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The red island and the seven dwarfs: Body size reduction in Cheirogaleidae

**Judith C. Masters¹, Fabien Génin¹, Daniele Silvestro^{2,3}, Adrian M. Lister⁴ and
Massimiliano DelPero⁵**

¹African Primate Initiative for Ecology and Speciation, Department of Zoology and Entomology, University of Fort Hare, Alice, South Africa

²Department of Plant and Environmental Sciences, University of Gothenburg, Gothenburg, Sweden

³Department of Ecology and Evolution, Biophore, University of Lausanne, Lausanne, Switzerland

⁴Earth Sciences Department, The Natural History Museum, London, UK

⁵Dipartimento di Scienze della Vita e Biologia dei Sistemi, Università degli Studi di Torino, Turin, Italy

Correspondence: Judith Masters, P.O. Box 12, Hogsback 5721, South Africa.

Abstract

Aim: Small body size in Madagascar's dwarf and mouse lemurs (Cheirogaleidae) is generally viewed as primitive. We investigated the evolution of body size in this family and in its sister-taxon, the Lepilemuridae, from phylogenetic, ontogenetic and adaptive perspectives.

Location: Madagascar.

Methods: We used a phylogenetic method to reconstruct the evolution of body size in lemurs, and allometric regression models of gestation periods and static and growth allometries in Cheirogaleidae and Lepilemuridae to test the hypothesis that dwarfing occurred as a result of truncated ontogeny (progenesis). We also examined adaptive hypotheses relating body size to environmental variability, life history, seasonality of reproduction, hypothermy (use of torpor), and a diet rich in plant exudates.

Results: Our results indicated that cheirogaleids experienced at least four independent events of body size reduction from an ancestor as large as living Lepilemuridae, by means of progenesis. Our interpretation is supported by the paedomorphic appearance and parallel ontogenetic trajectories of the dwarf taxa, as well as their very short gestation periods and increased fecundity. *Lepilemur* species that occupy more predictable environments are significantly larger than those occupying unpredictable habitats.

Main conclusions: Cheirogaleidae appear to be paedomorphic dwarfs, a consequence of progenesis, probably as an adaptation to high environmental unpredictability. Although the capacity to use hypothermy is related to small body size, this advantage is unlikely to have driven dwarfing in cheirogaleids. We propose that gummivory/exudativory co-evolved with body size reduction in this clade, probably from a folivorous ancestor. Their small size is derived, and their suitability as models for the 'ancestral primate' is therefore dubious.

Introduction

The currently popular model of a small, nocturnal primate ancestor was largely inspired by an extant family of Malagasy lemurs, the Cheirogaleidae, which includes the smallest living primates (30–400 g). Mouse lemurs (*Microcebus* spp.), in particular, are believed to have retained a series of primitive characters associated with their very small size (30–100 g): nocturnality, insectivorous/omnivorous diet, fast life history, nest-building, altricial infants carried by mouth, solitary social structure, and a promiscuous mating system (Charles-Dominique & Martin, [1970](#); Cartmill, [1972](#), [1974](#), [1992](#); Martin, [1972](#), [1990](#); Kappeler, [1998](#); Wimmer *et al.*, [2002](#); Gebo, [2004](#); Scheumann & Zimmermann, [2008](#); Montgomery *et al.*, [2010](#); but see Soligo, [2006](#); Masters *et al.*, [2007](#); Soligo & Martin, [2007](#)). This interpretation is frequently associated with a biogeographical scenario that posits that lemurs have evolved from a mouse lemur-like waif which colonized Madagascar from Africa by rafting (Charles-Dominique & Martin, [1970](#); Martin, [1972](#), [1990](#); Yoder, [1996](#); Kappeler, [2000](#)). In this contribution, we interrogate this model of lemur ancestry by examining the evolution of body size in the cheirogaleids and the closely related lepilemurids, from a phylogenetic, an ontogenetic and an adaptive perspective.

The main problem invoked by viewing the Cheirogaleidae and their life histories as primitive is that small size may also be adaptive and may evolve secondarily and convergently in different lineages: a phenomenon termed ‘dwarfism’ and frequently associated with island habitats as part of a syndrome known as the ‘island rules’ (Lomolino, [1985](#); Lister, [1996](#); Whittaker & Fernández-Palacios, [2007](#)). Insular dwarfs often have relatively smaller brains than their continental relatives (e.g. Balearic *Myotragus*, Malagasy *Hippopotamus*, Indonesian *Homo floresiensis*: Köhler & Moyà-Solà, [2004](#); Brown *et al.*, [2004](#); Bromham & Cardillo, [2007](#); Weston & Lister, [2009](#)). Insular dwarfism has also been described in primates (Bromham & Cardillo, [2007](#)), including *Homo floresiensis* (Brown *et al.*, [2004](#)). Within primates, dwarfism not associated with true insularity has been reported in Callitrichinae (marmosets and tamarins) (Ford, [1980](#); Leutenegger, [1980](#); Groves, [1989](#)), and was interpreted by Martin ([1992](#)) as an effect of unpredictable food availability. Using phylogenetic reconstructions, Montgomery & Mundy ([2013](#)) proposed that callitrichines and cheirogaleids have experienced ‘parallel dwarfism’.

Parallel evolution was described by Simpson ([1961](#), p. 103) as ‘the independent occurrence of similar changes in groups with a common ancestry and *because* they had a common ancestry’ (italics original). In more modern phylogenetic terms (e.g. Zhang & Kumar, [1997](#)), parallelism is the development of similar phenotypes in independent lineages from a shared ancestral state; convergence, on the other hand, is the development of similar phenotypes from different ancestral states. In this context, Montgomery & Mundy’s ([2013](#)) invocation of parallel evolution implies that small size is primitive for the primate clade. If cheirogaleids are not primitive strepsirrhines and callitrichines are not primitive haplorhines, however, the concept is inappropriate. Their phylogenetic distance suggests that these small primates present an example of ecological convergence; that is, non-related lineages that underwent convergent dwarfism, probably

as a result of similar environmental constraints (unpredictable conditions and fragmented habitats). In this study, we extend this idea to suggest that dwarfism *within* cheirogaleids is an example of true parallel evolution; that is, body size reduction along similar ontogenetic trajectories among the lineages making up a monophyletic group (Gould, [1977](#)).

The study of ontogenetic influences on lineage evolution has emphasized one kind of developmental bias: temporal changes in development, or heterochrony (Gould, [1977](#); McKinney & McNamara, [1991](#)). This focus has been criticized (Raff, [1996](#)), because developmental reprogramming may alter not only the timing but also the nature (heterotypy), the intensity (heterometry), and the location (heterotopy) of gene expression (Arthur, [2004](#)). McKinney & McNamara's ([1991](#)) generalization of heterochrony has been caricatured, but was based on sound arguments also used by Gould ([1977](#)): (1) development is highly co-ordinated and canalized, thus heterochrony is the most likely source of change; and (2) all evolutionary changes target one ontogenetic stage or another, and therefore have a heterochronic component. Selection targets processes rather than fixed phenotypes.

In this contribution, we adopt the terminology of McKinney & McNamara ([1991](#)), and focus on the life history hypothesis of Gould ([1977](#)), who proposed that environmental variability was the main driver of heterochrony. We make a clear distinction between environmental variability and its predictability; indeed, some types of variability (such as seasonality) are rendered highly predictable by the perception of photoperiodic changes and endogenous rhythms, while others are truly unpredictable because they are caused by recurrent, but irregular, change (El Niño oscillations, for instance) or long astronomical cycles. We examine specifically Gould's life history hypothesis of developmental drive, which posits that small body size may occur as a by-product of fast life history (Gould, [1977](#)). We also consider the alternative hypothesis of direct selection for small body size (Raff, [1996](#)), and assess the adaptive hypotheses of selection for gummivory and heterothermy, two habits frequently associated with dwarfed arboreal mammals occurring in fragmented and hypervariable habitats, notably in cheirogaleids and callithrichines (Génin, [2008](#); Génin *et al.*, [2010](#)).

Moreover, we adopt Gould's ([1977](#)) distinction between growth and development. Changes in growth may lead to facultative isometric changes in body size; that is, they do not affect the relative proportions of the descendants, and comprise faster (acceleration) or slower (neoteny) rates of growth than were shown by the ancestor. Growth changes can be diagnosed by a dissociation of the growth allometries of the ancestor and its descendants. By contrast, changes in development are changes affecting ontogeny without necessarily affecting the rate of growth. They comprise truncated (progenesis) or prolonged (hypermorphosis) ontogenies, and are often diagnosed by the association of static and growth bivariate allometries because they occur in late ontogeny. Such changes are accompanied by obligatory shifts in body size: progenesis with phyletic dwarfism and hypermorphosis with phyletic gigantism. Such body mass shifts reflect ancestral growth allometries and are linked to characteristic, parallel changes in shape.

The main hypothesis of our study is that the small size of Cheirogaleidae is phylogenetically derived; cheirogaleids are paedomorphs and show characters found in the juveniles of related lemur taxa. Our investigation took three approaches, corresponding to three fundamental levels of evolution. The phylogenetic context, based on recent phylogenies that group the Cheirogaleidae and the Lepilemuridae as a single clade (see Masters *et al.*, 2013), was used to reconstruct the evolution of body size in this group, leading to a hypothesis of recurrent dwarfism. We investigated the ontogenetic context, specifically the hypothesis of progenesis, by comparing the allometries of juvenile Lepilemuridae with static allometries of adult Cheirogaleidae. Finally, we examined Gould's (1977) hypothesis of small size as a by-product of fast life history selected in hypervariable environments, and two functional alternatives based on correlates of small body size in arboreal mammals: hypothermy and gummivory.

Materials and methods

Phylogenetic analysis and body mass reconstruction

We based our reconstruction of body mass evolution on the mtDNA phylogenies recovered by Chatterjee *et al.* (2009) and Masters *et al.* (2013) because these were the only studies to include all cheirogaleid genera. The trees were identical to one another, and congruent with that published by Perelman *et al.* (2011) based largely on nuclear sequences, but omitting the cheirogaleid genera *Allocebus* and *Phaner*. We extracted a sub-clade of 62 strepsirrhine species (i.e. Lorisiformes and Lemuriformes) from the maximum credibility tree of 219 species obtained using relaxed molecular clock analyses by Chatterjee *et al.* (2009). We inferred ancestral body masses using a comparative method recently developed by Lartillot & Poujol (2011) that combines divergence time estimates using a relaxed molecular clock, Brownian processes of evolution, and phylogenetically independent contrasts. This Bayesian method accounts for the potential correlation (estimated from the data) between the rates of molecular evolution and the value of a continuous trait, to perform a joint estimation of evolutionary rates (for both nucleotide substitution and phenotypic traits), divergence times and ancestral states. A uniform prior ranging from 72 to 35.9 Ma was assigned to the crown age of the strepsirrhine clade as a secondary calibration reflecting the respective 95% credibility interval obtained by Wilkinson *et al.* (2011) in their dating of the primate clade. The narrower range obtained by Chatterjee *et al.* (2009), i.e. 55.8 to 47.4 Ma, was also tested for comparison. A joint estimation of ancestral body masses and branching times was obtained by Markov chain Monte Carlo (MCMC) sampling as implemented in Coevol 1.3 (Lartillot & Poujol, 2011) assuming a model that allows for correlation between rates of molecular evolution and rates of change in log body mass. Sampling efficiency and convergence were assessed by calculating the effective sample size (ESS) and the relative discrepancies between two independent runs (Lartillot *et al.*, 2009). Marginal estimates of ancestral body masses were obtained by summarizing the MCMC samples and plotted on

to the phylogeny. MCMC cycles, after a burn-in phase of 1000 cycles, were run until ESS values were greater than 150 for all parameters, and relative discrepancies were smaller than 0.05.

The pattern of body mass evolution was further investigated by testing whether a directional change could be detected throughout strepsirrhine evolutionary history. Maximum likelihood analyses were run using BayesTraits 2 (Pagel & Meade, 2013) to compare the directional model (Model B; Pagel, 1999) of evolution against a Brownian (non-directional) model (Model A). The directional model needs to be run on a phylogram (i.e. with branch lengths expressed as expected numbers of substitutions), and estimates a regression coefficient for the trait that can take negative or positive values to indicate a trend towards smaller or greater values, respectively. Based on the tree topology used in the Coevol analyses and on the mtDNA alignment of Masters *et al.* (2013), we estimated the branch lengths using raxmlGUI under the GTRGAMMA model (Stamatakis, 2006; Silvestro & Michalak, 2012). Maximum likelihood scores were calculated under models A and B and compared using a likelihood ratio test (LRT). The analyses were repeated on the Lepilemuridae–Cheirogaleidae (LC) clade only, after pruning its sister clades.

Morphological data collection

We took measurements from cheirogaleid and lepilemurid specimens housed in the Natural History Museum (London) and the Muséum National d'Histoire Naturelle (Paris), the world's two most comprehensive collections of these taxa (Table 1, and see Appendix S1 in Supporting Information). The number of valid lemur species is a matter of great contention (Tattersall, 2007), as new species are often described on the basis of limited numbers of DNA sequences or museum specimens, and await more extensive biological verification. Cheirogaleid specimens are also relatively rare in museum collections, particularly juveniles, although no species is as rare as *Allocebus trichotis*, the hairy-eared dwarf lemur. [This taxon is represented by five specimens in three museums around the world; only two have skulls available for study, one of which is incomplete. The species was thought to be extinct until its rediscovery in 1989, and no additional museum specimens have been collected since then.] For these reasons, we used genera (or species-groups in the case of *Cheirogaleus*) rather than species in our analysis. This also allowed us to gain a broader appreciation of the size variation inherent in the genera/species-groups. Our sample comprised the following Cheirogaleidae species-groups: greater dwarf lemurs (*Cheirogaleus major*, *C. sebreei*), lesser dwarf lemurs (*C. medius*, *C. adipicaudatus*), giant mouse lemurs (*Mirza coquereli*), mouse lemurs (*Microcebus* spp.), hairy-eared dwarf lemurs (*Allocebus trichotis*), and fork-marked dwarf lemurs (*Phaner* spp.), as well as diverse Lepilemuridae (sportive lemurs). Sub-adults with adult cranial sizes but incompletely erupted dentitions were classified as adults. The sampling of *Lepilemur* spp. included four juvenile and five adult *Lepilemur ruficaudatus* specimens used to construct an ontogenetic model (Table 1). The skulls are illustrated diagrammatically in Fig. 1. Fifteen cranial measurements were taken from 96 adult and 7 juvenile skulls, and three hind limb measurements were taken from 51 adult skeletons. Total hind limb length was evaluated as femur shaft length + tibial shaft length +

calcaneal length. Linear measurements were recorded to an accuracy of 0.1 mm using digital callipers, and descriptions of the measurements are listed in Appendix S1. The area of the foramen magnum (FM) was estimated as that of a circle with a radius equal to half the average of the height and width measurements, and linearized with a square-root transformation. Cranial volume (CV) was measured to an accuracy of 1 ml using a 50:50 mixture of 1.5 mm and 2 mm polypropylene balls supplied by Precision Plastic Balls Company Ltd, Ilkley, UK. The volumetric estimates were linearized with a cube-root transformation.

Table 1. *Lepilemur* and cheirogaleid species included in this study. Hind limb lengths and basicranial lengths are geometric means.

Species	Body mass (g)*	Head–body length (mm)	Hind limb length (mm)	n	Basicranial length (mm)	n	DFA group**
LEPILEMURIDAE							
<i>Lepilemur dorsalis</i>	615	255	—	—	40.04 ± 0.58	4	L
<i>Lepilemur edwardsi</i>	1000	280	196.23 ± 5.51	4	46.93	1	L
<i>Lepilemur microdon</i>	1085	325	226.80 ± 0.43	2	49.91	2	L
<i>Lepilemur mustelinus</i>	809	325	226.39 ± 3.21	4	47.52 ± 0.72	12	L
<i>Lepilemur ruficaudatus</i>	807	280	195.45	1	47.17 ± 0.52	5	L
<i>Lepilemur ruficaudatus</i> juveniles	—	—	—	—	28.38 ± 42.65	5	L
CHEIROGALEIDAE							
<i>Allocebus trichotis</i>	83	145	78.38	1	30.37	2	H
<i>Cheirogaleus adipicaudatus</i>	—	170	—	—	36.32 ± 0.58	4	H
<i>Cheirogaleus major</i>	364	240	119.56 ± 2.38	11	46.80 ± 0.23	20	D
<i>Cheirogaleus medius</i>	188	215	87.43 ± 1.15	3	34.80 ± 0.24	19	H
<i>Cheirogaleus sabreei</i>	—	—	—	—	42.14	1	D
<i>Microcebus griseorufus</i>	57	123	—	—	26.09	1	H
<i>Microcebus murinus</i>	62	130	71.68 ± 0.51	10	26.95 ± 0.46	6	H
<i>Microcebus myoxinus</i>	40	125	68.36	1	25.83	1	H
<i>Microcebus rufus</i>	49	125	63.11 ± 3.21	3	25.81 ± 0.46	6	H
<i>Mirza coquereli</i>	308	250	122.87 ± 6.44	3	41.40 ± 0.32	11	D
<i>Phaner (furcifer) pallescens</i>	403	260	150.67 ± 3.88	8	42.88 ± 0.30	12	D

*Body masses from Mittermeier *et al.* (2010) and Rowe (1996); other data original; **discriminant function analysis (DFA) categories: L, *Lepilemur*; D, dwarf; H, hyper-dwarf.

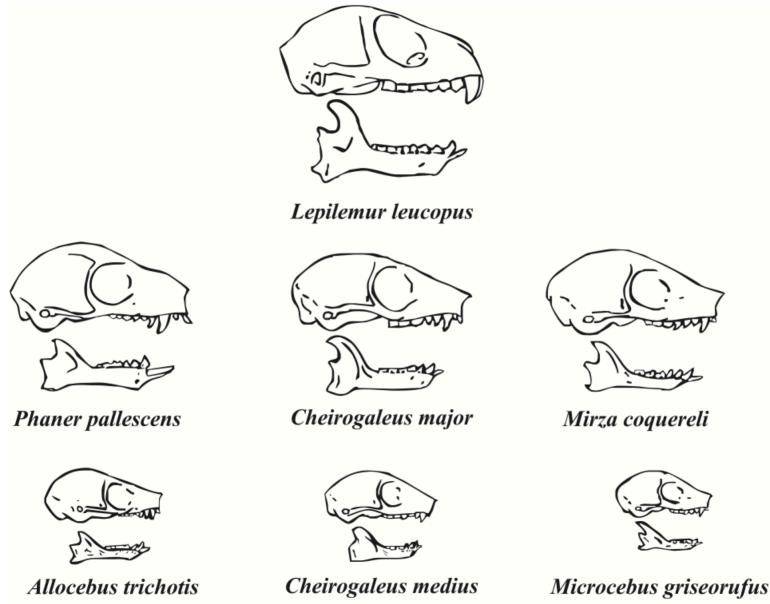


Figure 1. Diagrammatic representation of skulls of genera/species-groups making up the endemic Malagasy Lepilemuridae–Cheirogaleidae clade, drawn to scale.

Morphometric analyses

We constructed a relative time-based allometric model, under the assumption of parallel dwarfism (progenesis: static allometry is parallel to the ancestral ontogenetic allometry; Gould, 1977). For this, we plotted mean measurements of four species of cheirogaleids and *Lepilemur ruficaudatus* for five cranial and post-cranial measurements against developmental duration calculated as gestation + suckling periods: head–body length (HB), hind limb length (HL), basicranial length (BL), total cheek tooth row (CR) and cranial volume (CV). Data on body masses, durations of gestation and suckling periods, mating and birth seasons of Cheirogaleidae and Lepilemuridae were gleaned from Rowe (1996), Garbutt (2007) and Mittermeier *et al.* (2010). The plots allowed us to compare an estimate of *Lepilemur* neonatal size with the sizes of adult cheirogaleids using *Lepilemur* gestation duration as predictor and the time-based regression of adult measurements as a predictive model: an underestimation of *Lepilemur* neonatal size would mean that progenesis was associated with neoteny, while an overestimation would indicate ontogenetic acceleration. In addition, we compared the time-based allometries (predicted growth rate) of four characters with their size-based allometries: negative allometry should reveal early ontogeny relative to HB, while positive allometry should reveal late ontogeny relative to HB.

Because the juvenile specimens could not be aged, we used multivariate and bivariate analyses to investigate the size-based allometry of cheirogaleids and lepilemurs ('internal time' in the terminology of McKinney & McNamara, 1991). All means for cranial measurements are geometric means which have the advantage of scaling linearly and

being expressed in the original units. Using all 15 cranial variables and the 96 adult skulls, we performed a discriminant function analysis (DFA) to compare the taxa with one another in multivariate space, as well as a principal components analysis (PCA) on log-transformed data to determine the relative contributions of cranial variables to the overall variation in the sample. In the DFAs we used standardized data to test the hypothesis that cranial shape is constrained by cranial size. Standardization was achieved by dividing each value by the geometric mean of all measurements for an individual as a proxy for cranial size. The pre-defined groups for the DFA were the general size groups into which the focal taxa fell: (1) lepilemurids; (2) large cheirogaleid taxa ('dwarfs'); (3) small cheirogaleid taxa ('hyper-dwarfs') (see Table 1). To test the progenesis hypothesis, we performed a second DFA including all juvenile and adult specimens ($n = 103$). Because our hypothesis implies a shift in diet leading to a major change in dental size, we only used the nine non-dental cranial characters, also standardized, in this analysis.

Our hypothesis of progenesis requires juvenile specimens only of the taxon believed to represent the ancestral developmental pathway. We used an ontogenetic model based on nine skulls attributed to *Lepilemur ruficaudatus* (four juveniles and five adults) compared with the static allometry of cranial characters of cheirogaleid and lepilemur skulls. We used basicranial length (BL) as the independent factor (proxy for cranial size). The *Lepilemur* ontogenetic series was constructed using BL-based allometric regressions of cranial variables in the four juvenile specimens, with an average of the five adult *L. ruficaudatus* specimens making up the fifth point. Six characters did not show any growth within the range of variation of the *Lepilemur* ontogenetic series [tympanic aperture (TA) and tooth sizes (M1W, M1L, M3W and M3L)], or evinced a discrete growth pattern corresponding to tooth eruption times [cheek tooth row (CR)], and were excluded from the ontogenetic model. The model was constructed by selecting the 63 specimens that fell within the range of size variation of the *Lepilemur* ontogenetic series. We used 95% confidence intervals to compare the slopes and y-intercepts obtained in the regressions of adult allometries and the ontogenetic series. In addition, we included three juvenile specimens (one each of *Microcebus rufus*, *Mirza coquereli* and *Phaner pallescens*), and estimated relative growth based on each juvenile and the means of all available adult specimens, although this small sample size did not allow for statistical analyses.

We used the same ontogenetic regression model to predict nine cranial variables, with BL as predictor, and calculated percentages as predicted value/observed value $\times 100$. These percentages were averaged using geometric means for the 96 adult specimens (prediction per character), as well as for the Lepilemuridae (*Lepilemur* spp.) and the six cheirogaleid species-groups: *Phaner*, *Mirza*, the greater and lesser forms of *Cheirogaleus*, *Allocebus* and *Microcebus* spp. (prediction per character and species-group).

Body size and environmental predictability

To test the relationship between body size and habitat predictability, we used the predictability index (PI) calculated by Dewar & Richard (2007), which is the sum of intra- and inter-annual constancy indexes, and ranges from 0 to 1. We focused on

Lepilemur, which conveniently shows high diversity throughout Madagascar (i.e. 26 named species, making *Lepilemur* the most species-rich lemur genus; Mittermeier *et al.*, 2010). We calculated a specific predictability index (p) by averaging the PI-values of the Malagasy localities estimated by Dewar & Richard (2007) and included within the distribution ranges (or within 100 km of the locality and not separated from it by any geographical barriers) of 11 *Lepilemur* species: *L. edwardsi*, *L. fleuretae*, *L. hubbardorum*, *L. leucopus*, *L. microdon*, *L. mustelinus*, *L. petteri*, *L. randrianasoloi*, *L. scottorum*, *L. seali* and *L. septentrionalis*.

Results

The phylogenetic context: parallel dwarfing in Cheirogaleidae

Estimation of ancestral body weights at phylogenetic nodes

As shown in Fig. 2, lepilemurids are phylogenetically inseparable from Cheirogaleidae, and this is reflected in all recent phylogenies (Chatterjee *et al.*, 2009; Perelman *et al.*, 2011; Masters *et al.*, 2013). Lepilemurs are the second smallest lemurs after cheirogaleids, with the various species ranging from 600 g to ≥ 1 kg. The joint reconstruction of divergence times and body size evolution using Coevol indicated a weak negative correlation between the rates of nucleotide substitution and body mass, with a correlation coefficient $r = -0.267$ and a posterior probability = 0.944. The estimated ages of most nodes were (unsurprisingly) comparable to those of Chatterjee *et al.* (2009), but the more conservative calibration settings of Wilkinson *et al.* (2011) yielded larger uncertainty around the nodal age estimates (here reported as standard deviations; see Appendix S2). Body size reconstructions were found to be largely congruent under the two calibration settings, hence only the results obtained under Wilkinson's secondary calibrations are presented. Body size evolution reconstructed along the tree as marginal ancestral states (Fig. 2, Appendix S2) is likely to have involved repeated dwarfing events in the LC clade (blue lineages in Fig. 2): an initial dwarfing event from a common ancestor similar in size to living *Lepilemur* spp. to the three largest cheirogaleid forms (*Phaner*, *Mirza* and greater *Cheirogaleus*), followed by three hyper-dwarfing events leading to the smallest forms (lesser *Cheirogaleus*, *Allocebus* and *Microcebus*). The ancestral state reconstructions generated the following body mass estimates for the clade ancestors: 973 g (central 95% range: 259–1688 g) for the common ancestor of the Malagasy lemuriforms; 927 g (central 95% range: 409–1446 g) for the common ancestor to the non-daubentoniid lemuriforms, and 766 g (central 95% range: 319–1212 g) for the common ancestor to the LC clade. (Inclusion of the subfossil giant lemurs would double the reconstructed body weight of the lemuriform ancestor to c. 2 kg; see Masters *et al.*, 2007.)

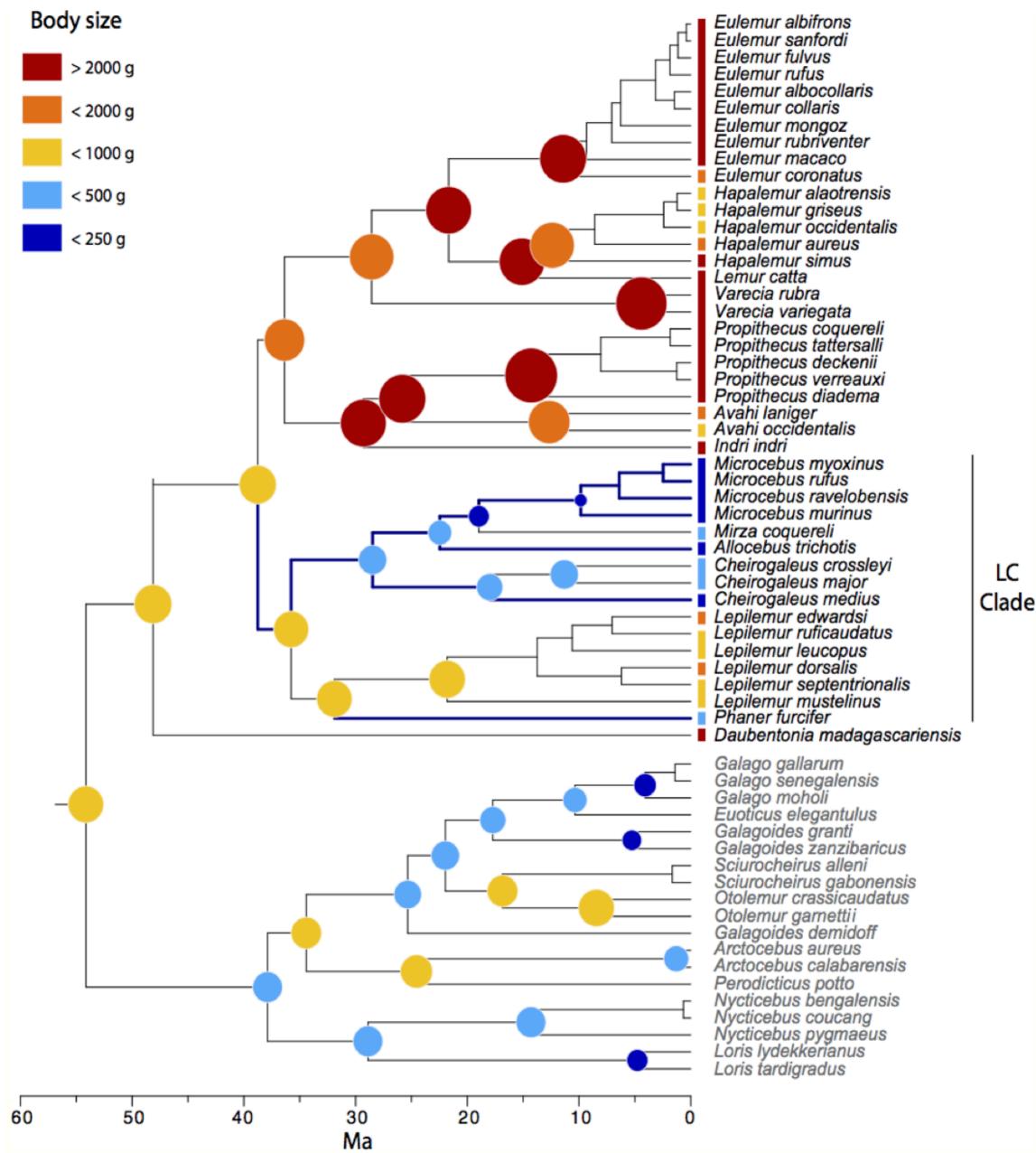


Figure 2. Ancestral body mass reconstructions in Strepsirrhini, based on the tree recovered by Chatterjee *et al.* (2009) using relaxed molecular clock analyses, and the comparative method of Lartillot & Poujol (2011). The latter combines divergence time estimates using a relaxed molecular clock, Brownian processes of evolution, and phylogenetically independent contrasts. LC clade = Lepilemuridae–Cheirogaleidae clade.

Our BayesTraits analyses also provided evidence of a trend towards body size reduction. The directional Model B was preferred against the standard Brownian Model A based on the entire strepsirrhine tree (log-likelihoods = $-60.69/-64.26$), as well as on the LC clade alone (log-likelihoods = $-17.50/-26.18$). In both cases Model A was rejected with a P -value < 0.01 based on the LRT. The regression coefficient, representing the slope of the evolutionary trend from the root to the tips, was estimated to be negative on both the entire tree and the LC clade (-19.23 and -22.29 , respectively) indicating a general reduction in body size from the ancestors to the extant descendants.

The DFAs of standardized adult cranial characters (Fig. 3a,b) produced a clear separation among the three size groups (*Lepilemur* spp. and the greater and lesser cheirogaleids). These groupings were not concordant with phylogenetic relatedness, indicating that strikingly similar, parallel changes in shape accompanied body size reduction in distinct lineages during the evolution of the LC clade, despite very different ecologies, i.e. parallel rather than convergent evolution (for canonical scores see supplementary data Appendix S3).

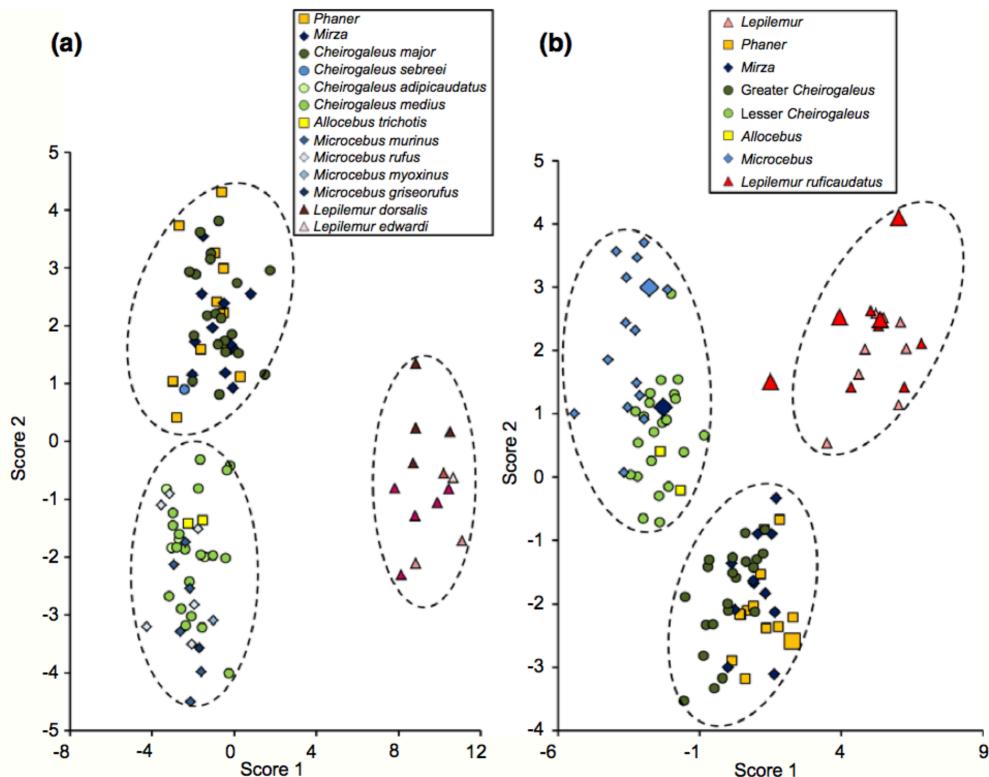


Figure 3. Graphical results of discriminant function analyses conducted on craniodental morphometrics of the Malagasy lemur families Cheirogaleidae and Lepilemuridae. The size/shape metrics cluster the taxa into three clearly distinguished groups that do not reflect phylogenetic affinities, indicating that shape is essentially determined by size in this clade. The clusters include respectively: lepilemurs; the larger cheirogaleids [*Cheirogaleus major* s.l., *Mirza* spp. and *Phaner* spp. ('dwarfs')]; and the smaller cheirogaleids [*Allocebus*, *C. medius* s.l. and *Microcebus* spp. ('hyper-dwarfs')]. (a) 15 standardized craniodental measurements of 96 adult specimens; (b) nine standardized non-dental cranial measurements including seven juvenile specimens (large symbols).

The seven dwarfs

Our ancestral state reconstructions estimated the body weight of the common LC ancestor as 766 g – similar to the average weight of extant *Lepilemur* spp. Although they are not sister-taxa, *Phaner* and *Allocebus* share several morphological similarities, and *Allocebus* resembles a miniaturized *Phaner* in many ways (Fig. 1; see also Schwartz & Tattersall, 1985). For example, *Phaner* spp. (fork-marked lemurs) are characterized by a dark dorsal stripe that forks over the eyes (Mittermeier *et al.*, 2010), and by striking adaptations for gummivory, including very large hands and feet, sharply pointed, keeled nails that allow them to cling vertically to tree trunks while feeding, as well as dental and digestive specializations (Charles-Dominique & Petter, 1980; Génin *et al.*, 2010). From our own field observations, hairy-eared dwarf lemurs, *Allocebus trichotis*, also have proportionally large hands and feet equipped with sharply pointed, keeled nails. *Allocebus* sometimes exhibits a true dorsal stripe, a character otherwise found only in *Phaner* among Malagasy lemurs. The dentitions of the two genera are extremely similar, with elongated, horizontal tooth combs, large upper canines, and enlarged, caniniform P²'s, interpreted as adaptations to gummivory on the basis of their convergence with the gummivorous African galagid *Euoticus* (Schwartz & Tattersall, 1985; Génin *et al.*, 2010). The close relationship between *Mirza* and *Microcebus* is widely accepted and indicated by both morphometric and genetic similarities. *Microcebus* is characterized by rounded nails, in contrast to the pointed nails observed in all other cheirogaleids and in *Lepilemur*, suggesting they are apomorphic (Soligo & Martin, 2007). Finally, the presence of greater and lesser species within *Cheirogaleus* suggests recent body size reduction in this genus. *Cheirogaleus adipicaudatus* and *C. medius* were not distinguished by our analysis, supporting the proposal that they represent a single species (Mittermeier *et al.*, 2010).

The ontogenetic context: paedomorphic dwarfism in Cheirogaleidae

Progenetic paedomorphosis in Lepilemuridae and Cheirogaleidae

In the LC clade, the smallest adult forms bear a striking resemblance to the juveniles of the largest forms, with typical paedomorphic traits: large heads, large eyes and shorter limbs (Gould, 1977; Appendix S3). When various cranial and post-cranial measurements are plotted against the total duration of ontogeny, the resulting graph can be interpreted as a paedomorphocline resulting from parallel evolution (Fig. 4a). In primates, the head shows fast development while the limbs show slow development relative to the rest of the body (Gould, 1977).

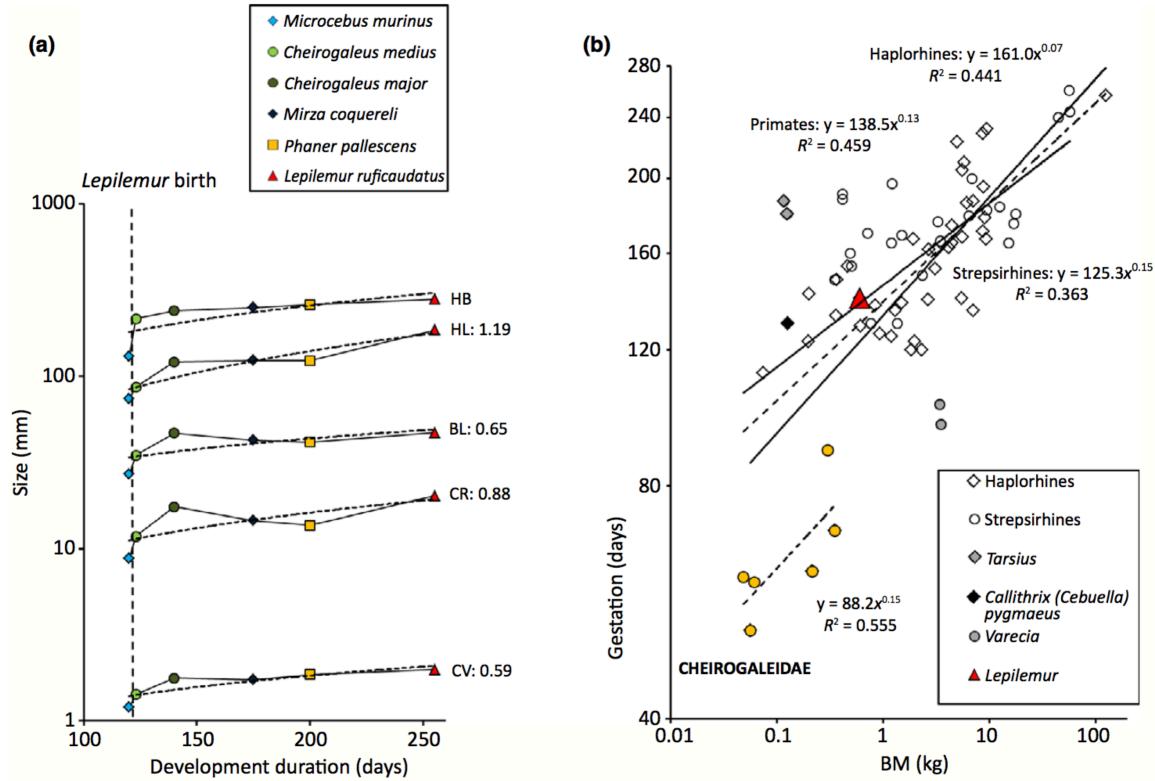


Figure 4. Madagascar's cheirogaleids evolved shorter development resulting in dwarfism. (a) Time-based model of parallel dwarfism for head–body length (HB) and hind limb length (HL) and three cranial characters [basicranial length (BL), total cheek tooth row (CR) and cranial volume (CV)] plotted against development duration. The vertical dashed line indicates the end of *Lepilemur* gestation. If the mean values for the five adult cheirogaleid taxa simply reflected stages in *Lepilemur* ontogeny (estimated ontogenetic trajectories indicated by solid lines), *Lepilemur* newborns should have the size of adult *Cheirogaleus medius* (for instance BL ± 35 mm; body mass ± 200 g). The model overestimates neonatal size, so development is likely to have been accelerated in hyper-dwarfed cheirogaleids (see '[Materials and methods](#)' for data sources). We also indicate time-based regression lines (dotted lines) compared with HB-based allometric exponents for four characters (Appendix S3). (b) Relationship between body mass (BM) and gestation duration in primates, showing lower y-intercepts in the Cheirogaleidae.

The size predicted for a newborn *Lepilemur* by this allometric model (Fig. 4a) is too large to fit a simple model of progenesis from a larger ancestor, and is close to the size of an adult *C. medius* (BL ± 35 mm; mass ± 200 g). Although we do not have body mass data for *Lepilemur* neonates, the smallest *L. ruficaudatus* juvenile skull we measured was probably not newborn but young enough to have encrypted molars, and its BL (28.4 mm) was shorter than that of any *C. medius* adult we measured. This suggests that at least the hyper-dwarfed cheirogaleids have also experienced ontogenetic acceleration. Cheirogaleids have altricial infants and the shortest gestation durations of all primates, even relative to their small body sizes, confirming that dwarfism involved changes in prenatal development (*t*-test on body mass-independent residuals: $t_{72} = 6.5$, $P < 0.001$; Fig. 4b). Because the paedomorphic appearance of cheirogaleids is more pronounced in the smaller forms, and their development is shorter, the most likely process involved in

the reduction of body size in the dwarfed and hyper-dwarfed forms is a truncation of development, or progenesis (Gould, [1977](#); Alberch, [1980](#); McKinney & McNamara, [1991](#)).

The ontogenetic model: a test of the progenesis hypothesis

The second DFA performed on all specimens, but excluding dental characters, yielded two misclassifications, which indicated that the youngest specimen of *Lepilemur ruficaudatus* was similar in shape to the greater cheirogaleids, while the youngest specimen of *Mirza coquereli* fell into the hyper-dwarfed category (Fig. [3b](#), Appendix S3.)

We performed a PCA on the 96 adult specimens, including all 15 non-standardized characters, and extracted the loadings of these characters on the first component. These loadings were then correlated with the relative growth of the same characters in *Lepilemur ruficaudatus*, evaluated as the difference between the average adult measurement ($n = 5$) and the measurements of the smallest juvenile specimen. Because only 10 characters showed a size increase in the *Lepilemur* juveniles, only 10 characters were used for this correlation. The two sets of variables were significantly and positively correlated ($r = 0.927, n = 10, P < 0.001$). The characters that developed late in *Lepilemur* ontogeny (and showed their highest growth rate in late ontogeny) were those that varied most in adult cheirogaleids and *Lepilemur* (Appendix S3). This result supports the contention that the evolution of cheirogaleid body size and shape is largely due to changes in their late ontogeny.

We assessed the general validity of the model by predicting the measurements of cranial characters, first among the 63 cheirogaleid specimens that fell within the juvenile *Lepilemur* size range (Table [2](#)), and then for the seven species-groups (Table [3](#)). We calculated the percentage size predicted for each BL by the *Lepilemur* ontogenetic series plus a single average point for all *L. ruficaudatus* adult measurements. The model was a good predictor (93%–103% actual size) for eight adult cheirogaleid cranial measurements out of nine, but highly overestimated cranial volume (CV, 78%) (Table [2](#)), especially in the smallest forms (Table [3](#); *Microcebus* = 48%, *Allocebus* = 51% and *C. medius* = 63%).

Table 2. Cranial measurements in *Lepilemur* and Cheirogaleidae: ontogenetic model using basicranial length as a proxy for cranial size ($n = 63$). Cranial characters: ZW, zygomatic width; PL, palatal length; MW, mastoid width; OD, orbital diameter; IO, interorbital width; TC, temporal constriction; CV, cranial volume; FM, foramen magnum

Cranial characters	% prediction	Slope		γ -intercept (mm)		R^2		
		Allometry	Ontogeny	Allometry	Ontogeny	Allometry	Ontogeny	Association
ZW	97 ± 1	0.726 ± 0.015	0.723 ± 0.086	0.192 ± 0.041	0.240 ± 0.013*	0.855	0.948	A
PL	103 ± 2	1.023 ± 0.023	0.986 ± 0.096	-0.347 ± 0.057	-0.328 ± 0.139	0.884	0.964	A
MW	99 ± 2	0.969 ± 0.021	1.189 ± 0.129*	-0.073 ± 0.054	-	0.883	0.955	D
OD	98 ± 2	0.896 ± 0.020	0.896 ± 0.175	-0.318 ± 0.050	-0.371 ± 0.015*	0.868	0.957	A
IO	96 ± 5	1.112 ± 0.023	0.825 ± 0.182*	-0.953 ± 0.062	-	0.727	0.839	D
TC	93 ± 4	0.993 ± 0.039	0.499 ± 0.113*	-0.378 ± 0.055	-	0.577	0.830	D
CV	78 ± 13	0.928 ± 0.048	0.598 ± 0.124*	-1.270 ± 0.052	-	0.843	0.854	D
FM	93 ± 3	0.750 ± 0.051	0.890 ± 0.180*	-0.391 ± 0.030	-	0.664	0.861	D

'Association' refers to non-significantly different allometric slopes (*significant), using a 95% confidence interval and adult cheirogaleid measurements: A, association; D, dissociation. 'Ontogeny' refers to the regression line fitted to *Lepilemur* ontogeny. 'Allometry' refers to the regression line fitted to adults of all taxa within the *Lepilemur* ontogenetic size range. '% prediction' is calculated using the measures predicted for a juvenile *Lepilemur* of the same basicranial length.

Table 3. Percentage of sizes predicted by the ontogenetic trajectories of *Lepilemur ruficaudatus* for adult specimens of Cheirogaleidae and Lepilemuridae genera

Group	<i>n</i>	Mastoid width (MW)	Palatal length (PL)	Zygomatic width (ZW)	Orbital diameter (OD)	Interorbital width (IO)	Temporal constriction (TC)	Foramen magnum area (FM)	Cranial volume (CV)
<i>Lepilemur</i>	13	99	100	100	99	98	98	96	93
<i>Phaner</i>	12	96	103	99	98	100	98	92	91
<i>Allocebus</i>	2	98	105	99	102	87	92	96	51
Greater <i>Cheirogaleus</i>	21	97	104	98	98	99	90	90	78
Lesser <i>Cheirogaleus</i>	23	97	103	101	98	93	88	93	63
<i>Mirza</i>	11	97	104	98	98	92	95	94	85
<i>Microcebus</i>	14	97	103	103	104	74	91	96	48

¹We used size groups in the case of *Cheirogaleus*.

Lepilemur ontogenetic and cheirogaleid adult allometries showed remarkable similarity (Fig. 5a). As expected, their relationships to BL in bivariate log-transformed space showed negative allometry or were close to isometry, and we observed close allometry/ontogeny association in three characters of overall shape that showed major growth in the late ontogeny of *Lepilemur*: Zygomatic width (ZW), palatal length (PL) and orbital diameter (OD) (Fig. 5a). 'Dissociation', inferred from significantly different allometric slopes between *Lepilemur* ontogenetic series and cheirogaleid adults using a 95% confidence interval, was observed in characters that grew early in *Lepilemur* ontogeny, supporting the interpretation of early acceleration.

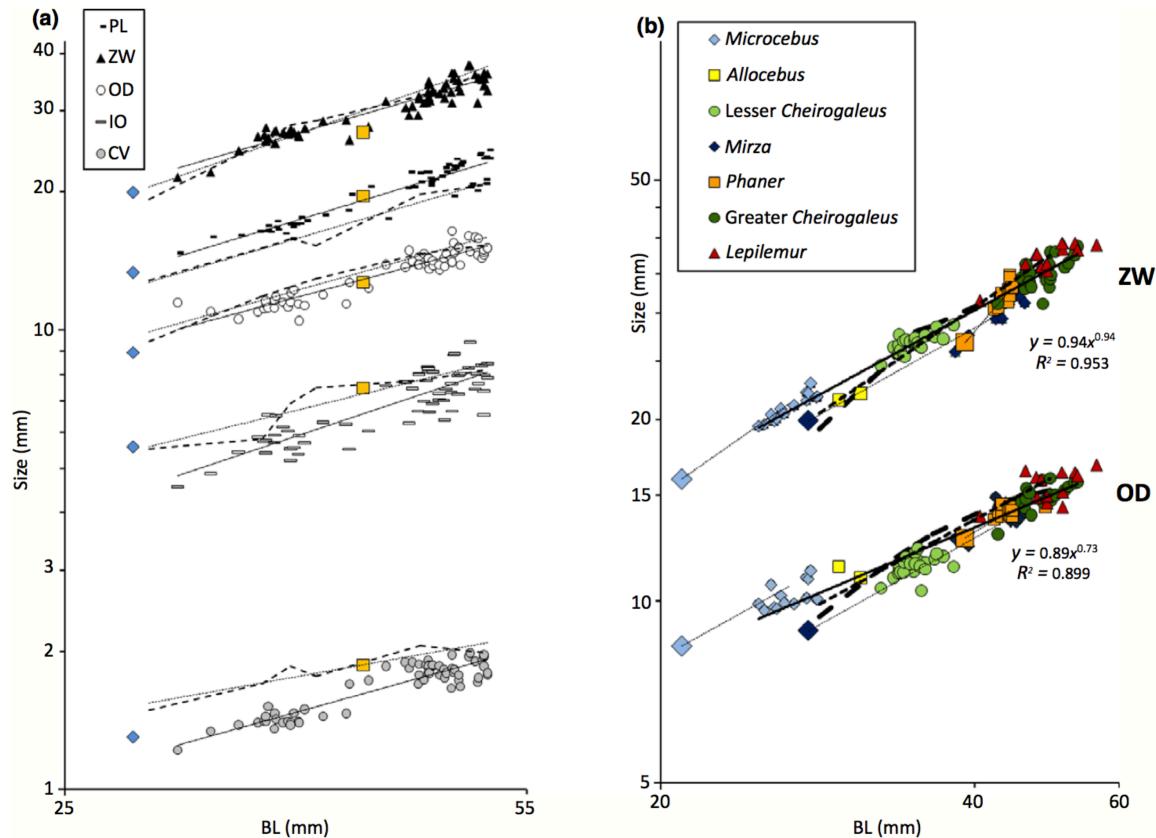


Figure 5. Ontogenetic model of dwarfism in Malagasy mouse and dwarf lemurs (Cheirogaleidae). (a) Cranial allometry in five characters [palatal length (PL), zygomatic width (ZW), orbital diameter (OD), interorbital width (IO) and cranial volume (CV)] from 63 adult specimens of Lepilemuridae and Cheirogaleidae (solid line: regression) and *Lepilemur* ontogenetic trajectory (dashed lines). The allometric regression of the ontogenetic series is in dotted lines. The different symbols refer to different characters. (b) The same relationship for the two best associated cranial characters [zygomatic width (ZW) and orbital diameter (OD)] showing allometric slopes (dotted lines) and the *Lepilemur* ontogenetic series (bold dashed lines), but with different taxa represented by different symbols. In both (a) and (b), juvenile specimens are indicated by large symbols: *Mirza* = dark blue diamonds; *Microcebus* = pale blue diamonds; *Phaner* = orange squares.

Although our sample size was too small for statistical analysis, we included three juvenile specimens (*Microcebus rufus*, *Mirza coquereli* and *Phaner pallescens*) to observe their positions on the plots, which needed to be extrapolated to fit the very small juvenile *M. rufus* specimen (Fig. 5b). The *Mirza* juvenile and subadults followed both the *Lepilemur* ontogenetic trajectory and the adult allometries of all cheirogaleids except *Microcebus* and *Phaner*. In contrast, the *Microcebus* ontogenetic and adult allometries were associated, but dissociated from the *Lepilemur* ontogenetic series and other adult allometries although they showed similar slopes, indicating ontogenetic acceleration (Fig. 5b). The *Phaner* ontogenetic and adult allometries were associated, and both were sometimes dissociated from (ZW and PL) and sometimes associated with (OD, IO, CV) the *Lepilemur* ontogenetic trajectories (Fig. 5a, b).

The adaptive context: natural selection and body size

Environmental hypervariability and progenesis: a test using Lepilemur

We tested our hypothesis that dwarfism in the LC clade evolved under the influence of environmental hypervariability using *Lepilemur*, which conveniently shows high diversity throughout Madagascar. We found a positive correlation between the specific habitat predictability index (p) and body mass (logarithmic correlation: $n = 11, r = 0.904, P < 0.001$; Fig. 6). The taxa found in the most unpredictable regions of the island (south, west and extreme north) are significantly smaller than the forms found in the east. The smallest forms, found in the western deciduous forest and the southern xerophytic thicket, also have relatively larger eyes and narrower snouts than the large eastern forms (Fig. 6).

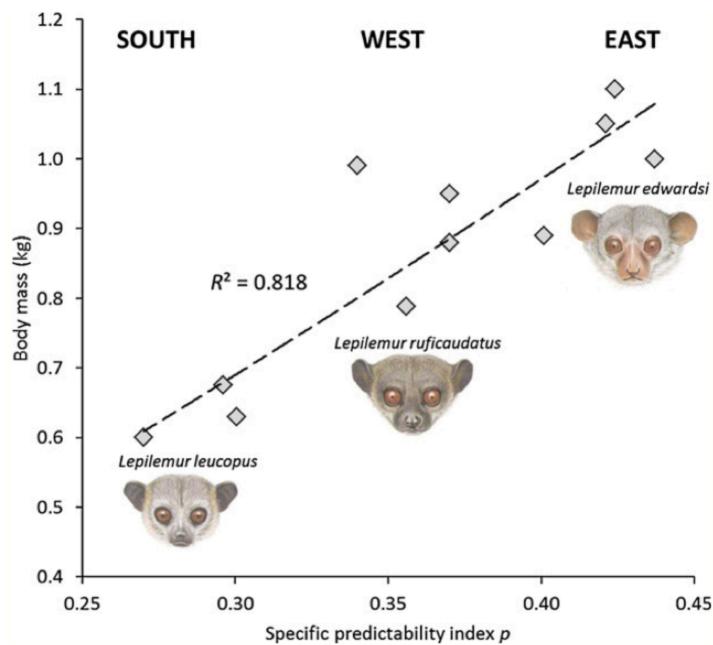


Figure 6. Correlation between body mass and the specific predictability index (p) calculated by averaging the rainfall predictability indexes of localities included within the ranges of 11 endemic Malagasy *Lepilemur* species (data from Dewar & Richard, 2007). *Lepilemur* illustrations are the copyright of Stephen D. Nash/IUCN/SSC Primate Specialist Group, used with permission.

Discussion

Environmental hypervariability and energy-saving strategies

One problem posed by Dewar & Richard's (2007) PI predictability index is that it conflates intra- and inter-annual variability. In fact, intra-annual variability (seasonality) is highly predictable: most animals use photoperiodic annual cycles to anticipate seasonal changes. Seasonality is the most satisfactory explanation for the bimodal frequency distribution of body size in mammals, and in primates in particular (Martin *et al.*, 2007), and for the observed discontinuity in life history strategies. Small primates have fast life histories (reproductive cycle \leq 1 year) and altricial infants, while large primates have slow life histories (reproductive cycle $>$ 1 year) and semi-precocial infants transported by their parents (Soligo & Martin, 2007). In cheirogaleids, dwarfism has involved a switch between a short-day breeding system typical of large mammals (with mating synchronized by short photoperiods) to an atypical long-day breeding system (with mating partly synchronized by long photoperiods) (Génin & Perret, 2003; Génin, 2008). In most lemurs, including *Lepilemur* and *Phaner*, animals mate at the beginning of the dry season and give birth in the heart of the rainy season, which implies very long gestation periods in *Lepilemur* (and probably *Phaner*) relative to their body sizes. Mouse lemurs mate at the end of the dry season. Females exhibit a circannual rhythm of reproduction synchronized by long photoperiods, while males show atypical testicular recrudescence prior to long photoperiod exposure (photo-refractoriness in *Microcebus murinus*; Perret & Aujard, 2001). This mixed photoperiodic response is likely to be transitional, indicating an ancestral short-day breeding system.

Dwarf and mouse lemurs of the genera *Cheirogaleus* and *Microcebus* are the only known heterothermic primates (Schmid, 2000; Génin & Perret, 2003; Dausmann *et al.*, 2004). The capacity to enter hypothermy is restricted to small endotherms (McNab, 2002), but this fact is unlikely to have provided the selective advantage for body size reduction in cheirogaleids, at least for the hyper-dwarfs, as the larger forms of *Cheirogaleus* almost certainly undergo hibernation (Blanco & Rahalinarivo, 2010). Heterothermy, as a means of energy saving, has evolved in many small tropical mammals found in climatically unpredictable regions, and particularly those regions subject to El Niño-related droughts (Lovegrove & Raman, 1998; McNab, 2002; Génin & Perret, 2003; Mzilikazi & Lovegrove, 2004). These animals (including cheirogaleids) rouse themselves from torpor using non-shivering thermogenesis, which takes place in brown adipose tissue (brown fat). The only cheirogaleid in which this process has been studied in detail is the grey mouse lemur (*Microcebus murinus*), in which the anatomical distribution of brown fat is very different from that found in non-primate mammals (Génin *et al.*, 2003), suggesting that non-shivering thermogenesis is not a homologous retention shared by cheirogaleids and other small mammals. Brown fat develops during early ontogeny in most mammals, including humans, but is lost later. Its presence in adult *Microcebus* specimens is a further indication that cheirogaleids have evolved by progenesis, and retained functional brown fat in the adult stage. Marmosets (callitrichines) also use non-shivering thermogenesis (Rothwell & Stock, 1985), but probably exclusively for cold acclimatization.

Environmental hypervariability and exudativory

Lepilemurs are the smallest known folivorous primates, weighing 650 g to 1 kg. This appears to be a minimal limit for folivores (Kay, [1984](#)), and lepilemurs have been shown to use caecotrophy to enhance their energy intake (Hladik *et al.*, [1971](#)), as is found in other small folivores like lagomorphs and rodents. Dwarfing in cheirogaleids would have necessitated a shift in diet, as is indicated by their reduced tooth sizes: all cheirogaleids consume various proportions of small animal prey, fruits and exudates including gum, nectar and the secretions of moth bugs (Flatidae, Heteroptera). In the case of the LC clade, therefore, we propose a reversal of Nash's ([1986](#)) hypothesis that gummivory was a digestive precursor to folivory, and propose instead that ancestral folivory pre-adapted cheirogaleids to the difficult digestion of gums, which accounts for the fact that cheirogaleids have retained large caeca. The robust tooth-comb employed by lepilemurs to strip leaves serves as a more than adequate gum-scraper/gleaner, and there is little evidence of breakage to the tooth-comb elements of cheirogaleid gummivores (J.C.M., pers. obs.). Whether gummivory in other primates (e.g. callitrichines) was derived from folivorous ancestors is less clear; most New World monkeys are primarily seed or fruit eaters, and there is no platyrhine equivalent of the leaf-eating colobines. If calitrichine ancestors were hard-seed predators, for example, the descendant taxa may share digestive adaptations with strepsirrhine gummivores (like large caeca), but are unlikely to share dental specializations with them. Callitrichines gouge bark to initiate gum flows, using a robust battery of scissor-like incisors and canines (Rosenberger, [2010](#)).

Lepilemurs consume their folivorous diet while clinging to vertical tree trunks, and this posture is made more secure by the evolution of pointed nails with strong median keels. Efficient gummivory, too, requires the ability to cling to vertical surfaces, and most cheirogaleids (as well as callitrichines) have pointed nails that can be implanted into bark, but lacking a median keel. The exception that proves the rule is *Microcebus*, the smallest living primates, whose light body weight does not require extra anchorage. *Microcebus* individuals have rounded nails.

Gummivorous primates, including lemurs, lorisoids and callithrichines, are often found in hypervariable regions subject to El Niño-related droughts (Génin *et al.*, [2010](#)). The fact the dwarfism and gum-feeding co-occur in unpredictable habitats is, in our view, no coincidence. Gums are some of the few foods available during the dry season, when fruits, leaves and insects are scarce; and gummivory and dwarfism are both survival strategies for hypervariable environments. A shift to gummivory could have allowed ancestral cheirogaleids to survive in dry deciduous forests, where gums are available all year round.

Body size reduction in cheirogaleids

We propose that the evolution of the family Cheirogaleidae has involved at least four independent dwarfing events from an ancestor equivalent in size to living *Lepilemur*, resulting in paedomorphism. The first event is linked to the evolution of the larger extant cheirogaleids [*Phaner*, *Mirza* and *Cheirogaleus major* s.l. (i.e. dwarfing)], while

subsequent events were involved in the emergence of *Allocebus*, *Microcebus* and the smallest *Cheirogaleus* (i.e. hyper-dwarfing). Szalay (1975) proposed that cheirogaleids evolved from a lepilemurid ancestor on the basis of skeletal anatomy, but was essentially ignored. Our study provides a new context for his prescient observations. Recent phylogenetic analyses indicate that hyper-dwarfs, and particularly mouse lemurs, are more derived than other cheirogaleids, and this is supported by several apomorphic character states, including the evolution of nails with rounded rather than pointed tips, and the partial fusion of the ectotympanic to the lateral bullar wall. In fact, ectotympanic fusion is likely to be a direct consequence of hyper-dwarfism. Vertebrates show a negative allometric relationship between the middle and inner ear components, and head size (Cartmill, 1975; Hanken & Wake, 1993). For purely mechanical reasons, these elements cannot be reduced proportionally with the skull. Cartmill (1975) therefore predicted that very small lemuriforms should have a relatively large tympanic ring, crowding the floor of the bulla inferiorly, and closely approximated to the lateral bullar wall. This is the condition seen in *Microcebus*.

Furthermore, we suggest that phyletic dwarfism in cheirogaleids is a secondary consequence of reduced developmental period (progenesis combined with ontogenetic acceleration), in response to the high levels of seasonality and year-to-year unpredictability (hypervariability) that characterize Madagascar (Dewar & Richard, 2007). Unpredictability (Martin, 1992) and progenesis (Groves, 1989) have similarly been proposed to explain dwarfing in Callitrichinae, and El Niño-induced unpredictability may also explain the small size of pygmy slow lorises (*Nycticebus pygmaeus*) (Génin *et al.*, 2010) and *Tarsius*. Dwarfing in cheirogaleids may have co-evolved with exudatovory, also observed in callitrichines and *Nycticebus*. Following Gould's (1977) model of dwarfing, the context of body size reduction in cheirogaleids suggests that it is a by-product of accelerated life history, rather than a result of direct selection for small body size (see also McKinney & McNamara, 1991).

Paedomorphosis as a consequence of truncated ontogeny is a better explanation for most peculiarities of the Cheirogaleidae than primitive retention. In primates, limb development is delayed relative to the rest of the body; hence the shorter limbs in the paedomorphic forms appear less specialized than the limbs of the larger forms. In accordance with von Baer's rule, paedomorphs often appear less specialized or less derived than their ancestors (Gould, 1977; McKinney & McNamara, 1991; Hanken & Wake, 1993). Further evidence of the shortened gestation period of *Lepilemur* and the cheirogaleids is the presence of altricial infants carried by mouth, and nest-building behaviour, also classically interpreted as primitive (Charles-Dominique & Martin, 1970; Kappeler, 1998).

Dwarfing in the Cheirogaleidae has apparently followed some aspects of the ‘island rules’, with a disproportional reduction in brain size (Roth, 1992; Brown *et al.*, 2004; Köhler & Moyà-Solà, 2004; Bromham & Cardillo, 2007; Weston & Lister, 2009; Montgomery *et al.*, 2010), which is not explained by the progenesis hypothesis. Present knowledge of Madagascar suggests that, despite its large size and old age, its biota is affected by insularity, particularly if sub-fossils are considered (Carlquist, 1974; Weston

& Lister, [2009](#)). Madagascar's insularity may be reinforced by its peculiar topography, which creates a high degree of local isolation, associated with very high local endemism (Martin, [1972](#); Masters *et al.*, [1995](#); Goodman & Ganzhorn, [2004](#)).

The small size of mouse and dwarf lemurs is hence derived, rather than ancestral. Many characters co-vary with body size (e.g. life history parameters, diet, use of heterothermy, and, at least partially, activity rhythm), and any similarities that might exist between the biology of cheirogaleids and that of a small primate or lemur ancestor would be homoplastic, rather than symplesiomorphic. Dwarfing has apparently occurred many times during primate evolution, complicating the reconstruction of ancestral body size. Reconstructions of the body size and characteristics of ancestral primates should direct more attention to the palaeoecological conditions that witnessed their emergence, than to trying to devise a 'model ancestor' from the living spectrum of strepsirrhine diversity (Génin & Masters, [2011](#)).

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Biosketch

The African Primate Initiative for Ecology & Speciation (APIES) is a research unit based at the University of Fort Hare, South Africa, dedicated to the study of past and present primate diversity and evolution.

Author contributions: J.C.M., F.G. and A.M.L. designed the project. J.C.M. is a strepsirrhine systematist, and collected the morphometric data from museum specimens. F.G. framed and conducted most of the morphometric/statistical analyses and contributed his expertise on cheirogaleid ecology and physiology. M.D.P. and D.S. provided the expertise in molecular evolution and phylogenetic methods, including ancestral state reconstructions. A.L.M. is a specialist in the evolution of body size in mammals, particularly on islands; he provided the logistical and intellectual context in which the study was conducted.

References

- Alberch, P. (1980) Ontogenesis and morphological diversification. *American Zoologist*, 20, 653–667.
- Arthur, W. (2004) Biased embryos and evolution. Cambridge University Press, Cambridge, UK.
- Blanco, M.B. & Rahalinarivo, V. (2010) First direct evidence of hibernation in an eastern dwarf lemur species (*Cheirogaleus crossleyi*) from the high-altitude forest of Tsinjoarivo, central-eastern Madagascar. *Naturwissenschaften*, 97, 945–950.
- Bromham, L. & Cardillo, M. (2007) Primates follow the ‘island rule’: implications for interpreting *Homo floresiensis*. *Biology Letters*, 3, 398–400.
- Brown, P., Sutikna, T., Morwood, M.J., Soejono, R.P., Jatmiko, Wayhu Saptomo, E. & DueRokus Awe (2004) A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. *Nature*, 431, 1055–1061.
- Carlquist, S. (1974) Island biology. Columbia University Press, New York.
- Cartmill, M. (1972) Arboreal adaptations and the origin of the order Primates. The functional and evolutionary biology of primates (ed. by R.H. Tuttle), pp. 97–122. Aldine-Atherton Press, Chicago, IL.
- Cartmill, M. (1974) Rethinking primate origins. *Science*, 184, 436–443.
- Cartmill, M. (1975) Strepsirrhine basicranial structures and the affinities of the Cheirogaleidae. *Phylogeny of the primates: a multidisciplinary approach* (ed. by W.P. Luckett and F.S. Szalay), pp. 313–354. Plenum Press, New York.
- Cartmill, M. (1992) New views on primate origins. *Evolutionary Anthropology*, 1, 105–111.
- Charles-Dominique, P. & Martin, R.D. (1970) Evolution of lemurs and lorises. *Nature*, 227, 257–260.
- Charles-Dominique, P. & Petter, J.J. (1980) Ecology and social life of *Phaner furcifer*. *Nocturnal Malagasy primates: ecology, physiology and behaviour* (ed. by P. Charles-Dominique, H.M. Cooper, A. Hladik, C.M. Hladik, E. Pagès, G.F. Pariente, A. Petter-Rousseaux, J.J. Petter and A. Schilling), pp. 3–38. Academic Press, New York.
- Chatterjee, H.J., Ho, S.Y.W., Barnes, I. & Groves, C. (2009) Estimating the phylogeny and divergence times of primates using a supermatrix approach. *BMC Evolutionary Biology*, 9, 259.
- Dausmann, K.H., Glos, J., Ganzhorn, J.U. & Heldmaier, G. (2004) Hibernation in a tropical primate. *Nature*, 429, 825–826.
- Dewar, R.E. & Richard, A.F. (2007) Evolution in the hypervariable environment of Madagascar. *Proceedings of the National Academy of Sciences USA*, 104, 13723–13727.
- Ford, S.M. (1980) Callitrichids as phyletic dwarfs, and the place of the Callitrichidae in Platyrrhini. *Primates*, 21, 31–43.
- Garbutt, N. (2007) Mammals of Madagascar – a complete guide. A & C Black, London.
- Gebo, D.L. (2004) A shrew-sized origin for primates. *Yearbook of Physical Anthropology*, 47, 40–62.

- Génin, F. (2008) Life in unpredictable environments: first investigation of the natural history of *Microcebus griseorufus*. *International Journal of Primatology*, 29, 303–321.
- Génin, F. & Masters, J.C. (2011) Mouse lemurs as model primate ancestors: the evolution of body size in Cheirogaleidae. In *The world at the time of Messel: puzzles in palaeobiology, palaeoenvironment and the history of early primates* (ed. by T. Lehrmann and S.F.K. Schaal), pp. 65–66. Senckenberg Gesellschaft für Naturforschung, Frankfurt.
- Génin, F. & Perret, M. (2003) Daily hypothermia in captive grey mouse lemurs (*Microcebus murinus*): effects of photoperiod and food restriction. *Comparative Biochemistry and Physiology B*, 136, 71–81.
- Génin, F., Nibbelink, M., Galand, M., Perret, M. & Ambid, L. (2003) Brown fat and nonshivering thermogenesis in the gray mouse lemur (*Microcebus murinus*). *American Journal of Physiology*, 284, R811–R818.
- Génin, F., Masters, J.C. & Ganzhorn, J.U. (2010) Gummivory in cheirogaleids: primitive retention or adaptation to hypervariable environments? The evolution of exudativory in primates (ed. by A.M. Burrows and L.T. Nash), pp. 123–140. Springer, New York.
- Goodman, S.M. & Ganzhorn, J.U. (2004) Biogeography of lemurs in the humid forests of Madagascar: the role of elevational distribution and rivers. *Journal of Biogeography*, 31, 47–55.
- Gould, S.J. (1977) *Ontogeny and phylogeny*. Belknap Press, Cambridge, MA.
- Groves, C.P. (1989) *A theory of human and primate evolution*. Clarendon Press, Oxford, UK.
- Hanken, J. & Wake, D.B. (1993) Miniaturization of body size: organismal consequences and evolutionary significance. *Annual Review of Ecology and Systematics*, 24, 501–519.
- Hladik, C.M., Charles-Dominique, P., Valdebouze, P., Delort-Laval, J. & Flanzy, J. (1971) La cœcotrophie chez un Primate phyllophage du genre *Lepilemur* et les corrélations avec les particularités de son appareil digestif. *Comptes Rendus de l'Académie des Sciences, Paris*, 272, 3191–3194.
- Kappeler, P.M. (1998) Nests, tree holes, and the evolution of primate life histories. *American Journal of Primatology*, 46, 7–33.
- Kappeler, P.M. (2000) Lemur origins: rafting by groups of hibernators? *Folia Primatologica*, 71, 422–425.
- Kay, R.F. (1984) On the use of anatomical features to infer foraging behavior in extinct primates. *Adaptations for foraging in nonhuman primates* (ed. by P.S. Rodman and J.G.H. Cant), pp. 21–53. Columbia University Press, New York.
- Köhler, M. & Moyà-Solà, S. (2004) Reduction of brain size and sense organs in the fossil insular bovid *Myotragus*. *Brain, Behavior and Evolution*, 63, 125–140.
- Lartillot, N. & Poujol, R. (2011) A phylogenetic model for investigating correlated evolution of substitution rates and continuous phenotypic characters. *Molecular Biology and Evolution*, 28, 729–744.
- Lartillot, N., Lepage, T. & Blanquart, S. (2009) PhyloBayes 3: a Bayesian software package for phylogenetic reconstruction and molecular dating. *Bioinformatics*, 25, 2286–2288.

- Leutenegger, W. (1980) Monogamy in callitrichids: a consequence of phyletic dwarfism. *International Journal of Primatology*, 1, 95–98.
- Lister, A.M. (1996) Dwarfing in island elephants and deer: processes in relation to time of isolation. *Symposia of the Zoological Society of London*, 69, 277–292.
- Lomolino, M.V. (1985) Body size of mammals on islands: the island rule re-examined. *The American Naturalist*, 125, 310–316.
- Lovegrove, B.G. & Raman, J. (1998) Torpor patterns in the pouched mouse (*Saccostomus campestris*; Rodentia): a model animal for unpredictable environments. *Journal of Comparative Physiology B*, 168, 303–312.
- Martin, R.D. (1972) Adaptive radiation and behaviour of the Malagasy lemurs. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, 264, 295–352.
- Martin, R.D. (1990) Primate origins and evolution: a phylogenetic reconstruction. Princeton University Press, Princeton, NJ.
- Martin, R.D. (1992) Goeldi and the dwarfs: the evolutionary biology of the small New World monkeys. *Journal of Human Evolution*, 22, 367–393.
- Martin, R.D., Soligo, C. & Tavaré, S. (2007) Primate origins: implications of a Cretaceous ancestry. *Folia Primatologica*, 78, 277–296.
- Masters, J.C., Rayner, R.J. & Tattersall, I. (1995) Pattern and process in strepsirrhine phylogeny. *Creatures of the dark: the nocturnal prosimians* (ed. by L. Alterman, G.A. Doyle and M.K. Izard), pp. 31–44. Plenum Press, New York.
- Masters, J.C., Lovegrove, B.G. & de Wit, M.J. (2007) Eyes wide shut: can hypometabolism really explain the primate colonization of Madagascar? *Journal of Biogeography*, 34, 21–37.
- Masters, J.C., Silvestro, D., Génin, F. & DelPero, M. (2013) Seeing the wood through the trees: the current state of higher systematics in the Strepsirrhini. *Folia Primatologica*, 84, 201–219.
- McKinney, M.L. & McNamara, K.J. (1991) *Heterochrony: the evolution of ontogeny*. Plenum Press, New York.
- McNab, B.K. (2002) *The physiological ecology of vertebrates: a view from energetics*. Cornell University Press, Ithaca, NY.
- Mittermeier, R.A., Louis, E.E., Jr, Richardson, M., Schwitzer, C., Langrand, O., Rylands, A.B., Hawkins, F., Rajaobelina, S., Ratsimbazafy, J., Rasoloarison, R., Roos, C., Kappeler, P.M., Mackinnon, J. & Nash, S.D. (2010) *Lemurs of Madagascar*, 3rd edn. Conservation International, Washington, DC.
- Montgomery, S.H. & Mundy, N.I. (2013) Parallel episodes of phyletic dwarfism in callitrichid and cheirogaleid primates. *Journal of Evolutionary Biology*, 26, 810–819.
- Montgomery, S.H., Capellini, I., Barton, R.A. & Mundy, N.I. (2010) Reconstructing the ups and downs of primate brain evolution: implications for adaptive hypotheses and *Homo floresiensis*. *BMC Biology*, 8, 9.
- Mzilikazi, N. & Lovegrove, B.G. (2004) Daily torpor in free-ranging rock elephant shrews, *Elephantulus myurus*: a year-long study. *Physiological and Biochemical Zoology*, 77, 285–296.
- Nash, L.T. (1986) Dietary, behavioural, and morphological aspects of gummivory in primates. *Yearbook of Physical Anthropology*, 29, 113–137.

- Pagel, M. (1999) Inferring the historical patterns of biological evolution. *Nature*, 401, 877–884.
- Pagel, M. & Meade, A. (2013) BayesTraits v. 2. Computer program and documentation. Available at: <http://www.evolution.rdg.ac.uk/BayesTraits.html> (accessed 12 July 2013).
- Perelman, P., Johnson, W.E., Roos, C., Seuánez, H.N., Horvath, J.E., Moreira, M.A.M., Kessing, B., Pontius, J., Roelke, M., Rumpler, Y., Schneider, M.P.C., Silva, A., O'Brien, S.J. & Pecon-Slattery, J. (2011) A molecular phylogeny of living primates. *PLoS Genetics*, 7, e11342.
- Perret, M. & Aujard, F. (2001) Regulation by photoperiod of seasonal changes in body mass and reproductive function in gray mouse lemurs. *International Journal of Primatology*, 22, 5–24.
- Raff, R.A. (1996) *The shape of life: genes, development, and the evolution of animal form*. University of Chicago Press, Chicago, IL.
- Rosenberger, A.L. (2010) Adaptive profile versus adaptive specialization: fossils and gummivory in early primate evolution. *The evolution of exudativory in primates* (ed. by A.M. Burrows and L.T. Nash), pp. 273–295. Springer, New York.
- Roth, V.L. (1992) Inferences from allometry and fossils: dwarfing of elephants on islands. *Oxford Surveys in Evolutionary Biology*, 8, 259–288.
- Rothwell, N.J. & Stock, M.J. (1985) Thermogenetic capacity and brown adipose tissue activity in the common marmoset. *Comparative Biochemistry and Physiology – Part A*, 81, 683–686.
- Rowe, N. (1996) *The pictorial guide to the living primates*. Pogonias Press, East Hampton, NY.
- Scheumann, M. & Zimmermann, E. (2008) Sex-specific asymmetries in communication sound perception are not related to hand preference in an early primate. *BMC Biology*, 6, 3.
- Schmid, J. (2000) Daily torpor in the gray mouse lemur (*Microcebus murinus*) in Madagascar: energetic consequences and biological significance. *Oecologia*, 123, 175–183.
- Schwartz, J.H. & Tattersall, I. (1985) Evolutionary relationships of living lemurs and lorises (Mammalia, Primates) and their potential affinities with European Eocene Adapidae. *Anthropological Papers of the American Museum of Natural History*, 60, 1–100.
- Silvestro, D. & Michalak, I. (2012) RaxmlGUI: a graphical front-end for RAxML. *Organisms, Diversity & Evolution*, 12, 335–337.
- Simpson, G.G. (1961) *Principles of animal taxonomy*. Columbia University Press, New York.
- Soligo, C. (2006) Correlates of body mass evolution in primates. *American Journal of Physical Anthropology*, 130, 283–293.
- Soligo, C. & Martin, R.D. (2007) Adaptive origins of primates revisited. *Journal of Human Evolution*, 50, 414–430.
- Stamatakis, A. (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, 22, 2688–2690.

- Szalay, F.S. (1975) Phylogeny of primate higher taxa. The basicranial evidence. *Phylogeny of the primates: a multidisciplinary approach* (ed. by W.P. Luckett and F.S. Szalay), pp. 91–125. Plenum Press, New York.
- Tattersall, I. (2007) Madagascar's lemurs: cryptic diversity or taxonomic inflation? *Evolutionary Anthropology*, 16, 12–23.
- Weston, E.M. & Lister, A.M. (2009) Insular dwarfism in hippos and a model for brain size reduction in *Homo floresiensis*. *Nature*, 459, 85–88.
- Whittaker, R.J. & Fernández-Palacios, J.M. (2007) Island biogeography: ecology, evolution, and conservation, 2nd edn. Oxford University Press, Oxford, UK.
- Wilkinson, R.D., Steiper, M.E., Soligo, C., Martin, R.D., Yang, Z. & Tavare, S. (2011) Dating primate divergences through an integrated analysis of palaeontological and molecular data. *Systematic Biology*, 60, 16–31.
- Wimmer, B., Tautz, D. & Kappeler, P.M. (2002) The genetic population structure of the gray mouse lemur (*Microcebus murinus*), a basal primate from Madagascar. *Behavioral Ecology and Sociobiology*, 52, 166–175.
- Yoder, A.D. (1996) The use of phylogeny for reconstructing lemuriform biogeography. *Biogéographie de Madagascar* (ed. by W.R. Lourenço), pp. 245–258. Editions de l'ORSTOM, Paris.
- Zhang, J. & Kumar, S. (1997) Detection of convergent and parallel evolution at the amino acid sequence level. *Molecular Biology and Evolution*, 14, 527–536.