Seeing the Wood through the Trees: The Current State of Higher Systematics in the Strepsirhini

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Abstract

Strepsirhines comprise 10 living or recently extinct families, ≥50% of extant primate families. Their phylogenetic relationships have been intensively studied, but common topologies have only recently emerged; e.g. all recent reconstructions link the Lepilemuridae and Cheirogaleidae. The position of the indriids, however, remains uncertain, and molecular studies have placed them as the sister to every clade except *Daubentonia*, the preferred sister group of morphologists. The node subtending Afro-Asian lorisids has been similarly elusive. We probed these phylogenetic inconsistencies using a test data set including 20 strepsirhine taxa and 2 outgroups represented by 3,543 mtDNA base pairs, and 43 selected morphological characters, subjecting the data to maximum parsimony, maximum likelihood and Bayesian inference analyses, and reconstructing topology and node ages jointly from the molecular data using relaxed molecular clock analyses. Our permutations yielded compatible but not identical evolutionary histories, and currently popular techniques seem unable to deal adequately with morphological data. We investigated the influence of morphological characters on tree topologies, and examined the effect of taxon sampling in two experiments: (1) we removed the molecular data only for 5 endangered Malagasy taxa to simulate 'extinction leaving a fossil record'; (2) we removed both the sequence and morphological data for these taxa. Topologies were affected more by the inclusion of morphological data only, indicating that palaeontological studies that involve inserting a partial morphological data set into a combined data matrix of extant species should be interpreted with caution. The gap of approximately 10 million years between the daubentoniid divergence and those of the other Malagasy families deserves more study. The apparently contemporaneous divergence of African and non-daubentoniid Malagasy families 40-30 million years ago may be related to regional plume-induced uplift followed by a global period of cooling and drying.

Keywords: Lemuriforms Lorisiforms Madagascar Phylogenetics Strepsirhini Taxonomy

Introduction

To most primate systematists, the order Primates comprises two suborders: the Haplorhini (with simple nostrils) and the Strepsirhini (with twisted nostrils). Of these subdivisions, the most diverse in terms of lifestyle characteristics are the Strepsirhini, living members of which are referred to as tooth-combed primates because of their highly derived lower anterior dentition; and by far the major part of strepsirhine diversity (at all taxonomic levels) is endemic to the island of Madagascar. The Afro-Asian mainland is occupied by the sister families Lorisidae (lorises and pottos, distributed patchily from West to East Africa and in South-East Asia) and Galagidae (galagos or bushbabies, confined to sub-Saharan Africa). In Madagascar, living strepsirhines are generally held to fall into 5 readily distinguishable families [Fleagle, 1999; Groves, 2001; Garbutt, 2007]: the mouse and dwarf lemurs (Cheirogaleidae), the aye-ayes (Daubentoniidae), the indris and sifakas (Indriidae), the ‘true' lemurs (Lemuridae) and the sportive or weasel lemurs (Lepilemuridae). The subfossil remains of 3 families of giant lemurs have been discovered in karstic cave deposits, and dated between 26,000 and approximately 100 years old [Godfrey and Jungers, 2002]: the monkey lemurs (Archaeolemuridae), koala lemurs (Megaladapidae) and sloth lemurs (Palaeopropithecidae). These 8 extant or recently extinct Malagasy families can be compared with 3 families of monkeys and apes in the Old World, and 2-4 monkey families in the New World, depending on taxonomic predilection.

Family Level Taxonomy of Living Strepsirhini

John Gray, Keeper of Zoology at the British Museum (Natural History) from 1840 to 1874, defined most of the extant strepsirhine families. In 1821 he designated Loridae (now referred to as Lorisidae) for lorises, tarsiers and galagos, and Lemuridae for *Lemur catta* and *L. indri* [Gray, 1821]. The ‘Indridae' (now referred to as Indriidae) were separated out by Burnett [1828] because he believed the lemurids had 6 incisors in the lower jaw, while the indriids had only 4. (Burnett and other systematists of this period identified the 6 teeth of the non-indriid tooth comb as incisors; it is now generally accepted that the outer teeth are canines.) Gray recognized the family Daubentoniidae, with its single surviving representative [Gray, 1863], and separated the cheirogaleids at the subfamilial level [Gray, 1872]. The latter were upgraded to a family by Petter [1962]. But the family with the most recent - and most tortuous - history is the monotypic Lepilemuridae.

For most of its taxonomic life *Lepilemur* was grouped with the true lemurs, although it was variously allied with subgroups within the family. For example, after a detailed examination of lemur postcrania, Mivart [1873, p. 490] wrote: ‘... *Lepilemur* seems to be that genus of the *Lemurinae* which most approximates to the *Indrisinae*' [italics original]. Stephan and Bauchot [1965] classified *Hapalemur* and *Lepilemur* together in the tribe Lepilemurini by dint of their shared low degree of encephalization (i.e. brain weight relative to body weight), an association supported by shared elongation of the navicular [Mivart, 1873], but contra-indicated by major differences in the alimentary systems of the 2 genera [Davies and Osman Hill, 1954]. Studies of digital pad morphology [Rumpler and Rakotosamimanana, 1972] and karyotypes [Rumpler, 1974; Rumpler and Albignac, 1978] led Rumpler and his coworkers to propose a subfamily within Lemuridae for the lepilemurs, i.e. Lepilemurinae, ‘corresponding to the tribe Lepilemurini Stephan and Bauchot, 1965' [Rumpler, 1974],

although *Hapalemur* was no longer included. Petter et al. [1977] elevated the subfamily to family level (Lepilemuridae), recognized by Tattersall in 1982, although he renamed the family Megaladapidae a few years later [Schwartz and Tattersall, 1985; Tattersall, 1986], subsuming *Lepilemur* and subfossil *Megaladapis* within a single taxon on the basis of uniquely shared morphological characters (loss of permanent upper incisors; double articulation of the mandibular condyle). Studies of ancient DNA by Yoder et al. [1999] and Karanth et al. [2005] failed to support this relationship, and most lemur biologists have reverted to the use of Lepilemuridae.

Strepsirhine Phylogenetic Relationships

Relationships among strepsirhine families have been the focus of ongoing research over the past three and a half decades [Tattersall and Schwartz, 1975; Schwartz and Tattersall, 1985; Yoder, 1994; Yoder et al., 1996; Porter et al., 1997; Stanger-Hall and Cunningham, 1998; DelPero et al., 2001; Pastorini et al., 2003; Roos et al., 2004; DelPero et al., 2006; Horvath et al., 2008; Chaterjee et al., 2009; Perelman et al., 2011; Montagnon, 2012], attracting more interest than any other mammalian suborder excluding our own. One of the reasons for this persistent attention has been an absence of consensus given rampant morphological and molecular homoplasy at deep phylogenetic divergences (i.e. anywhere between 80 and 32 million years [Yoder et al., 1996; Porter et al., 1997; Roos et al., 2004; Chatterjee et al., 2009; Perelman et al., 2011; Montagnon, 2012]). A second is a fascination with reconstructions of the ancestor of the primate clade. Since the divergences among crown strepsirhines are much deeper than those among crown haplorhines, the belief that extant strepsirhines are ‘primitive' and good models for primate ancestors is widely shared.

Strepsirhines have thus received concentrated systematic study despite the fact that most of this radiation has occurred in situ on one of the world's most impassable islands, but consensus has been elusive, possibly because of sampling problems. Few studies have included all extant families let alone genera, and incomplete or biased taxon sampling is known to generate misleading results [Plazzi et al., 2010]. Some recent studies have included DNA from the recently extinct subfossil families to increase their taxon database, but this has been at the expense of sequence length, which also biases phylogenetic reconstruction (e.g. Orlando et al. [2008] based their analysis on 94- to 539-bp sequences from 2 mtDNA genes). A substantial number of strepsirhine sequences is available on GenBank, but sampling is spotty, and rare species are poorly represented; few genes have been sequenced across the systematic spectrum, and the rarer taxa tend to be represented by different genes. Strepsirhine systematists working with molecular data sets hence have an invidious choice: to include more taxa and fewer sequences, or more sequences and fewer taxa.

To probe the factors underlying phylogenetic inconsistencies, we compiled a test data set including 20 strepsirhine taxa and 2 outgroups (table 1) represented by 3,543 bp, and 43 morphological characters that have been used by strepsirhine systematists over the >250 years that the field has existed (see online suppl. Appendix 1; for all online suppl. material, see www.karger.com/doi/10.1159/000353179). We aimed to maximize the representation of generic and specific groups, particularly among the least studied family Cheirogaleidae, and especially *Phaner* and *Allocebus*, and this decision left us with only mtDNA sequences, not the most reliable genetic data for characterizing deep phylogenetic nodes. To increase the phylogenetic range of our data [Jenner, 2004], we combined our molecular data set with a

set of morphological characters selected for their importance to past systematists, and analysed them separately and together using a range of techniques. We assessed our results in the light of other recently published topologies, using our results as a comparative base. Our combined data set further enabled us to investigate the usefulness of morphology for clarifying ambiguous molecular nodes, and to explore the consequences of including fossils with no molecular data in combined molecules + morphology data sets, as is often done by palaeontologists. We calculated clade divergence times on the basis of recently published dates for primate origins, and assessed the relative likelihood of these dates in terms of palaeoecological events.

Table 1. Taxa included in the data sets

Outgroup/ingroup	Species group	Species included
Outgroup (Platyrrhini)	*Aotus*	*A. azarai, A. infulatus, A. lemurinus, A. nancimaae, A. trivirgatus*
Outgroup (Tarsiiformes)	*Tarsius*	*T. bancanus, T. dentatus, T. lariang, T. syrichta*
Ingroup (Strepsirhini)	*Allocebus*	*A. trichotis*
	Avahi	*A. laniger, A. occidentalis*
	Lesser *Cheirogaleus*	*C. medius*
	Greater *Cheirogaleus*	*C. major*
	Daubentonia	*D. madagascariensis*
	Eulemur	*E. macaco*
	Galago	*G. senegalensis*
	Hapalemur	*H. griseus*
	Indri	*I. indri*
	Lemur	*L. catta*
	Lepilemur	*L. aeeclis, L. ankaranensis, L. dorsalis, L. edwardsi, L. leucopus, L. microdon, L. mitsinjoensis, L. mustelinus, L. otto, L. randrianasoli, L. ruficaudatus, L. sahamalazensis, L. seali, L. septentrionalis*
	Loris	*L. tardigradus*
	Microcebus	*M. berthae, M. griseorufus, M. lehilahytsara, M. murinus, M. myoxinus, M. ravelobensis, M. rufus, M. sambiranensis, M. tavaratra*
	Mirza	*M. coquereli*
	Nycticebus	*N. bengalensis, N. coucang, N. pygmaeus*
	Otolemur	*O. crassicaudatus*
	Phaner	*P. furcifer*
	Perodicticus	*P. potto*
	Propithecus	*P. coquereli, P. deckenii, P. diadema, P. edwardsi, P. tattersalli, P. verreauxi*
	Varecia	*V. variegata*

Compiling the Test Data Set

The number of valid species in lemurs is a matter of great contention [Tattersall, 2007], and much of the posited variation on which new ‘species' are based is cryptic and untested. We therefore chose species groups or genera rather than species for our test taxa.

Molecular Data Collection

Our genetic data set was assembled from GenBank, which presents its own set of problems. In some taxa hundreds of individuals had been sampled, whereas others were represented by 1 or 2 individuals. For the highly sampled taxa, there was often a high level of intraspecific variability, forcing us to confront its effects on phylogenetic reconstruction. Our solution was to calculate a 75% consensus sequence for each species group or genus from the sequences available in GenBank as of March 1, 2012. Since different sequences had been sampled for different taxa, we compromised between maximizing numbers of sequences and numbers of taxa. Our study is based on 20 strepsirhine taxa (table 1) and the following mtDNA sequences: the complete cytochrome b gene; part of the COIII gene; complete sequences for the NADH-dehydrogenase subunits 3, 4L, and 4 (ND3, ND4L, and ND4); and the $tRNA^{Gly}$, $tRNA^{Arg}$, $tRNA^{His}$, $tRNA^{Ser}$, and partial $tRNA^{Leu}$ genes. Sequences were aligned with CLUSTAL 2.0 [Larkin et al., 2007] and adjusted by eye. The resulting trimmed alignment was 3,529 bp, and is available from the authors on request.

Morphological Data Collection

The morphological data matrix consisted of 43 multistate characters recorded from strepsirhine primates housed in the American Museum of Natural History (New York), the Natural History Museum (London) and the Muséum National d'Histoire Naturelle (Paris). Details of the characters and coding are described in online supplementary Appendices 1 and 2. The characters were chosen for their independence and consistency, and on the basis of their use as systematic markers by earlier systematists.

Outgroups

We included 2 outgroups on the basis of their potential to inform character state polarities: (a) *Tarsius* is an ancient taxon that appears to have retained many of its morphological features for at least 45 million years. It is still considered by some evolutionary primatologists to represent a primitive grade of primate organization; in the tree resulting from a supermatrix analysed by Chatterjee et al. [2009], *Tarsius* emerges as the sister taxon to living strepsirhines; (b) *Aotus* is considered a generalized platyrrhine (New World monkey), once even linked to lorisoid strepsirhines: ‘The most primitive platyrrhine known is *Aotus*, which has retained the nocturnal habits and retinal structure of its lorisoid ancestors... Although *Aotus* is a platyrrhine, it is almost a lorisoid' [Regan, 1930, p. 389]. While we do not share the view that *Aotus* had lorisoid ancestors, we think it is possible that its adaptations to nocturnal life may converge to some extent with those of nocturnal strepsirhines, or at the very least, not lead to marked adaptive divergences. Major morphological differences, therefore, would be more likely to encode phylogenetic history.

Analysing the Test Data Set

The substitution model GTR + G + I was chosen as most appropriate by the Akaike information criterion test, and implemented using the program MrModeltest, version 2.3 [Nylander, 2004]. Bayesian inference (BI) was performed using MrBayes version 3.2 [Ronquist et al., 2012]. Four independent runs of Markov chain Monte Carlo, each with 1 cold and 3 incrementally heated chains, were run for 20 million generations, sampling trees every 1,000th generation. Convergence among runs was assessed when the average deviation of split frequencies reached values lower than 0.01. The first 2 million Markov chain Monte Carlo generations were discarded as burn-in, and the remaining trees were used to construct a majority rule consensus tree and estimate the nodal support values (posterior probabilities). Maximum parsimony (MP) reconstructions were obtained through heuristic searches using PAUP* [Swofford, 2002] with 1,000 random addition sequence replicates and branch swapping via tree bisection reconnection. We checked our MP results by running an analysis using TNT [Goloboff et al., 2000], using both data sets, and the morphological and molecular data sets combined. Maximum likelihood (ML) analyses were performed using RaxML version 7.3.0 [Stamatakis, 2006] via its graphical interface raxmlGUI [Silvestro and Michalak, 2011], assuming a GTR + Gamma substitution model. In both MP and ML analyses, 1,000 bootstrap replicates were run to compute nodal support values. Finally, tree topology and divergence times were jointly estimated by Bayesian molecular clock analyses as implemented in BEAST version 1.7.1 [Drummond and Rambaut, 2007]. We applied the log-normal relaxed clock model and a birth-death prior on the node ages. The trees were calibrated to an absolute time scale by assigning normally distributed priors on the root age as secondary calibrations. Two calibration settings dating the haplorhine-strepsirhine split were tested: 77.5 million years (95% credibility interval 93.2-65.9) [Chatterjee et al., 2009]; 87.2 million years (95% credibility interval 98.6-75.9) [Perelman et al., 2011]. Both analyses were run for 20 million Markov chain Monte Carlo generations, sampling every 1,000th. The posterior samples were combined in maximum clade credibility trees after excluding the initial 3 million generations as burn-in phase.

To investigate the effect of taxon sampling on phylogenetic reconstruction, we performed a series of ML analyses simulating ‘pseudo-extinctions' by removing taxa regarded as vulnerable or endangered [Mittermeier et al., 2010] from our data set, i.e. *Daubentonia*, *Hapalemur*, *Indri*, *Propithecus* and *Varecia*. We excluded each taxon individually, and then simulated a ‘mass extinction' by excluding them all. In the first phase we simulated extinction leaving a fossil record by excluding the molecular data and including the morphological data for the 5 taxa. In the second phase, we removed both the molecular and morphological data for these taxa. The ML settings were as before. The MULTIGAMMA model with GTR substitution matrix was applied for morphological characters.

Results of Analyses of the Test Data Set

Trees derived from the combined morphological + molecular data set were topologically identical to those obtained using the molecular data set alone for each analytical technique, and support values were only marginally improved (fig. 1), indicating that morphology played little to no role in our reconstructions. Both the PAUP* and TNT MP analyses found a single most parsimonious tree, and the identical tree was recovered using both techniques (fig. 1). The TNT bootstrap values were slightly lower than those recovered with PAUP*, but showed minor improvement when morphological data were added.

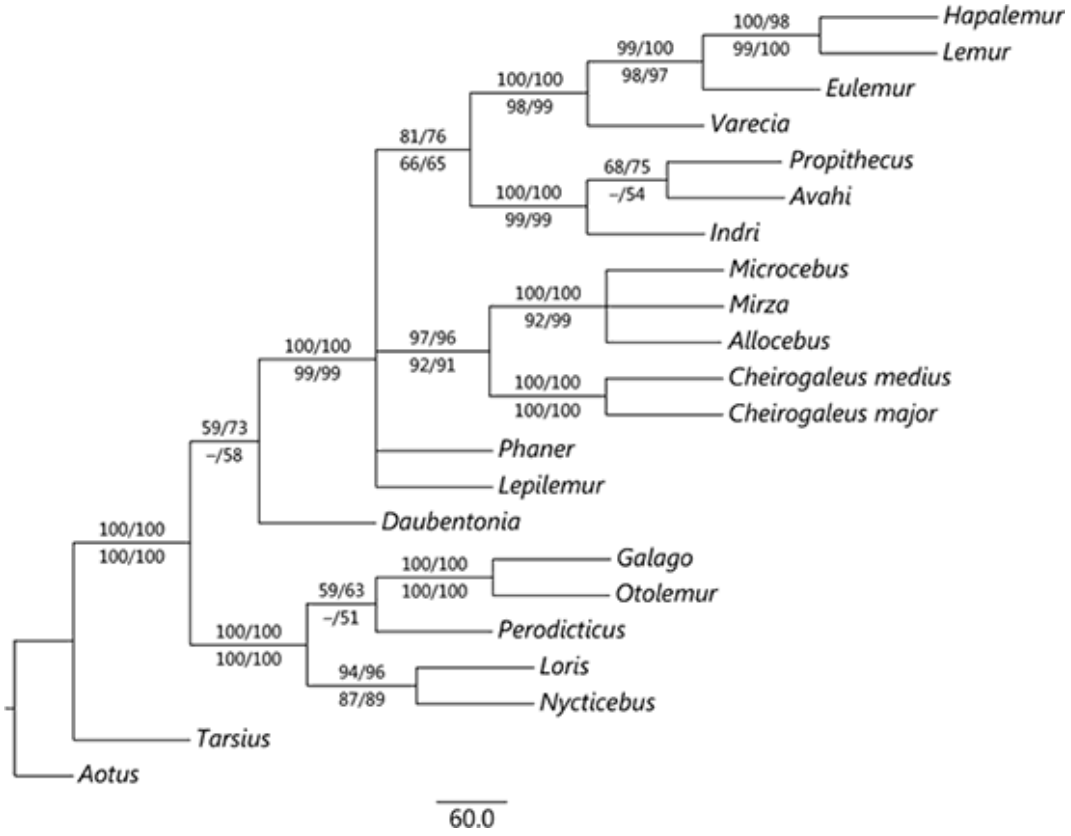

Fig. 1 MP phylogeny for 20 strepsirhine taxa. MP analyses were performed using both PAUP* and TNT. Both procedures resulted in a single most parsimonious tree, shown here. Bootstrap support values based on mtDNA only (left) and combined mtDNA + morphological data (right) are reported above and below branches, and refer to PAUP* and TNT analyses, respectively.

In our experience, using phylogenetically conserved morphological characters in combination with molecular data to anchor deep nodes in phylogeny reconstruction [Jenner, 2004; Lee and Camens, 2009] is not realistic using current analytical techniques. MP showed the greatest influence of morphology, but also yielded the least resolved tree (fig. 1). Model-based approaches were better supported (fig. 2, 3), but not always consistent with one another. Nevertheless, all trees were congruent, yielding compatible evolutionary histories. Each approach generated a tree with at least 1 well-supported clade that was not well supported in other reconstructions, probably because different analytical models have different assumptions which are violated by the data to some extent. Thus, clade support is not an objective quantity, but also reflects how data conform to analytical assumptions.

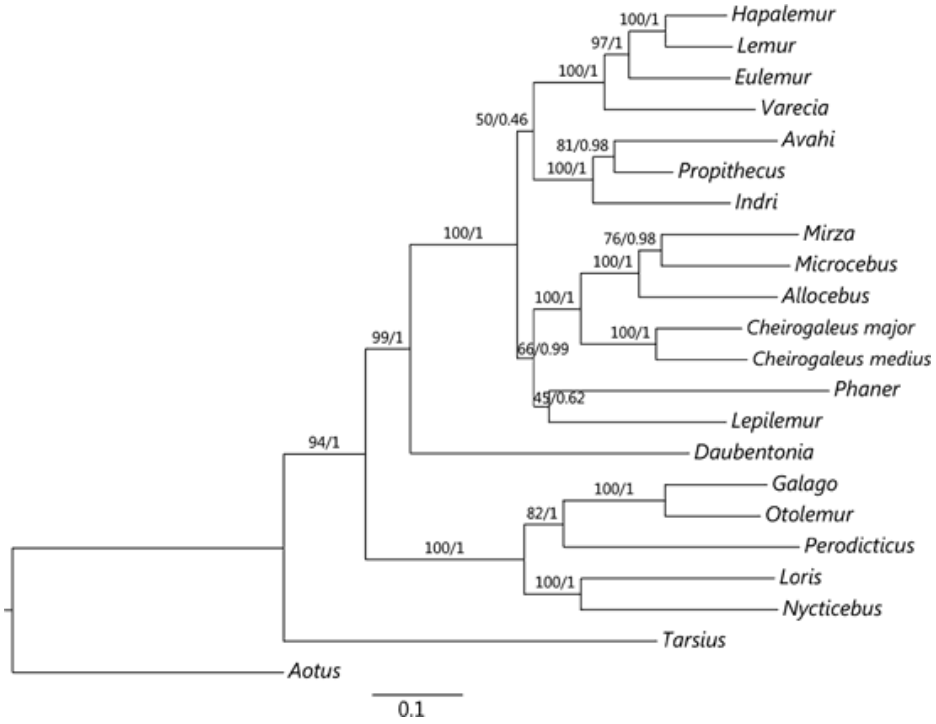

Fig. 2 ML tree derived from mtDNA data. The BI tree had the identical topology. ML bootstrap support values are shown above branches on the left, and BI posterior probabilities on the right.

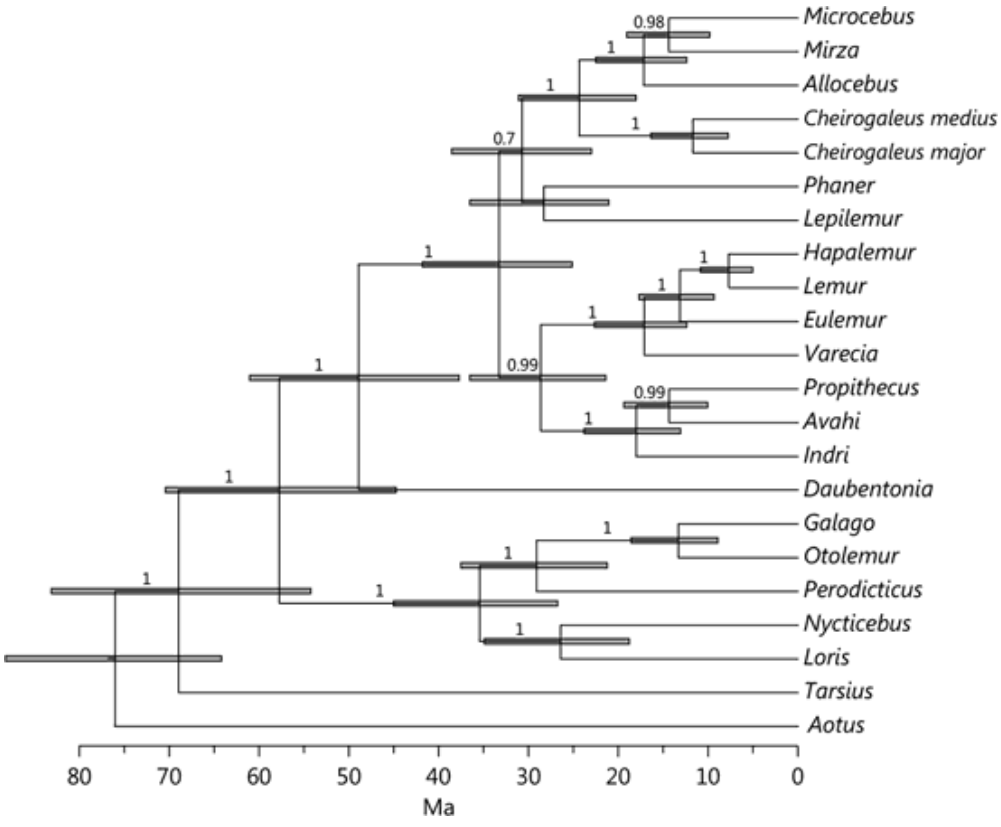

Fig. 3 Maximum credibility tree from relaxed molecular clock analysis calibrated to absolute time according to the primate origin date estimated by Chaterjee et al. [2009] of 77.5 million years. The bars on the nodes

represent the 95% credibility interval around the age estimates, and values above branches are posterior probabilities expressing topological support. Ma = Million years ago.

Major Strepsirhine Clades

In all recent analyses including our own test data set, the living Strepsirhini form a well-supported clade [Yoder et al., 1996; Roos et al., 2004; Horvath et al., 2008; Chatterjee et al., 2009; Perelman et al., 2011] with 2 subgroups: the series of Gregory [1915], Lemuriformes and Lorisiformes. In our study, the aye-aye *(Daubentonia)* and the remaining Malagasy taxa formed a clade that was strongly supported in all model-based analyses, but weakly (59 BS) or moderately (73 BS) supported under MP using the molecular and combined data sets, respectively. A clade including Indriidae, Lemuridae, Cheirogaleidae and Lepilemuridae is consistently recovered. Within these major clades, however, inconsistencies are commonly detected.

The Afro-Asian Lorisiforms

In our reconstruction, the Lorisidae did not form a clade exclusive of the Galagidae, but *Perodicticus*, the potto, clustered with the galagids with moderate to high support. This failure of the lorisids and galagids to form well-supported, exclusive clades is a common result [Yoder et al., 2001; Roos et al., 2004; Masters et al., 2007; Chatterjee et al., 2009], and the lorisid node appears to be fairly labile. Even the reconstruction of Perelman et al. [2011], based on >35,000 nuclear base pairs, managed to obtain only moderate bootstrap support (71-80%) for this node. The Lorisidae are grouped unambiguously by a suite of morphological characters, both craniodental and skeletal, and our inability to reconstruct it with certainty here testifies to the lack of influence of morphological characters in modern combined analyses.

Position of Daubentonia

In all molecular analyses undertaken to date, *Daubentonia* has emerged as the first divergence of the Malagasy lemuriform clade, whereas morphological reconstructions [Schwartz and Tattersall, 1985] have allied it with the indriids, and indeed, when we removed the *Daubentonia* molecular data set only, it was reconstructed as a member of the indriid clade. This is a classic case of molecular/morphological conflict. However, unless *Daubentonia* has a substantially elevated rate of nucleotide substitution relative to other extant strepsirhines, the fact that its divergence is reconstructed as having occurred 10 million years earlier than those of the other families argues against any such affiliation. We discuss this further below.

The Cheirogaleidae-Lepilemuridae Clade

Almost all recent sequence-based studies reconstruct the Cheirogaleidae and Lepilemuridae as a single clade. In our test study, these 2 families were grouped with 0.99 posterior probability (PP) using BI (fig. 2), although this node received only moderate support under BEAST (0.7 PP) and ML (66 BS), and the cheirogaleids did not form a clade, with or without lepilemurids, under MP. When both *Lepilemur* and *Phaner* are included in the analyses [Roos et al., 2004; Chatterjee et al., 2009; our analysis], they tend to form a sister group; in the absence of *Phaner*, *Lepilemur* forms the basal divergence of the cheirogaleid clade, generally with strong bootstrap support [Horvath et al., 2008; Perelman et al., 2011].

This result is also congruent with molecular trees published by DelPero et al. [2001, 2006] and Pastorini et al. [2003].

The Position of the Indriidae

Placing the Indriidae relative to the other lemuriform families remains the grail of strepsirhine systematics. Our analyses grouped the Indriidae and Lemuridae with moderate support (81 BS) under MP and strong support in the molecular clock analysis (BEAST, 0.99 PP), but no support was found for this relationship under BI or ML. An indriid-lemurid clade was also identified in trees presented by DelPero et al. [2001], Roos et al. [2004] and Chatterjee et al. [2009], again without strong support. A relationship between lemurids and indriids would make sense in terms of Godfrey's [1988] derivation of indriid hindlimb morphology from a quadrupedal, lemurid-like ancestor. Additionally, von Hagen [1978] identified a suite of skeletal (skull and scapular features), physiological (throat glands), pelage (bright, bold colours) and behavioural (vocal) characters shared by *Varecia*, the earliest branch of the Lemuridae, with the Indriidae.

An alternative topology is to place the indriids as sister to the cheirogaleid/lepilemurid-lemurid group, emerging as the second divergence after *Daubentonia* [Pastorini et al., 2003; Perelman et al., 2011]. This topology received strong support in the Pastorini analysis (2,400 mtDNA base pairs), but had no support in the Perelman analysis using a much larger data set including both nuclear and mitochondrial sequences. This arrangement would imply lemurid-like quadrupedalism was plesiomorphic for the Malagasy clade - not an unlikely scenario. Less likely is the plesiomorphic status of the striking pelage patterning shared by *Varecia*, *Indri* and *Propithecus* - a scenario which contradicts the ‘metachromism' model of pelage evolution [Hershkovitz, 1968; von Hagen, 1978]. The metachromism hypothesis posits agouti colouration as the ancestral pelt colour for mammals, which has been variously modified in different lineages. Other shared characters (gular glands, skeletal forms, vocalizations) would also be plesiomorphic according to this topology. A similar interpretation arises from a third reconstruction by Horvath et al. [2008] on the basis of a 16,000-bp data set, 9,000 bp of which were nuclear. Their reconstruction places indriids as the sister group to the lepilemurid/ cheirogaleid clade, and this group is sister to the lemurids. While reconstructing the ancestor to the non-daubentoniid Malagasy lemurs in accordance with characters likely to have been present in the common ancestor to indriids and *Varecia* is not beyond the abilities of an active imagination, finding characters that align indriids with the lepilemurid/cheirogaleid clade is a lot more difficult - particularly deriving a vertical clinging and leaping strategy based on tarsal elongation from one based on the elongation of the femur. In the light of this additional, non-genetic evidence, we believe that an indriid-lemurid sister grouping is the most likely evolutionary relationship, subject to confirmation by new phylogenetic information.

The Role of Morphology, Pseudo-Extinctions and the Inclusion of Fossils

For almost 200 years, strepsirhine family groupings were defined on the basis of morphology alone. The fact that these groups are largely supported by molecular da-ta - and that congruence between morphological and molecular clades is viewed as evidence for the success of molecular reconstructions - is a strong indicator of the important role that

morphology has played, and continues to play, in strepsirhine systematics. Nevertheless, when combined with molecular data and analysed using currently popular statistical techniques, morphological characters played no obvious role in our reconstructions. There were indications that the effect of the morphological data set was not negligible; for example, when we excluded the molecular data for a taxon, its morphological data were sufficiently informative to assign it to its appropriate family, except in the case of *Daubentonia*. In the absence of its genetic data set, *Daubentonia* was reconstructed within the Indriidae clade with moderate support (fig. 4a), although its extreme branch length testifies to its morphological uniqueness [Groves 1974, 1989].

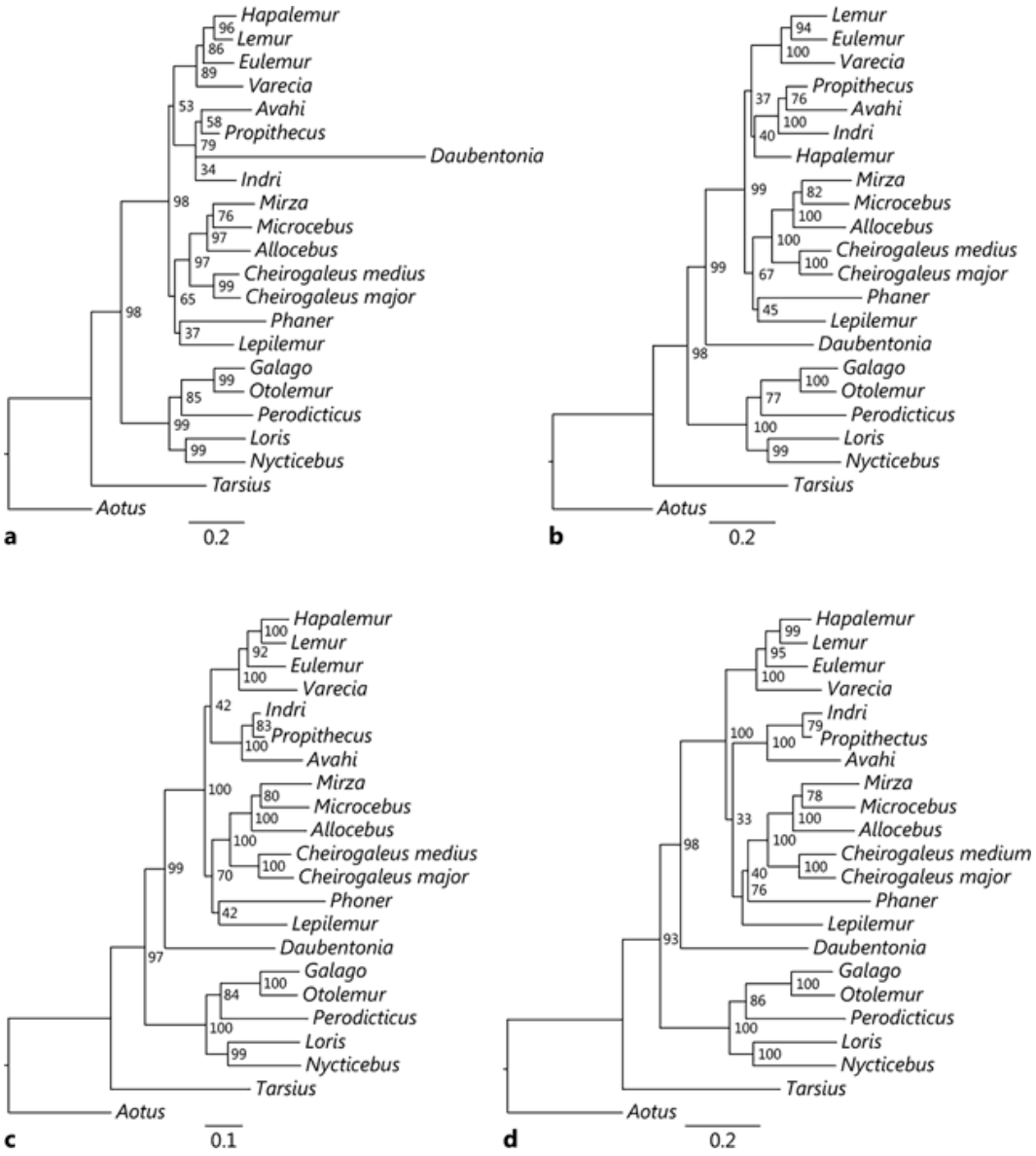

Fig. 4 Representative results of the 'pseudo-extinction' tests with a 'fossil record'. Genetic data were excluded from the analyses for selected taxa, which were represented only by morphological data, and analysed using ML. Bootstrap support values are shown above branches. 'Extinct' taxa with missing sequence data are: *Daubentonia* (a), *Hapalemur* (b), *Indri* (c) and *Propithecus* (d).

A second indicator of the recondite effect of morphology lies in our observation that removal of both molecular and morphological data for a given taxon did not influence the tree topology, whereas removing the molecular data and retaining the morphological data was more disruptive. Exclusion of the molecular data for *Hapalemur* dissolved its relationship to *L. catta* (which previously had 100 BS support), and reduced the already weak support for the indriid-lemurid clade (fig. 4b). When either *Indri* or *Propithecus* was represented only by morphological data, the genera grouped with one another to the exclusion of *Avahi* (fig. 4c, d), whereas *Avahi* and *Propithecus* (indriids with tails) consistently formed a sister group in molecular analyses. Similarly, removal of the *Varecia* genetic data grouped it with *L. catta* to the exclusion of *Hapalemur*. Removal of the genetic data for all 5 taxa simultaneously destroyed the structure of the phylogeny, with most clades losing support.

These observations indicate that the palaeontological practice of inserting fossils into phylogenies reconstructed using combined data sets from extant relatives may appear to be informative, but is not necessarily reliable. The results of our simulated mass extinction imply additionally that reliable phylogenetic assignments of fossils are only feasible in combination with adequate taxon sampling in the molecular data set, and when the number of morphologically defined taxa is limited; otherwise the tree structure will become unstable.

Timing of the Strepsirhine Radiation

We estimated clade divergence times based on two published calibration settings dating the haplorhine-strepsirhine split: 77.5 million years [Chatterjee et al., 2009] and 87.2 million years [Perelman et al., 2011]. The BEAST reconstructions generated the same topology, although the time scale differed by around 10 million years. The results are illustrated in figure 3, and compared in table 2.

Table 2 Divergence ages with credibility intervals (in parentheses) based on highest posterior density

Lineage divergence	CHA	PER
Daubentonia	48.94 (37.7–61.02)	63.97 (47.41–79.92)
Asian-African Lorisidae	35.45 (26.77–45.08)	46.15 (58.84–32.94)
Lepilemuridae/Cheirogaleidae/ Lemuridae/Indriidae clade	33.29 (25.07–41.76)	43.02 (31.73–54.49)
Cheirogaleidae/Lepilemuridae clade	30.73 (22.97–38.54)	39.76 (29.81–50.73)
Perodicticus potto-Galagidae	29.08 (21.18–37.48)	37.72 (26.84–49.72)
Lemuridae-Indriidae	28.59 (21.41–36.52)	36.98 (26.81–47.78)
Indri-Propithecus/Avahi clade	17.97 (12.98–23.82)	23.11 (16.01–31.19)
Varecia/Eulemur-Hapalemur-Lemur clade	17.09 (12.31–22.65)	22.16 (15.69–29.8)
Galago/Otolemur	13.29 (8.86–18.54)	17.21 (11.24–24.51)

Two sets of dates were calculated in the relaxed molecular clock analysis using the estimates for the origin of the primate clade taken from Chatterjee et al. [2009] (CHA; origin = 77.5 million years) and Perelman et al. [2011] (PER; origin = 87.2 million years) as calibration settings. The tree is illustrated in figure 4.

Depending on the calibration point, the daubentoniids are most likely to have diverged from the other lemurs shortly after the strepsirhine-haplorhine split, between about 64 and 49 million years ago (Early Palaeocene to Early Eocene). The remaining Malagasy and Afro-Asian families all appear to have diverged within a restricted temporal period between the Mid-Eocene and Early Oligocene approximately 43-29 million years ago. The evolutionary or biogeographic reasons for this vast gap in divergence times have seldom excited interest, although it must be significant for the story of lemur evolution. Montagnon [2012] proposed that the discrepancy in timing indicates that lemurs invaded Madagascar twice from Africa. While this idea is intriguing, it cannot be tested with currently available data.

Extant and subfossil *Daubentonia* are the only known primates to have continuously growing upper and lower incisors. Godinot [2006] postulated a link between the extinct *Plesiopithecus* recovered from site L-41 in the Fayum Depression, Egypt (approx. 40 million years, Late Eocene) and the origins of *Daubentonia*. *Plesiopithecus* had a single pair of large, procumbent lower anterior teeth (probably canines [Simons and Rasmussen, 1994]), although nothing is known of its upper anterior teeth. Any such link would be undermined by the fact that the aye-aye lineage divergence apparently antedates the appearance of plesiopithecids by at least 10 million years. Additionally, large incisors were also present in extinct plesiadapiforms, omomyids and anaptomorphids.

Madagascar's complex topography has undoubtedly influenced the high level of diversification that has occurred on the island [Martin, 1972, 1990; Masters et al., 1995; Pastorini et al., 2003; Wilme et al., 2006], rendering it a biodiversity hot spot [Myers et al., 2000]. De Wit [2003] has described it as a young landscape, consisting of a number of distinct erosion surfaces ranging from near sea level to the grasslands at 1,200-1,500 m. Although dating these erosion surfaces is not possible with the data currently available, there is evidence to suggest that the uplift is not older than the Cenozoic: de Wit attributed ‘the deep young canyons that cut into Cenozoic sediments' as ‘possibly related to the onset of regional plume-induced uplift in East Africa around 30-35 Ma.' Furthermore, ‘[y]oung uplift is also implied by the Neogene-Quaternary age of volcanic activity and associated seismic activity in central and northern Madagascar', the volcanic fields of which ‘stand at least 1,000 m above the surrounding highlands. …enhanced seismic activity and uplift may have triggered a significant increase in erosion rate and induced changes in local climates that in turn may have played a significant role in changes to the vegetation cover of the island' [de Wit, 2003, p. 238].

If major lineage divergences are adaptive responses to climatic and vegetational upheavals, and the primary uplift of Madagascar's central highlands occurred between 35 and 30 million years ago in concert with the uplift in East Africa, this could explain why the mainland and Malagasy families diverged at around the same time (fig. 3). If this interpretation has validity, then the divergence dates we calibrated from the 77.5 million years date for the origin of the primate clade [Chatterjee et al., 2009] accord better with the tectonic history of Africa and Madagascar than do those based on the 10 million years older origin date of Perelman et al. [2011]. The end of the Eocene was also marked by a dramatic period of global cooling and drying (the Grande Coupure) that coincided with the near extinction of the infraorder Adapiformes, the Eocene 'lemurs' of the northern latitudes [Fleagle, 1999], making this period both the beginning and the end for different parts of the strepsirhine radiation.

The Implications of Phylogenetic Advances for Strepsirhine Systematics

The relationship between phylogenetic reconstruction and zoological nomenclature has been clearly articulated. Simpson [1945, p. 12] advised that '...the groups to be recognized in classification should be as nearly as possible valid phylogenetic entities...'. Molecular information regarding phylogenetic relationships should, therefore, feed into our classifications, although there is often great resistance to nomenclatural change. In Simpson's words, '...the rapid advance of taxonomy makes it both inevitable and desirable that it should quickly become outmoded' [1945, p. 3].

The most significant insight into strepsirhine relationships yielded by molecular phylogenetics is the close relationship between lepilemurids and cheirogaleids, to the extent that, when all genera from the two families are sampled, cheirogaleids are paraphyletic. But while this may seem like a novel idea, a review of the systematic literature shows it is anything but. Gray [1863, 1870] viewed *Lepilemur* as a synonym of *Microcebus* (mouse lemurs), including under it *L. murinus (Microcebus murinus)*, *L. myoxinus (M. myoxinus), L. mustelinus* and *L. furcifer(Phaner furcifer)* before erecting the genus *Phaner* in the Appendix to his *Catalogue of the Mammals* a couple of years later. Milne Edwards, Grandidier and Filhol [1897], the great 19th century pioneers of Madagascar's natural history, compiled a folio of exquisite drawings of Malagasy mammals for Grandidier's *Histoire physique, naturelle et politique de Madagascar*. In their atlas, lepilemurs are not included among the species illustrating the diversity of the genus *Lemur*; instead, they appear in a separate part, alongside the Cheirogaleidae. We reproduce their plate 259 here as figure 5.

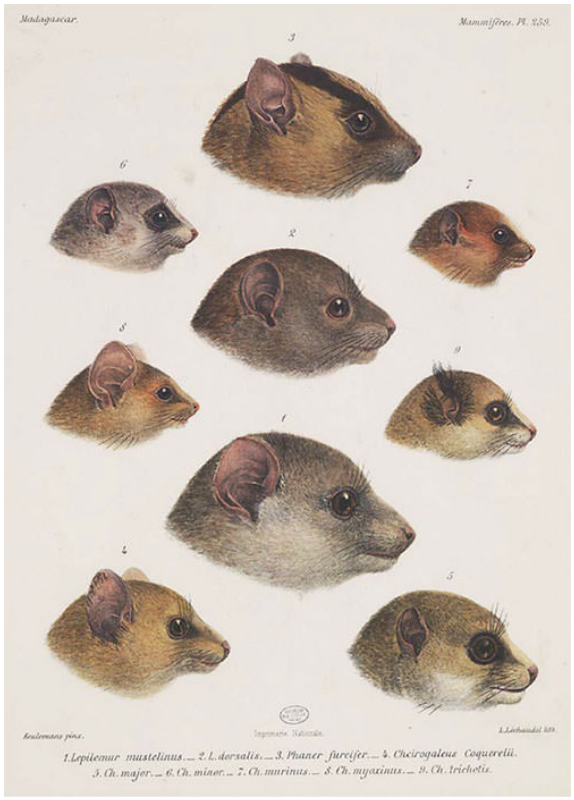

Fig. 5 Plate 259 copied from Milne Edwards et al. [1897] demonstrating the striking similarities in skull conformation shared by lepilemurs and cheirogaleids.

In the early days of the phylogenetic renaissance, Szalay [1968, 1975], on the basis of detailed studies of basicranial morphology, proposed that cheirogaleids had evolved from a lepilemurid ancestor, but was essentially ignored. Results summarized here indicate that it has taken us more than 35 years, countless hours of human effort, and the development of sophisticated methods of molecular and statistical analysis, to catch up with him.

Monotypic families are not particularly informative phylogenetically. They do not assist in reconstructions of clade evolution as they are based on degree of divergence and autapomorphies, rather than shared, derived character states. There is therefore little to be gained by maintaining Lepilemuridae as a separate family, and we recommend that it be subsumed within Cheirogaleidae. *Phaner*, the fork-marked dwarf lemur, shows many transitional traits between *Lepilemur* and cheirogaleids, from its basicranial structures to its hindlimb proportions, and is sometimes placed in its own subfamily Phanerinae [Rumpler and Albignac, 1972]. Resurrecting the subfamily Lepilemurinae, this time as a subfamily of Cheirogaleidae, is appropriate given our current knowledge of strepsirhine affinities.

The relationship between *Lepilemur* and *Megaladapis* remains a mystery. Molecular studies using short DNA sequences deny any relationship between the two genera, but their cranial anatomy argues against this. Both taxa apparently use the vertebral artery for their main cranial blood supply, and both have a complex, identical double system of articulation between the mandible and the glenoid fossa. This conundrum deserves further study.

Molecular data further indicate that the Daubentoniidae diverged far back in strepsirhine history - at least 10 million years before the other extant Malagasy families. This age

discrepancy led Chatterjee et al. [2009] to follow Groves' [2001] taxonomy, placing the genus in its own infraorder, Chiromyiformes. The uniqueness of *Daubentonia*'s morphology certainly suggests that there is a lot we do not know about the evolution of this extraordinary group.

Conclusions

Phylogenetic reconstructions based on nucleotide sequence data indicate that *Lepilemur* species are closely allied to the cheirogaleids, and belong in the same family. The most likely phylogenetic position for the Indriidae is as sister taxon to the Lemuridae, although even the largest molecular data sets have so far been unable to secure this node. The node subtending the Afro-Asian lorisids has been similarly elusive. Hence, although model-based systems may generate resolved but partially unsupported trees, the unresolved trees generated by MP may be closer to the truth. Techniques currently in use for phylogenetic reconstruction seem unable to deal adequately with morphological data, making it difficult to realize the theoretical goal of combined analyses. The gap of approximately 10 million years between the daubentoniid divergence and those of the other Malagasy families warrants greater biogeographic and phylogenetic attention. The emergence of the non-daubentoniid strepsirhine families within a restricted temporal period from the Mid-Eocene to Early Oligocene (approx. 43-29 million years ago) may be related to the onset of regional plume-induced uplift in East Africa around 30-35 million years ago, as well as a dramatic period of global cooling and drying. The forces that drove the extinction of early strepsirhines may thus have been the same ones that drove the emergence of the extraordinarily diverse living lemur fauna, now facing fate similar to that of its Palaeogene forebears.

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