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Review

Special issue: Comparative biogeography of Neotropical primates

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ABSTRACT

New research presented in this special issue of *Molecular Phylogenetics and Evolution* on the "Phylogeny and Biogeography of Neotropical Primates" greatly improves our understanding of the evolutionary history of the New World monkeys and provides insights into the multiple platyrrhine radiations, diversifications, extinctions, and recolonizations that have taken place over time and over space in the Neotropics. Here, we synthesize genetic and biogeographic research from the past several years to construct an overarching hypothesis for platyrrhine evolution. We also highlight continuing controversies in Neotropical primate biogeography, such as whether the location of origin of platyrrhines was Africa or Asia; whether Patagonian fossil primates are stem or crown platyrrhines; and whether cis- and trans-Andean Neotropical primates were subject to vicariance through Andes mountain building, or instead diversified through isolation in mountain valleys after skirting around the Andes on the northwestern coast of South America. We also consider the role of the Amazon River and its major tributaries in shaping platyrrhine biodiversity, and how and when primates from the Amazon reached the Atlantic Forest. A key focus is on primate colonizations and extirpations in Central America, the Andes, and the seasonally dry tropical forests and savannas (such as the Llanos, Caatinga, and Cerrado habitats), all ecosystems that have been understudied up until now for primates. We suggest that most primates currently inhabiting drier open habitats are relatively recent arrivals, having expanded from rainforest habitats in the Pleistocene. We point to the Pitheciidae as the taxonomic group most in need of further phylogenetic and biogeographic research. Additionally, genomic studies on the Platyrrhini are deeply needed and are expected to bring new surprises and insights to the field of Neotropical primate biogeography.

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1. Introduction

This special issue of *Molecular Phylogenetics and Evolution* on the "Phylogeny and Biogeography of Neotropical Primates" marks a watershed moment in our understanding of the evolutionary history of the New World monkeys, or suborder Platyrrhini. Schneider and Sampaio's (2015) comprehensive review article on the history of research on platyrrhine systematics ends with a look toward the future of Neotropical primate biogeography. But the future is now, and with the new research presented in this issue we begin to form a comprehensive picture of the multiple New World monkey radiations, diversifications, extinctions, and recolonizations that have taken place over time and over space in the Neotropics. Here, we synthesize genetic and biogeographic research – both new research from this special issue and results from other key papers published over the past several years – to construct a comprehensive hypothesis for platyrrhine evolution. We also highlight continuing controversies in Neotropical primate biogeography, such as the location of origin of platyrrhines, the relationship of Patagonian fossil primates to living platyrrhines, and the influence of the formation of the Amazon River and its major tributaries in shaping platyrrhine biodiversity. We also identify the taxonomic groups most in need of further research, most pressingly the Pitheciidae. Nuclear – and especially genome-wide – studies at the species and population levels are deeply needed and are expected to bring new surprises and insights to the field of Neotropical primate biogeography.

2. Overview and synthesis of Neotropical primate biogeography

2.1. Arrival and spread of primates in the neotropics

Platyrrhines form a monophyletic clade of non-human primates found in Mexico, Central America, and South America. Their origin has been contentious, because the timing of their arrival to South America based on the fossil record is believed to have occurred since 34 Ma, in a time interval after the breakup of Gondwanaland, when South America was isolated by water from all other continents. Kay (2015) supports the long-standing and prevailing view of an African origin for platyrrhines, based on his phylogenetic analyses of molecular and morphological data on living platyrrhines, combined with morphological data from fossil platyrrhines, stem anthropoids, and parapithecids. Kay's analysis suggests that the cranial and dental anatomy of Late Eocene African primate taxa is quite similar to what would be expected in the last common ancestor of catarrhines and platyrrhines. In his phylogenetic tree, fossil and extant catarrhines (including *Aegyptopithecus*, *Hylobates*, *Miopithecus*, *Presbytis*, *Apidium*, and *Simonsius*) form a monophyletic sister clade to living and fossil Platyrrhini. He also argues against the late Middle Eocene Amphipitheciidae of South Asia as belonging to the Catarrhini, and thus does not include Asian fossil primates in his comparative dataset (see also Kay, 2012).

In contrast to the African dispersal hypothesis (Kay, 2015; Oliveira et al., 2009; Poux et al., 2006), as well as the less favored North American dispersal through Central America hypothesis (Simpson, 1945) or the Antarctic migration hypothesis (Houle, 1999), Jameson Kiesling et al. (2015) propose an intriguing novel hypothesis that South America may have been colonized through waif or sweepstakes dispersal from proto-platyrrhines in Asia that dispersed across the Pacific Ocean. Several recent studies have suggested an Asian origin for anthropoid primates (Beard et al., 2009; Chaimanee et al., 2012; but see Kay, 2012), and Jameson Kiesling et al. (2015) reconstruct a western Amazonian ancestor to all living platyrrhines. Fossil evidence congruent with the Asian origin hypothesis includes the earliest known fossil primate in the Neotropics, *Branisella*, from Bolivia in the western Amazon, dating to ~26 Ma. Although great progress in our understanding of platyrrhine evolution has been achieved by combining information from morphological and molecular data, and from fossil and living primates, we still require further evidence that will allow for testing among the distinct hypotheses on platyrrhine origin.

2.2. Relationship of fossil primates to living Platyrrhini

2.2.1. Patagonian fossils

The taxonomic position of *Branisella* and of many Miocene primates from the Southern Cone are subjects of debate among primate paleontologists. In his recent phylogenetic reconstruction, Kay (2015) concludes that neither *Branisella* from Bolivia nor any of the Miocene primate fossils from Chile or Argentina (except *Proteropithecia*) belong within crown platyrrhines. Rather, he argues that all of these forms represent stem platyrrhines that branched off before the last common ancestor of extant New World primates. In fact, Kay (2015) argues that Eocene platyrrhines evolved first in tropical regions of South America and then later, in the Early Miocene, expanded (perhaps several times independently) into Patagonia through the Paraná Portal, and that all taxa in Patagonia subsequently were extirpated during the Middle Miocene due to climatic and geological changes. By contrast, Rosenberger and colleagues (e.g., Rosenberger, 2002; Rosenberger et al., 2009) argue that many of the Patagonian primates can be accommodated as old forms within the radiation of extant platyrrhines, specifically within the Pitheciidae. The conflicting inferences about platyrrhine evolutionary history keep us waiting for new fossil evidence to resolve the relationship of the Patagonian fossils to modern primates. One point of commonality is the inferred time of origin of modern Platyrrhini. Kay's scenario suggests modern platyrrhines originated after ~21 Ma, which coincides roughly with the estimates obtained by Jameson Kiesling et al. (2015) without using a *Branisella* calibration point (16.5 Ma, with 15.8–18.0 95% CI), as well as with those of other recent molecular studies (e.g., Hodgson et al., 2009; Pozzi et al., 2014; Di Fiore et al., 2015).

2.2.2. Antilles fossils

The relationships of fossil primates from the Greater Antilles to living platyrrhines are also discussed in this special issue. Kay's (2015) phylogenetic reconstruction places all of the Antillean fossils as stem primates, nested between the Patagonian forms and the extant radiation. Kay (2015) also considers Jamaican *Xenothrix* as the sister taxon to living platyrrhines, and the Cuban *Paralouatta* and Hispaniolan *Antillothrix* as sister species, together forming a