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Variation in guenon skulls (I): species divergence, ecological and genetic differences

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Abstract

Guenons are the most diverse clade of African monkeys. They have varied ecologies, include arboreal and terrestrial species, and can be found in nearly every region of sub-Saharan Africa. Species boundaries are often uncertain, with a variable number of species and subspecies mostly recognised on the basis of their geographic distribution and pelage. If guenon soft tissue patterns show high variability, the same does not seem to hold for skull morphology. Guenon skulls are traditionally considered relatively undifferentiated and homogeneous. However, patterns of variation in skulls have never been examined using a large number of specimens sampled across the breadth of species diversity. Thus, in the present study, skulls of adult guenons and two outgroup species are analysed using three-dimensional geometric morphometrics. Three-dimensional coordinates of 86 anatomical landmarks were measured on 1,315 adult specimens belonging to all living guenon species except *Cercopithecus dryas*. Species are well-discriminated using shape but the best discrimination occurs when species have either a long evolutionary history (e.g., *Allenopithecus nigroviridis*) or represent extremes of size variation (*Miopithecus* sp. and *Erythrocebus patas*). Interspecific phenetic relationships reflect size differences. Four main clusters are found that mainly correspond to four size groups: the smallest species (*Miopithecus* sp.), the largest species (*E. patas* plus the study outgroups), a group of medium-small arboreal guenons, and a group of medium-large arboreal and terrestrial guenons. Correlations between interspecific shape distances and interspecific differences in size are higher than between shape distances and genetic distances. However, if only the component of interspecific shape variation which is not correlated to evolutionary allometry is used in the comparison with genetic distances, correlations are up to 1.4 times larger than those including allometric shape. The smallest correlations are those between shape and ecological distances, which is consistent with the lack of clusters clearly reflecting broad ecological specialisations (e.g., arboreality versus terrestriality). Thus, size, which is generally considered more evolutionarily labile than shape, seems to have played a major role in the evolution of the guenons. The incongruence between interspecific shape differences and phylogeny might be explained by a large proportion of shape changes having occurred along allometric trajectories that tend to be conserved within this clade.

Keywords: Allometry; Cercopithecids; Geometric morphometrics; Size and shape; Morphological distinctiveness; Phylogenetic signal

Introduction

The highly speciose guenons (Primates, Cercopithecini), widespread in sub-Saharan Africa, are an ecologically and behaviourally varied tribe (Butynski, 2002). Their skull morphologies, in contrast, appear to be much less diverse. The Cercopithecini primarily comprises arboreal species, many of which are distinguished on the basis of pelage and calls (Kingdon, 1997). Craniodental features are seen as being poor species discriminators, at least within the species-rich genus *Cercopithecus* (Verheyen, 1962; Wood and Richmond, 2000), and have been the subject of remarkably few studies. Given the interest in the taxonomy, ecology, behaviour, and biogeography of guenons, perceptions of craniodental uniformity must surely have contributed to this lack of attention.

The most comprehensive study of guenon craniodental morphology to date was conducted by Verheyen (1962), who

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analysed 221 adult specimens of 13 guenon species using linear measurements of cranial, mandibular, and dental characters. Along with noting their general uniformity, lack of diagnostic characters, and pronounced sexual dimorphism [explored further in Cardini and Elton (in press)], he found that allometry had a strong influence on guenon skull morphology. Intergeneric comparisons of the ratio between interorbital width and glabella-prosthion length, which best discriminated among genera, indicated roughly parallel size-based trajectories within the majority of the clade (Verheyen, 1962). The links between body size and morphology in guenons were further highlighted by Martin and MacLarnon (1988), who, after removing the effects of body size through the use of residual values of cranial and dental dimensions, found that adults of the smallest guenon, *Miopithecus talapoin*, grouped with the largest, *Erythrocebus patas*. It thus appears likely that evolutionary or interspecific allometry (sensu Klingenberg, 1996, 1998) makes an important contribution to the morphological divergence of guenon taxa. It has also been suggested that ontogenetic scaling contributes to differences in skull form within the clade. In a comparison of *M. talapoin* and *C. cephus*, Shea (1992) determined that skull proportions differed significantly between the two species, attributing this to a decrease in growth rates and resultant smaller adult body size in *M. talapoin*.

The effects of allometric scaling on primate skull morphology have been the focus of considerable research, reviewed extensively elsewhere (Singleton, 2002). Many studies (e.g. Cheverud and Richtsmeier, 1986; Shea, 1992; O'Higgins and Collard, 2001; Leigh et al., 2003; Leigh, 2006) have investigated the role of ontogenetic allometry in determining cranial and mandibular form. Others (e.g., Marroig and Cheverud, 2001, 2005; Singleton, 2002; Frost et al., 2003; McNulty, 2004) have concentrated on assessing how size contributes to interspecific variation within adults of closely related species. In neotropical primates, allometry was found to account for 20–40% of all morphological variation within each genus, with only small divergence ($\approx 30°$) of allometric vectors between and within genera, despite at least 30 million years of evolutionary diversification and considerable variation in absolute size (Marroig and Cheverud, 2001, 2005). This indicates that although phenotypic means changed during the evolution of South American monkeys, covariance structure of their skulls remained relatively constant. The diversification of skull shape occurred mainly along lines of least evolutionary resistance (Schluter, 2000) defined by size variation, which, in turn, was generally associated with dietary shifts. When evolution did not occur along lines of least evolutionary resistance, the amount and pace of morphological changes were, respectively, small and slow. In Old World primates, size also appears to contribute to shape differences between taxa (Singleton, 2002; Frost et al., 2003; McNulty, 2004). However, in contrast to the conserved patterns evident in neotropical primates, there appears to be significant diversity in morphological scaling, both ontogenetic (O'Higgins and Collard, 2001) and, to a lesser degree, static (Singleton, 2002), within the sister clade of the guenons, the Papionini. Specifically, ontogenetic scaling appears to differ between mandrills and the other 'dog-faced' monkeys (O'Higgins and Collard, 2001), and adult mangabeys (*Cercocebus* and *Lophocebus*) may share a divergent static scaling pattern when compared to larger-bodied papionins (Singleton, 2002). This indicates that the relationship between size and shape in primates is not necessarily straightforward or evolutionarily conserved across the majority of taxa. Investigating the effects of allometry on the skulls of the behaviourally and ecologically diverse guenons, which [as discussed in Cardini and Elton (in press)] exhibit a wide range of body masses, will therefore help to shed further light on the links between size and shape in primate morphology.

Examining guenon skull morphologies will also assist in determining whether hard tissue features of the skull map onto the species boundaries that are indicated by calls, ecology, geographic range, and soft tissue. Geometric morphometrics is an ideal tool for this: demonstrated to be powerful enough to identify and quantify small inter- and intraspecific differences in primate morphology (e.g., Frost et al., 2003; Cardini et al., 2007). Nonetheless, traditional morphometric studies have identified highly divergent taxa, including *Allenopithecus nigroviridis* (Verheyen, 1962; Martin and MacLarnon, 1988) and *Miopithecus* (Verheyen, 1962), found in molecular analyses to probably be basal members of the guenon clade (Tosi et al., 2005). The patas monkey, which is ecologically and morphologically distinctive, tends also to be separated at the generic level, although recent molecular data suggest that as *E. patas* forms a monophyletic group with the other terrestrial guenons (the *Cercopithecus lhoesti* group and *C. aethiops*), it would be better placed in a more inclusive terrestrial guenon genus, possibly *Chlorocebus* (Tosi et al., 2004). The majority of guenon species are included in the apparently cranially homogeneous *Cercopithecus*. These hard tissue similarities, alongside a sparse fossil record prior to 1 Ma (Leakey, 1988), suggest rapid, recent divergence within *Cercopithecus* and possibly guenons as a whole. However, recent genetic studies have indicated that the tribe has a relatively long evolutionary history (Tosi et al., 2005). Based on evidence from X-chromosomal DNA, *Allenopithecus* split from the rest of the guenons at 9.3 ± 1.0 Ma, with divergence of *Miopithecus*, the terrestrial guenons, and the arboreal guenons occurring at 8.1 ± 1.0 Ma (Tosi et al., 2005). At 4.8 ± 1.2 Ma, the three 'terrestrial' guenon taxa (*E. patas*, *C. aethiops*, and the *C. lhoesti* group) diverged, followed by the separation of the major arboreal lineages (the *Cercopithecus mona*/*C. neglectus*/*C. diana* group and the *Cercopithecus mitis*/*C. cephus* group) at 4.6 ± 0.7 Ma. Speciation within the arboreal guenons probably happened relatively rapidly during the Plio-Pleistocene, with the differentiation of *C. mona*, *C. neglectus*, and *C. diana* at 3.5 ± 0.6 Ma, and *C. mitis* and *C. cephus* at 2.2 ± 0.6 Ma. The Central African forest belt is commonly seen as the region where much Plio-Pleistocene guenon evolution took place (Hamilton, 1988), with the subsequent dispersal of some taxa, including *C. aethiops* and *C. mitis*, to other parts of sub-Saharan Africa (Elton, 2007).

The study reported here has two main aims. First, similarities in skull shape (phenetic analyses) are used to group species, with similarity relationships of females compared to