Molecular Phylogenetics and Evolution 82 (2015) 455–466

Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

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

The effects of ecology and evolutionary history on robust capuchin morphological diversity

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ARTICLE INFO

Article history:
Received 26 March 2013
Revised 25 June 2014
Accepted 8 August 2014
Available online 4 September 2014

Keywords:
Sapajus
Robust capuchin monkeys
Morphological variation
Evolution
Cebidae
Platyrrhini

ABSTRACT

Recent molecular work has confirmed the long-standing morphological hypothesis that capuchins are comprised of two distinct clades, the gracile (untufted) capuchins (genus *Cebus*, Erxleben, 1777) and the robust (tufted) capuchins (genus *Sapajus* Kerr, 1792). In the past, the robust group was treated as a single, undifferentiated and cosmopolitan species, with data from all populations lumped together in morphological and ecological studies, obscuring morphological differences that might exist across this radiation. Genetic evidence suggests that the modern radiation of robust capuchins began diversifying ~2.5 Ma, with significant subsequent geographic expansion into new habitat types. In this study we use a morphological sample of gracile and robust capuchin craniofacial and postcranial characters to examine how ecology and evolutionary history have contributed to morphological diversity within the robust capuchins. We predicted that if ecology is driving robust capuchin variation, three distinct robust morphotypes would be identified: (1) the Atlantic Forest species (*Sapajus xanthosternos*, *S. robustus*, and *S. nigritus*), (2) the Amazonian rainforest species (*S. apella*, *S. cay* and *S. macrocephalus*), and (3) the Cerrado–Caatinga species (*S. libidinosus*). Alternatively, if diversification time between species pairs predicts degree of morphological difference, we predicted that the recently diverged *S. apella*, *S. macrocephalus*, *S. libidinosus*, and *S. cay* would be morphologically comparable, with greater variation among the more ancient lineages of *S. nigritus*, *S. xanthosternos*, and *S. robustus*. Our analyses suggest that *S. libidinosus* has the most derived craniofacial and postcranial features, indicative of inhabiting a more terrestrial niche that includes a dependence on tool use for the extraction of imbedded foods. We also suggest that the cranial robusticity of *S. macrocephalus* and *S. apella* are indicative of recent competition with sympatric gracile capuchin species, resulting in character displacement.

1. Introduction

Morphological evidence has long supported the division of capuchin monkeys into two types: the gracile or untufted capuchins (here and throughout referred to as genus *Cebus*, Erxleben, 1777), and the robust or tufted capuchins (referred to throughout as genus *Sapajus*, Kerr, 1792). While species diversity has always been recognized in the gracile capuchins, until recently the widespread robust capuchins were treated as a single species. The lumping of all robust capuchins into one species for data analyses has obscured any patterns of geographical or phylogenetic variation in this group (Lynch Alfaro et al., 2014). Here we review the history of morphological studies of the robust capuchins, as well as recent molecular and biogeographic evidence for the evolutionary history of this clade. Then we provide hypotheses about expected trends in morphological

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http://dx.doi.org/10.1016/j.ympev.2014.08.009
1055-7903/

variation within robust capuchins on the basis of ecology and phylogeny, and test these hypotheses using phylogenetic principal components analysis on craniofacial character variation across robust capuchin species. We also offer preliminary data analyses of robust capuchin postcranial material in a comparative biogeographic context using ancestral state reconstructions (ASR) of postcranial indices.

1.1. Morphological studies establishing differences between gracile and robust capuchins

In 1913, Elliot first proposed a deep separation between what was then referred to as the "untufted" (gracile) and "tufted" (robust) capuchins. In 1939, Tate identified a number of cranial characteristics specific to tufted capuchins, and Hershkovitz (1949, 1955) confirmed the tufted and untufted forms as distinct, with some modification to which species had tufts or not. Subsequent craniodental work by Kinzey (1974) further distinguished the tufted capuchins from the untufted forms by describing, for the first time, the tufted forms as "robust" and the untufted forms as "gracile". Following this morphologically relevant distinction offered by Kinzey, for the remainder of the text, we will continue to use the synonyms "gracile" for *Cebus* and "robust" for *Sapajus*.

To date all studies of the craniodental morphology of capuchins have identified significant differences between robust and gracile species in mandibular robusticity (Kinzey, 1974; Hershkovitz, 1977; Bouvier, 1986; Cole, 1992; Daegling, 1992), craniofacial shape (Masterson, 1996), masticatory muscle leverage (Wright, 2005), canine robusticity (Plavcan and van Schaik, 1992), tooth root size (Spencer, 2003), enamel thickness (Wright, 2005) and occlusal surface area (Anapol and Lee, 1994; Wright, 2005). In every case these analyses have found that robust capuchins differ from the gracile species in exhibiting wider and deeper mandibular corpora and symphyses (both externally and internally), anteroposteriorly shorter and mediolaterally broader faces, increased leverage for the masseter and temporalis muscles, shorter and thicker canines, larger canine roots, thicker dental enamel, and greater molar surface area. In addition, dental microwear texture analyses found *Sapajus* (previously lumped in *Cebus apella*, sensu lato) to exhibit complex wear surfaces indicative of hard food feeding (Scott et al., 2005).

Few studies have compared postcranial morphology between or within the robust and gracile capuchins, and in common with previous studies of craniodental traits, the robust capuchins have always been lumped into a single species (*Cebus apella*, sensu lato). Although one study found that the robust group shares some similarities in postcrania with some of the gracile forms, including brachial index (robust capuchins are similar to *C. capucinus*) and some features of the calcaneus and astragalus (robust capuchins are similar to *C. olivaceus*) (Ford and Hobbs, 1996), other data suggest that for a number of postcranial features, robust capuchins are postcranially distinct from gracile capuchins, exhibiting a greater degree of postcranial robusticity as well as relatively shorter fore- and hind limbs (Ford and Hobbs, 1996; K. Wright, 2005, 2007). This divergent pattern appears early in development (Jungers and Fleagle, 1980).

In summary, there is long-standing evidence of morphological differences between gracile and robust capuchin monkeys, but there has been much less attention paid to diversity among the robust capuchins.

1.2. Morphological studies of geographic variation within robust capuchins

Elliot (1913) initially recognized several distinct species of robust capuchins, but ever since studies by Cabrera (1957) and Hill (1960) placed all of the robust forms into one species, *Cebus apella*, morphological variation within the robust group has largely been ignored, with subsequent research tending to lump robust capuchins together irrespective of place of origin (e.g. Cole, 1992; Daegling, 1992; Ford and Hobbs, 1996; Masterson, 1996; Scott et al., 2005; Wright, 2005; K. Wright, 2005, 2007). A watershed moment for understanding robust capuchin diversity came with Torres de Assumpção's (1983) recognition of significant morphological variation based on geography. Subsequent analyses of pelage patterns and skeletal characters strongly supported multiple distinct species among the robust capuchins (Groves, 2001; Silva Jr., 2001, 2002a, 2002b; Rylands et al., 2005, 2012; Rylands and Mittermeier, 2009). The robust capuchin group is now considered by most taxonomists to be comprised of several species (Silva Jr., 2001; Groves, 2001; Rylands and Mittermeier, 2009; Rylands et al., 2005, 2012). The IUCN recognizes eight species of robust capuchins (which they currently still designate as belonging to the genus *Cebus*) (IUCN, 2012). These species include those largely restricted to the Atlantic Forest: *Sapajus flavius*, the blonde capuchin; *S. nigritus*, the black-horned capuchin; *S. robustus*, the robust tufted capuchin; *S. xanthosternos*, the yellow-breasted capuchin; those found in rainforests in Amazonia and the Guianas: *Sapajus apella*, the brown capuchin; *S. macrocephalus*, the large-headed capuchin; *S. cay*, Azara's capuchin; and *S. libidinosus*, the bearded capuchin, found in the drier habitats of Cerrado and Caatinga (Fig. 1). These species differ in ecogeographic niches (IUCN; Fig. 2). If ecology is driving morphological diversity in robust capuchin monkeys, we expect that the Atlantic Forest species will cluster together, those from the Amazon will form another cluster, and *S. libidinosus*, from much drier open habitats, will be the most morphologically distinct.

1.3. Molecular and biogeographic analyses of robust capuchin diversity

Recent molecular work (Perelman et al., 2011; Lynch Alfaro et al., 2012a,b; Ruiz-García et al., 2012; Springer et al., 2012) has confirmed the long-standing morphological hypothesis that capuchins are comprised of two distinct clades. Molecular data has provided support for a split during the Miocene, both from nuclear markers (6 Ma, 3.13–9.35 Ma 95% HPD: Perelman et al., 2011) and mitochondrial markers (6.15 Ma, 4.21–7.86 Ma 95% HPD: Lynch Alfaro et al., 2012a,b). A statistical phylogeographic analysis by Lynch Alfaro et al. (2012a,b) recovered the last common ancestor (LCA) of modern capuchins as most likely to have occurred in north-west Amazonia. Lynch Alfaro et al. (2012a,b) argue that the ancestral robust capuchin stock subsequently became isolated in the Atlantic Forest. At 2.65 Ma (1.57–3.8 Ma 95% HPD), the capuchin lineage leading to all modern robust species began to diversify along the Atlantic Coast of Brazil near the present-day range of *S. robustus*. Robust capuchins were restricted to the Atlantic Forest until about 0.40 Ma (0.21–0.67 Ma 95% HPD) when they "exploded," radiating north and west through Amazonia, into the Guianas as well as into the Cerrado–Caatinga (Lynch Alfaro et al., 2012a,b). The recent expansion of robust capuchins into the Amazon and Guianas led to broad sympatry with gracile capuchins (Lynch Alfaro et al., 2012a,b). Recently Cáceres et al. (2013) used geometric morphometric analysis of seven *Sapajus* and two *Cebus* species to assess the influence of climate and cranial size on craniofacial diversity among capuchins. They argued that capuchin species in drier southern habitats had narrower anteroposteriorly longer faces and that more recently diversified northern dwelling *Sapajus* species were more craniofacially similar to northern dwelling *Cebus* species. While latitude may play a role in selecting for particular craniofacial characteristics we have opted to develop our hypotheses based on differences in habitat and ecology and on the most recent molecular phylogenetic evidence.