CHAPTER FOURTEEN

Biogeographic Origins of Primate Higher Taxa

Christopher P. Heesy, Nancy J. Stevens, and Karen E. Samonds

ABSTRACT

Cladistic character reconstruction has become an increasingly popular method used to infer areas of origin in biogeographic studies. However, no study to date has assessed the role that fossils play in center-of-origin reconstructions for the order Primates. Fossils preserve more information about the 'where' and the 'when' key extinct groups were present than would be apparent in analyses that focused solely on extant taxa. This paper examines the sensitivity of cladistic character reconstruction to ingroup and outgroup tree topologies when critical fossil taxa are included in the cladistic analysis of Primates. Specifically, reconstruction sensitivity is examined at the basal primate, strepsirrhine, haplorhine and anthropoid nodes to outgroup choice. Results demonstrate that biogeographic reconstructions are extremely sensitive to outgroup choice and internal tree topology and suggest caution in interpretations of areas of origin from phylogenies that do not include fossil taxa.

Key Words: Outgroup, topology, character evolution, area of origin, fossils

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INTRODUCTION

On which continent did primates originate? Relationships between historical events and biogeographic patterns have long been of interest to natural historians (e.g., Wallace, 1876; Perrier de la Bathie 1936; Paulian, 1961; Simpson, 1965). A number of methodologies exist to examine the biogeographical history of a given taxonomic group (reviewed in Crisci *et al.*, 2003). For example, dispersal approaches emphasize the importance of the movement of organisms through space and time, considering the dispersal abilities of individual taxa to result in the present distribution patterns (Myers and Giller, 1988). In contrast, proponents of vicariance biogeography assert that biogeographic patterns result primarily when habitats and their resident biota are split by the emergence of barriers. Evolution in these now-separate biotas occurs in isolation via allopatric speciation and drift results in differing distribution patterns at different places. When vicariance patterns of many groups of unrelated taxa conform with one another, it may be inferred that abiotic processes have intervened to separate habitats (Pielou, 1979; Myers and Giller, 1988).

It is likely that both dispersal and vicariance mechanisms contribute to the biogeographic patterns observed today, and it is difficult to unravel their individual roles in the evolution of a taxonomic group. For this reason, several recent studies of vertebrate distributions have relied on phylogenetic vicariance biogeography approaches (e.g., Raxworthy and Nussbaum, 1994, 1996; Raxworthy *et al.*, 1998, 2002). In these studies, an understanding of taxonomic relationships among groups precedes the understanding of biogeographical patterns, and endemic taxa are the "derived characters" that allow one to reconstruct biogeographical history (Myers and Giller, 1988).

Such approaches are convenient in that they can utilize existing phylogenies to examine the biogeographic history of a group. In addition, cladistic data can be used to infer the center of origin of a group (Bremer, 1992, 1995; Crisci *et al.*, 2003). Using this approach, the areas inhabited by the group are optimized onto the tree using maximum parsimony. It can be inferred from the optimization analysis that the more primitive members of the group are found closer to the center of origin for that group (Hennig, 1966; Bremer, 1992, 1995; Crisci *et al.*, 2003). Yet no study to date has assessed the role that fossils play in reconstructions of center of origin. Moreover, the effects of differing tree topologies and outgroup taxa upon the robusticity of biogeographic inferences are not well understood.

Most recent work on eutherian supraordinal biogeography is based on molecular phylogenies (e.g., Springer *et al.*, 1997; Murphy *et al.*, 2001a). For our focus on the area of origin of primates, a molecular phylogeny seems a particularly inadequate starting point. This becomes clear when comparing the distributions of extant and fossil primate taxa. Extant nonhuman primates are found in Madagascar, southern Asia, sub-Saharan Africa, and South America (Fleagle, 1999). However, many Eocene- and Oligocene-age primate fossils are known from broader distributions in Asia and Africa, as well as North America, Europe, and continental India (Fleagle, 1999; see also Marivaux *et al.*, 2001). For the purposes of phylogenetic reconstruction, it has been argued that fossils preserve characters more closely approximating the ancestral condition, in addition to features entirely absent in extant taxa (Gauthier *et al.*, 1988; Donoghue *et al.*, 1989). The same could also be suggested for biogeographic reconstruction; fossils preserve more about "where" and "when" those primates existed than would a simple consideration of extant primates alone. This point is further illustrated in Table 1. When continent of origin is optimized onto various morphologically and molecularly based phylogenies of eutherians, the majority of the molecular phylogenies imply an Asian origin of primates as well as strepsirrhines, haplorhines, and anthropoids. However, two fossil-based morphological phylogenies reconstruct a North American origin, which is not implied by any of the molecular phylogenies. This difference emphasizes the importance of including fossil taxa and character states in biogeographic reconstructions.

The most comprehensive work to date on the biogeographic origin of primates using fossil data is by Beard (1998; see also Beard, this volume), who reconstructed an Asian origin for primates and at least 12 other placental groups. The congruence of the analyses is surprising. Of considerable interest is the topology of the primate tree used in Beard's analysis. The topology is based in part upon his Primatomorpha hypothesis (Beard, 1993), in which Dermoptera + Plesiadapiformes (broadly considered) and Primates are sister taxa. These relationships have been called into question based primarily on otic and postcranial evidence (Bloch and Silcox, 2001; Silcox, 2002). Other prominent studies of primate phylogeny are also incongruent with Beard's tree (e.g., Shoshani *et al.*, 1996; Kay *et al.*, 1997; Ross *et al.*, 1998). This lack of consensus erodes confidence not only in Beard's biogeographic reconstruction, but also in any such reconstruction. In other words, are area of origin reconstructions overly sensitive to tree topology? As is shown in Table 1, many but not all tree topologies suggest an Asian origin for the Order Primates. However, none

Primate Biogeography

Table 1. Continent of Origin for Major Primate Nodes, by Advocated Phylogeny

Study	Primates node	Strepsirrhini node	Haplorhini node	Anthropoidea node	Type of data
Arnason et al., 2002	Asia	Asia	—	Asia	molecular-various
Beard, 1998	Asia	Asia	Asia	equivocal	morphological-MP
Bloch and Boyer, 2002	Asia	—	—	—	morphological-MP
Eizirik et al., 2001	Laurasia	—	—	—	molecular-MP,ML
Gunnell et al., 2002	North America	—	—	Africa	morphological-MP
Kay et al., 1992	Asia	—	—	—	morphological-MP
Liu et al., 2001	Asia	—	—	—	matrix representation
Madsen et al., 2001	Africa	—	—	—	molecular-ML
Marivaux et al., 2001	North America	equivocal (Asia, Africa)	—	—	morphological-MP
Murphy et al., 2001a	Asia	—	Asia	Asia	molecular-MP,ML,D
Murphy et al., 2001b	Asia	—	—	—	molecular-Bayesian
Ni et al., 2004	North America	North America	Asia	Asia/Africa[1]	morphological-MP
Norejko, 1999	Asia	—	—	—	morphological-MP
Novacek, 1992	Asia	—	—	—	morphological-T
Novacek and Wyss, 1986	Asia	—	—	—	morphological-MP
Purvis, 1995a; - and Webster, 1999	—	Asia	Asia	Asia	matrix representation
Ross et al., 1999 (preferred)	Asia	Asia	Asia	equivocal (Asia, Africa)	morphological-MP
Shoshani et al., 1996	Asia	Asia	Asia	Asia	morphological and molecular-MP

Studies in bold indicate those that incorporate data on fossil taxa.

MP = maximum parsimony, ML = maximum likelihood, D = distance, T = taxonomic

[1] The area of origin for anthropoids reconstructed using the Ni et al. (2004) topology depends on whether *Eosimias* is considered an anthropoid. If so, then anthropoids originated in Asia, if not, then anthropoids originated in Africa.

of these studies represents both living and fossil diversity. Inclusion of fossil taxa can have dramatic impact on biogeographic reconstructions (Stewart and Disotell, 1998). It is also true that we are uncertain of the outgroup for the primate order.

This study employs a dense representative phylogeny to examine the robusticity of reconstructions of primate biogeographic area of origin. It systematically evaluates the biogeographic origin of the Order Primates, as well as its major subgroups (e.g., Strepsirrhini, Haplorhini, and Anthropoidea). The purpose is to examine the sensitivity of character reconstruction at the basal primate, strepsirrhine, haplorhine, and anthropoid nodes to outgroup choice. In order to do this, we first generate a composite cladistic phylogeny of extant and fossil primate taxa using published data sets. We then evaluate the biogeographic implications of this phylogeny using multiple assumption sets of outgroup taxa. Finally, we discuss the relative support for the various reconstructions of the basal primate and anthropoid nodes.

MATERIALS AND METHODS

Matrix Representation Using Parsimony

Cladistic biogeography relies upon robust phylogenies. To date, no study has generated a cladistically based phylogeny of all major primate clades, including both extant and extinct taxa resolved to the generic or species level. A phylogeny encompassing fossil taxa is desirable in the reconstruction of trait evolution because fossils often preserve characters in states that more closely approximate the ancestral condition or that are entirely absent in extant taxa (Gauthier et al., 1988). In addition, a phylogeny that includes modern and fossil taxa offers the opportunity to analyze biogeographic distributions through time.

For this reason a composite phylogeny of extant and extinct primates was generated for this analysis using a cladistically based method, matrix representation using parsimony (Baum, 1992; Ragan, 1992; Purvis, 1995a,b). Following this method, a matrix was constructed by recoding source cladistic, phenetic (e.g., UPGMA), and taxonomic studies and scoring each taxon in a clade with "1," each taxon in the sister clade with "0," and all others with "?" (Purvis, 1995a,b; see also Sanderson et al., 1998). These data are hereafter known as "matrix elements" (Bininda-Emonds and Bryant, 1998), because they code for

node/clade membership and do not directly represent phylogenetic character information. Subjecting the matrix elements to parsimony analysis produces trees that are the most parsimonious representations of the hierarchical information derived from the source analyses (Baum, 1992; Ragan, 1992; Purvis 1995a,b; Bininda-Emonds and Bryant, 1998). Trees are rooted by scoring an all-"0" outgroup (Ragan, 1992; Purvis, 1995b). For this analysis, phylogenetic sources of data incorporating both extant and extinct taxa were used in order to generate a composite tree of living and fossil primates. The following studies were used as sources of phylogenetic information: Fleagle and Kay (1987), Beard *et al.* (1991, 1994), Jungers *et al.* (1991), Begun (1995), Purvis (1995a), Rose (1995a), Begun and Kordos (1997), Benefit and McCrossin (1997), Kay *et al.* (1997), Horovitz and Meyer (1997), Jaeger *et al.* (1998), Harris and Disotell (1998), Kay *et al.* (1998), Ross *et al.* (1998), Purvis and Webster (1999), Horovitz *et al.* (1998), Fleagle (1999), Horovitz (1999), Horovitz and MacPhee (1999), Gebo *et al.* (2000), Ross (2000 (summary of analysis in press)), Seiffert *et al.* (2000). In the cases of *Eosimias*, *Archaeolemur*, *Palaeopropithecus*, and *Megaladapis*, each of which was present in some analyses as resolved to the generic level, the generic monophyly was assumed and species were manually inserted as sister taxa.

The data matrix of 226 matrix elements for 165 extant and extinct primate taxa was subjected to maximum parsimony analysis in PAUP 3.0s+1 (Swofford and Begle, 1993) with the following parameters: Branch and Bound search algorithm using the furthest addition sequence, unordered matrix elements, uninformative matrix elements ignored, and collapse option enabled. In addition, the analysis was conducted without weighting or partitioning the matrix elements.

Character Mapping of Biogeographic Data

The areas of biogeographic origin were reconstructed for primate higher taxa in MacClade 4.0 by optimizing geographic area (continent) onto each tree using maximum parsimony, which reconstructs the most parsimonious sequence of changes to produce the observed character state distribution (Maddison and Maddison, 1992, 2000). This method of optimization has been successfully applied to biogeographic analyses where continents or subcontinents were the minimum geographic unit coded as a trait (Beard, 1998; Strait and Wood, 1999; Murray, 2001). Character and taxon coding are described in the Appendix

(sections 1 and 2). Continental distribution was treated as an unordered, multistate character. No constraints on dispersal were applied. In other words, taxa in this analysis could theoretically disperse from Asia to South America. For illustrative purposes, major clades, such as the Lemuriformes, Platyrrhini, and Catarrhini, were condensed when the reconstructed node value was unequivocal. The maximum parsimony option in MacClade yields the set of equally most parsimonious solutions to the optimization of a trait for a given phylogeny. Nodes and internodes for which multiple solutions are possible are reconstructed as equivocal. This set of equally most parsimonious solutions includes optimizations that favor parallelisms (accelerated transformations, or ACCTRAN) and reversals (decelerated transformations, or DELTRAN) as well as all other parsimonious solutions. ACCTRAN and DELTRAN are specific models of character optimization and do not necessarily demonstrate the most appropriate solution to the evolution of the trait of interest because they may not apply to all characters simultaneously.

Putative outgroup taxa include Plesiadapiformes (e.g., Bloch and Boyer, 2002), Scandentia (e.g., Jacobs, 1980), and Dermoptera (e.g., Beard, 1993). The effects of outgroup choice on the biogeographic reconstruction of major primate nodes were explored by varying outgroup combinations. Outgroup variations were coded for major continents from which fossil and living primates are known, those being Africa, Asia, North America, and Europe. Equivocal node reconstructions were considered unresolvable based on the current data.

RESULTS

Composite Phylogeny of Primates

The maximum parsimony analysis yielded 29 equally most parsimonious composite trees of 235 steps. The summary of the strict consensus composite tree with Lemuroidea, Lorisoidea, Ceboidea, Cercopithecinae, Colobinae, and Hominoidea compressed is shown in Figure 1. The complete strict consensus summary file is presented in the Appendix (section 3). The Rescaled Consistency Index is 0.95 (CI = 0.96, RI = 0.99), and is a measure of the congruence of source trees rather than of matrix element homoplasy (Bininda-Emonds and Bryant, 1998). These values are high because composite trees contain far fewer homoplastic and uninformative matrix elements than the characters used in the original phylogenetic analyses.
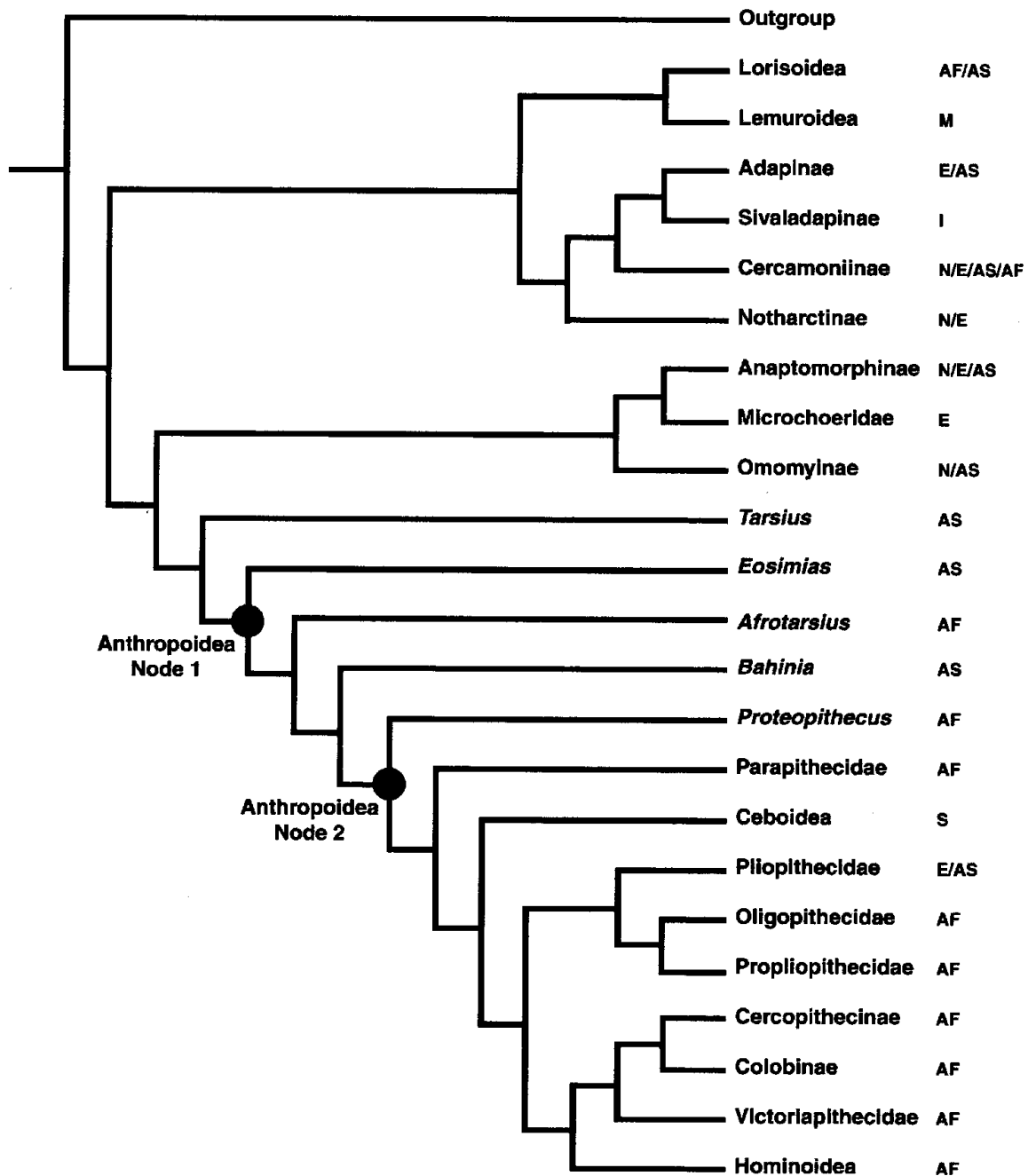
Figure 1. Summary composite tree of Primates with Lorisoidea, Lemuroidea, Ceboidea, Cercopithecinae Colobinae, and Hominoidea compressed. Continents to which taxa are endemic are indicated to the right. Abbreviations are: N—North America, E—Europe, As—Asia, Af—Africa, S—South America, M—Madagascar, and I—India. The definition of Anthropoidea is controversial. In this study, we reconstruct area of origin based on two node definitions of anthropoids: Anthropoidea Node 1 is defined by considering *Eosimias* and *Bahinia* as undisputed anthropoids. Anthropoidea Node 2 does not include *Eosimias* and *Bahinia* in Anthropoidea. The node is defined as *Proteopithecus* + all later anthropoids.

The monophyly of Strepsirrhini and Haplorhini are supported (Figure 1). Adapoidea is the sister group to all other strepsirrhines, and Omomyoidea is the sister group to all other haplorhines. *Eosimias*, *Afrotarsius chatrathi*, and *Bahinia pondaungensis* are "basal" anthropoids, or are sister taxa to a [*Proteopithecus* [Parapithecidae [Catarrhini + Platyrrhini]]] clade. The [Pliopithecidae [Oligopithecidae + Propliopithecidae]] clade is the sister group to all other catarrhines (Figure 1).

Results of Character Mapping of Biogeographic Data

Basal Primates

Reconstruction of the continental area of origin for all primates using various outgroup assumption sets yields seven unequivocal solutions (Table 2). These outgroup assignments also have varying effects on the reconstruction of strepsirrhine areas of origin (haplorhine origins are discussed with anthropoids, see below). A European origin of primates is supported by assigning either Europe or Europe + North America character states to the outgroups. A European origin of primates also reconstructs the Adapiformes + Strepsirrhini node as arising in Europe. An African origin of primates is supported when either Africa or Africa + North America character states are assigned to the outgroups. An African outgroup also reconstructs Adapiformes + Strepsirrhini as African. Three outgroup character state assignments lead to a reconstructed Asian origin: Asia (Scandentia + Dermoptera), Asia ((Scandentia + Siwaliks tupaiid) + Dermoptera), and Asia + North America. In these three cases, the strepsirrhine-based nodes are equivocal.

Anthropoidea

Assigning varying outgroup character states to the entire primate tree is largely irrelevant for node reconstructions of haplorhines and anthropoids (Table 2). The majority of haplorhine nodes are reconstructed as Asian in origin, with the minority exceptions for those that generate equivocal reconstructions. The primary anthropoid node reconstructions are completely consistent and unequivocal. If *Eosimias* and *Bahinia* are considered undisputed anthropoids, then anthropoids originated in Asia. If, however, the basal primate node is defined by *Proteopithecus* + all later anthropoids, then anthropoids originated in Africa.

Table 2. Continent of Origin for Major Primate Nodes Using Maximum Parsimony Character Reconstruction

Outgroup assumption set	Primates node	Strepsirrhini node	Adapiformes +Strepsirrhini	Haplorhini node	Omomyiformes+ Haplorhini	Anthropoidea node 1	Anthropoidea node 2
Asia (Scan+Derm)	Asia	equivocal	equivocal	Asia	Asia	Asia	Africa
Asia ((Scan+fossil)+Der)	Asia	equivocal	equivocal	Asia	Asia	Asia	Africa
Africa	Africa	Africa	Africa	Asia	Asia	Asia	Africa
North America	equivocal	equivocal	equivocal	equivocal	equivocal	Asia	Africa
Europe	Europe	equivocal	Europe	equivocal	equivocal	Asia	Africa
Asia+Africa	equivocal	equivocal	equivocal	Asia	Asia	Asia	Africa
Asia+North America	Asia	equivocal	equivocal	Asia	Asia	Asia	Africa
Asia+Europe	equivocal	equivocal	equivocal	Asia	equivocal	Asia	Africa
Africa+North America	Africa	Africa	Africa	Asia	Asia	Asia	Africa
Africa+Europe	equivocal	equivocal	equivocal	Asia	equivocal	Asia	Africa
North America+Europe	Europe	equivocal	Europe	Asia	equivocal	Asia	Africa

Anthropoidea Node 1 = includes *Eosimias* and *Bahinia* as undisputed anthropoids. **Anthropoidea Node 2** = does not include *Eosimias* and *Bahinia*. The node is defined as *Proteopithecus* + all later anthropoids.

DISCUSSION

Based on the results of this study, primates could be suggested to have originated in Africa, Asia, or Europe. These reconstructions based on theoretical outgroup choices are not unwarranted by fossil evidence. An African origin of primates is consistent with the suggestion that *Altiatlasius* is a basal primate (Gingerich, 1990; Sige *et al.*, 1990). The phylogenetic position and significance of *Altiatlasius* is, however, highly debatable with some researchers suggesting omomyid affinities (e.g., Sige *et al.*, 1990), and others plesiadapiform affinities (Hooker *et al.*, 1999). Similarly, an Asian origin of primates is consistent with the suggestion that *Altanius* from Mongolia is a basal primate (Dashzeveg and McKenna, 1977; Gingerich *et al.*, 1991). However, the affinities of *Altanius* are also debated, quite possibly because it shares similarities with both omomyids and adapids, and plesiadapiformes (Rose and Krause, 1984; Gingerich *et al.*, 1991; reviewed in Gunnell and Rose, 2002; Ni *et al.*, 2004).

The earliest undisputed Adapiformes and Omomyiformes appeared nearly simultaneously in Europe and North America (Rose and Fleagle, 1981; Rose *et al.*, 1994; Rose, 1995b;). This distribution seemingly would provide potential resolution to the question of origin. However, it is important to consider but one example that was very tentatively suggested by Covert (2002) that either the Asian *Altanius* or the African *Altiatlasius* represent the stem group from which Omomyiformes and Adapiformes originated. In such cases, the geographic distribution of later prosimians is irrelevant to reconstructing the area of origin of earlier groups.

The largely unequivocal results for anthropoid origins illustrate both the strengths and major weaknesses of cladistic biogeography using character reconstruction methodology. The hypothesis that basal anthropoids originated in Asia is based primarily on the disputed phylogenetic position of *Eosimias* (e.g., Kay *et al.*, 1997; Ross *et al.*, 1998; see also Beard, 2002). As with any fossil taxon of this importance, the affinities of *Eosimias* have been disputed from the beginning (Culotta, 1992; Godinot, 1994; Simons and Rasmussen, 1994; Simons, 1995a). The *Eosimias* problem illustrates the weight that one taxon with an unusual character state can have on subsequent reconstructions. The vast majority of fossils and data on early anthropoid evolution come from North Africa (Simons, 1995b). If in the future the position of *Eosimias* should be resolved differently, then reconstruction of the area of origin using an approach like that of this study will likely suggest an African origin of anthropoids.

Character reconstruction using a parsimony algorithm (e.g., Heesy and Ross, 2001) is a second stage process that is entirely dependent on topological resolution of the tree. If ambiguity or error is present in a base tree, then the resulting character reconstruction data are probably not robust. We would also argue that cladistic biogeography using the character reconstruction method is especially sensitive to missing data. Just as fossils may contain important features for the purposes of phylogenetic reconstruction and comparative analysis that are not found in extant taxa (Gauthier *et al.*, 1988; Donoghue *et al.*, 1989), our results suggest that fossils also represent geographic distribution data not necessarily found among extant taxa. These results call into question all biogeographic hypotheses based solely on molecular phylogenies (e.g., Springer *et al.*, 1997). However, at present, our results suggest that biogeographic reconstruction using character reconstruction when simultaneously considering both fossil and living taxa can only add potential sources for areas of origin, not discriminate among those that have been suggested for primate higher taxa.

CONCLUSIONS AND SUMMARY

Primates are among the best-documented taxa in the mammalian fossil record. As such, they provide a useful test case for understanding effects of different phylogenetic interpretations upon biogeographic reconstructions. This study has used multiple competing phylogenies, including a new comprehensive composite tree incorporating fossil taxa to evaluate the area of origin of primate higher taxa. It has examined the robusticity of biogeographic inferences, based on the sensitivity of such reconstructions to tree topology. Results demonstrate that biogeographic reconstructions are extremely sensitive to outgroup choice and internal tree topology and suggest caution in interpretations of primate and anthropoid areas of origin from phylogenies that do not include fossil taxa. Moreover, it has been shown that even a single taxon can have a powerful effect upon area of origin interpretations. Perhaps not surprisingly, it is only with greater phylogenetic resolution that a clearer understanding of the biogeographic origins of primate higher taxa will emerge.

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APPENDIX

Character Description and States.

One character, continental distribution of taxa, was coded as: North America = 1, Europe = 2, Asia = 3, Africa = 4, South America = 5, Madagascar = 6, and India = 7. Note that some taxa were coded as a multistate because representatives are found on multiple continents.

Taxon Coding

Tupaiinae 3; Ptilocercinae 3; *Lemur* 6; *Hapalemur* 6; *Eulemur* 6; *Varecia variegata* 6; *Varecia v. rubra* 6; *Lepilemur* 6; *Avahi* 6; *Indri* 6; *Propithecus verreauxi* 6; *Propithecus v. coquereli* 6; *Microcebus* 6; *Mirza* 6; *Cheirogaleus* 6; *Allocebus* 6; *Phaner* 6; *Daubentonia* 6; *Galago* 4; *Otolemur* 4; *Euoticus* 4; *Galagoides* 4; *Arctocebus* 4, *Loris* 3, *Nycticebus* 3, *Perodicticus* 3, *Tarsius* 3; *Trachypithecus* 3; *Presbytis* 3; *Semnopithecus* 3/7; *Nasalis* 3; *Simias* 3; *Rhinopithecus* 3; *Pygathrix* 3; *Piliocolobus* 4; *Colobus* 4/7; *Papio* 4; *Theropithecus* 4; *Lophocebus* 4; *Cercocebus* 4; *Macaca* 2/3; *Mandrillus* 4; *Cercopithecus* 4; *Chlorocebus* 4; *Miopithecus* 4; Hominoidea 3/4; *Callithrix* 5; *Cebuella* 5; *Saguinus* 5; *Callimico* 5; *Leontopithecus* 5; *Saimiri* 5; *Cebus* 5; *Aotus* 5; *Tremacebus* 5; *Callicebus* 5; *Pithecia* 5; *Cacajao* 5; *Chiropotes* 5; *Alouatta* 5; *Brachyteles* 5; *Lagothrix* 5; *Ateles* 5; Notharctinae 1/2; Cercamoniinae 1/2/3/4; Adapinae 2/3; Sivaladapinae (*Sivaladapis/ Indraloris*) 7; Microchoeridae 2; Anaptomorphinae 1/2/3; Omomyinae 1/3; *Eosimias* 3; *Afrotarsius* 4; *Proteopithecus* 4; Parapithecidae 4; Oligopithecidae 4; Pliopithecidae 2/3; Propliopithecidae 4; Victoriapithecidae 4; *Komba* 4; *Mioeuoticus* 4; *Progalago* 4; *Bahinia* 3; *Mohanamico* 5; *Lagonimico* 5; *Patasola* 5; *Carlocebus* 5; *Cebupithecia* 5; *Nuciruptor* 5; *Paralouatta* 5; *Antillothrix* 5; *Proteropithecia* 5; *Stirtonia* 5; *Archaeolemur* 6; *Hadropithecus* 6; *Palaeopropithecus* 6; *Megaladapis* 6.

Summary Tree File Generated in this Study.

((Ptilocercinae, Tupaiinae), (((Notharctinae, (Cercamoniinae, (Adapinae, Sivaladapinae))), (((((*Galago, Galagoides*), *Otolemur, Euoticus*), *Komba*),

((((*Arctocebus, Loris*), *Nycticebus*), *Perodicticus*), *Mioeuoticus, Progalago*)), (*Daubentonia*, (((((*Microcebus, Mirza*), *Cheirogaleus*), (*Allocebus, Phaner*)), (((((*Lemur, Hapalemur*), *Eulemur*), (*Varecia_v._rubra, Varecia_variegata*)), ((*Lepilemur, Megaladapis*), (((*Avahi*, (*Indri*, (*Propithecus_verreauxi*, Pro-pithecus_v._coquereli*))), *Palaeopropithecus*), (*Archaeolemur, Hadropithe-cus*))))))))), (((Microchoeridae, Anaptomorphinae), Omomyinae), (((*Tarsius, Tarsius_eocaenus*), *Xanthorhysis, Afrotarsius*), (*Eosimias*, (*Bahinia*, (*Proteopithecus*, (Parapithecidae, (((((((*Callithrix, Cebuella*), *Saguinus*, ((*Callimico, Patasola*), *Carlocebus*), *Leontopithecus, Mohanamico, Lagonimico*), (*Saimiri, Cebus*)), (*Tremacebus, Aotus*)), (((*Callicebus*, (*Paralouatta, Antillothrix*)), (((((*Pithecia*, (*Cacajao, Chiropotes*)), *Cebupithecia*), *Proteropithecia*), *Nu-ciruptor*)), ((*Alouatta, Stirtonia*), (*Brachyteles*, (*Lagothrix, Ateles*)))))), (((Oligopithecidae, Propliopithecidae), Pliopithecidae), ((Victoriapithecidae, (((((((*Trachypithecus, Presbytis*), *Semnopithecus*), (*Nasalis, Simias*)), (*Rhino-pithecus, Pygathrix*)), (*Piliocolobus, Colobus*)), (((((*Papio, Theropithecus*), *Lophocebus*), (*Cercocebus, Mandrillus*)), *Macaca*), ((*Cercopithecus, Chlorocebus*), *Miopithecus*)))), Hominoidea)))))))))))

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