 2009a,b; Begun, 2007, 2010; Alba et al., 2010b; Senut, 2010; Casanovas-Vilar et al., 2011). This is especially true for the controversial phylogenetic position of the dryopithecinae clade that some researchers closely relate to the African great apes (Homininae, hominines; Begun et al., 1997, 2012; Begun, 2009, 2010), while others relate to the Asian pongines (Ponginae; Moyà-Solà and Köhler, 1995; Alba et al., 2010b; Casanovas-Vilar et al., 2011). The case of *Oreopithecus*, an insular fossil hominoid that lived in the Tusco-Sardinian paleobioprovince of Italy during the late Miocene, is no exception (Delson, 1987; Harrison and Rook, 1997; Köhler and Moyà-Solà, 1997; Moyà-Solà et al., 2005; Williams, 2008, 2013). *Oreopithecus* has been associated with extant and Late Miocene great apes (hominids; Harrison and Rook, 1997; Moyà-Solà and Köhler, 1997; Williams, 2008), in contrast to the hypothesis that it might belong to a separate clade with no living descendants (Begun et al., 1997; Begun, 2002). Less controversial, however, is the fossil superfamily Pliopithecoidea, a primitive catarrhine group with no extant descendants that spread from northeastern Spain to China from about 17 to 7 million years ago (Crusafont-Pairó, 1975, 1978; Begun, 2002; Alba et al., 2010a; Harrison, 2010, 2013; Marigó et al., 2014). Among Miocene Cercopithecoidea, the fossil colobine *Mesopithecus* spread from Western Europe to Central and South Asia at least 8.5 Ma (Pan et al., 2004; Koufos, 2006), apparently surviving in Europe until the Early Pliocene (Delson et al., 2005; Merceron et al., 2009).

Geometric morphometrics (GM) is a powerful tool for studying the shape changes of morphological traits in biological structures and their associated implications for ontogeny, phylogeny, and ecological adaptations (Vidarsdottir et al., 2002; Zelditch et al., 2004; Macholán, 2006; Gómez-Robles et al., 2007; Astúa, 2009; White, 2009; Baab et al., 2012). GM is a suite of methods for the acquisition, processing, and analysis of variables that retain the geometric information of shape contained within the data (Slice, 2005). It is an especially useful technique for describing spatial aspects of morphological variation (Adams et al., 2004, 2013; Zelditch et al., 2004; Slice, 2005; Gómez-Robles et al., 2007; Baab et al., 2012) and for directly visualizing shape differences (Klingenberg, 2013). Detailed information on the mathematics involved in GM can be found in the literature (e.g., Bookstein, 1989, 1991; Richtsmeier et al., 2002; Adams et al., 2004, 2013; Zelditch et al., 2004; Slice, 2007; Mitteroecker and Gunz, 2009). Despite its utility, GM studies of dental shape in non-human primates are relatively scarce (White, 2009; Cooke, 2011; Singleton et al., 2011) and none have focused on catarrhine molar shape, including fossil specimens.

The aim of the present study was to explore the geometric morphometric characteristics of the occlusal shapes of lower molars (M_1 and M_2) in a large sample of extant catarrhine primates in order to assess their phylogenetic signal for exploring the affinities of Miocene fossil taxa with extant species. In particular, this study explored the position of the Pliopithecoidea within the catarrhine primates, including the recently described *Barberapithecus* (Alba and Moyà-Solà, 2012) and the affinities of *Mesopithecus* with either African (Strasser and Delson, 1987; Hohenegger and Zapfe, 1990) or Asian colobines (Jablonski, 1998, 2002; Pan et al., 2004). In addition, the affinity of the insular *Oreopithecus* with extant and Late Miocene great apes (Begun et al., 1997; Harrison and Rook, 1997; Moyà-Solà and Köhler, 1997; Begun, 2002; Williams, 2008) and the phylogenetic position of the dryopithecine clade (Moyà-Solà and Köhler, 1995; Begun et al., 1997, 2012; Begun, 2009, 2010; Alba et al., 2010b; Casanovas-Vilar et al., 2011; Alba, 2012) were analyzed.

2. Material and methods

2.1. The sample

Lower first (M_1; $N = 334$) and second (M_2; $N = 427$) molars (one tooth per individual) from osteological collections were analyzed in a sample of both extant (M_1, $N = 303$; M_2, $N = 386$; Table 1) and fossil (M_1, $N = 31$; M_2, $N = 41$; Table 2) catarrhine primates. The extant primates were grouped by genera, including one or more species, in multivariate and phylogenetic trees analyses, with the exception of *Semnopithecus* (grouped with *Trachypithecus*), *Chlorocebus* (grouped with *Erythrocebus*), and *Symphalangus* (grouped with *Hylobates*) in order to maximize sample sizes for these genera and based on previous phylogenetic and morphological affinities (Strasser and Delson, 1987; Page et al., 1999; Swindler, 2002; Perelman et al., 2011; Nova-Delgado et al., 2012).

High-resolution dental replicas of whole crowns were obtained following standardized procedures described in Galbany et al. (2004, 2006). Enamel surfaces of original tooth crowns were cleaned with pure acetone and rinsed with ethanol (95%) using cotton swabs. Molds were obtained using polyvinylsiloxane (Colténe® President Microsystem-Regular body) impression materials and positive casts were made from the molds using epoxy Epo-Tek #301 or polyurethane Feropur PR55+E55 (Feroca®) resins, which have been shown to have high stability and resolution detail (see Galbany et al., 2006 for details). Digital images of occlusal crown surfaces of these casts were taken using a Nikon D70 digital camera with a 60 mm optical lens from a minimum distance of 50 cm (to prevent image deformation) using a metallic stand at the Centres Científics i Tecnològics (CCiT) of the University of Barcelona. The casts were held horizontally on the stand