A New Species of Dwarf Lemur (Cheirogaleidae: *Cheirogaleus medius* Group) from the Ankarana and Andrafiamena-Andavakoera Massifs, Madagascar

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Abstract: A new species of dwarf lemur, *Cheirogaleus shethi* sp. nov., of the *C. medius* group is described from the dry and transitional forests of northern Madagascar. This species can be found along the forest corridor from Ankarana Special Reserve east to the Analamerana Special Reserve down to the Bekaraoka forest in the Loky-Manambato Protected Area. This species is genetically distinct from other members of the *C. medius* species group and is sister to a poorly known lineage in Sambava. The identification of this new species highlights the importance of northern Madagascar as a reservoir of biodiversity.

Key Words: Dwarf lemurs, primate, Strepsirrhini, taxonomy

Introduction

Dwarf lemurs (Cheirogaleidae: *Cheirogaleus*) are small, arboreal, nocturnal strepsirrhine primates endemic to the island of Madagascar (Groves 2000; Lei *et al.* 2014). The genus *Cheirogaleus* has recently been the focus of in-depth field research combined with genetic analyses that revealed greater species diversity within this genus than previously suspected (Groves 2000; Hapke *et al.* 2005; Groeneveld *et al.* 2009, 2010; Thiele *et al.* 2013; Lei *et al.* 2014, 2015). Field expeditions undertaken from the Ankarana Special Reserve (SR) east to the Analamerana SR have resulted in the identification of a distinct dwarf lemur in this region (Lei *et al.* 2014). This lineage was recognized previously (Hapke *et al.* 2005; Thiele *et al.* 2013) and is described here as a new species, although with a slightly different circumscription than initially suggested (Thiele *et al.* 2013).

Taxonomic expansion has occurred in other lemur genera, in particular *Microcebus* and *Lepilemur* (Louis *et al.* 2006a, 2006b, 2008; Rasoloarison *et al.* 2013; Hotaling *et al.* 2016). The proliferation of new lemur species has been addressed in

the scientific literature, both supportively by those who view it as justified and critically by those who do not (Thalmann 2007; Tattersall 2007, 2013). A combination of factors has led to controversy about species status in dwarf lemurs. The arboreal and nocturnal habits of Cheirogaleus make them difficult to study in the wild. Additionally, the small number of available museum specimens and their spottily documented collection localities often limit their utility. Based on morphology, Groves (2000) recognized seven species of Cheirogaleus: C. major É. Geoffroy Saint-Hilaire, 1812; C. medius É. Geoffroy Saint-Hilaire, 1812; C. crossleyi Grandidier, 1870; C. adipicaudatus Grandidier, 1868; C. sibreei (Forsyth Major, 1896); C. ravus Groves, 2000; and C. minusculus Groves, 2000. Groeneveld et al. (2009) subsequently synonymized C. ravus into C. major, and C. adipicaudatus into C. medius. Groves' (2000) specific delimitation can, however, now be seen as overly conservative based on recent fieldwork and genetic research (Hapke et al. 2005; Groeneveld et al. 2009, 2010; Thiele et al. 2013; Lei et al. 2014, 2015). Lei et al. (2014, 2015) proposed four new species, including the recently described Cheirogaleus andysabini Lei et al., 2015, and

resurrected *C. thomasi* (Forsyth Major, 1894) (corresponding in large part to *C. adipicaudatus*). Thiele *et al.* (2013) also described a new species, *C. lavasoensis*, bringing the current number of accepted species to eight. It is likely that other species remain to be described, with an ever-growing enumeration presented in the "Species groups of *Cheirogaleus*" section of Lei *et al.* (2014; pp.17–22). Gardner and Jasper (2015) reported a possible new *Cheirogaleus* lineage from the island of Nosy Hara in northern Madagascar.

Hawkins *et al.* (1990) mentioned a dwarf lemur in Ankarana Special Reserve in northern Madagascar and referred to it as "*Cheirogaleus*? *medius*." They suggested trapping to clarify the species' identification, as it could also have been *C. major*. Hapke *et al.* (2005) incorporated a genetic sample from Ankarana that was taken from the Collection des specimens morts, Parc Botanique et Zoologique Tsimbazaza in Antananarivo. The Ankarana species was confirmed to be a member of the *C. medius* group (designated CmeB in that study, GenBank accession number AY605904), but Hapke *et al.* (2005) hinted that this individual may be a member of an independent lineage based on genetic distance, but did not propose designating it as such. Groeneveld *et al.* (2009, 2010) expanded the dataset with additional samples from northern Madagascar, Sambava and Bekaraoka. The individuals from Sambava were placed as sister to those from Ankarana and Bekaraoka, and all were identified as *C. medius*. Thiele *et al.* (2013) also expanded the dataset with the inclusion of genetic data from dwarf lemurs in southern Madagascar. Although they did not supplement the northern dataset, additional analytical tools were applied in Thiele *et al.*'s work (2013) that also supported the sister relationship of Sambava to Bekaraoka within the *C. medius* group. The Ankarana individual (Hapke *et al.* 2005; Groeneveld *et al.* 2009, 2010) was not included, possibly due to missing data. Thiele *et al.* (2013) recognized that dwarf lemurs in the Sambava (subgroup CmeA) and Bekaraoka (CmeB) area of Madagascar represented a separate lineage and gave it the interim designation of *Cheirogaleus* sp. Bekaraoka Sambava (CmeA+CmeB).

Multiple field expeditions from the Ankarana SR east to the Analamerana SR, crossing through the Andrafiamena-Andavakoera Protected Area augmented the *Cheirogaleus* dataset (Lei *et al.* 2014). In this study, genetic data grouped individuals from Ankarana and Bekaraoka into one clade; the lineage was identified as a probable new species of dwarf lemur (C. sp. nov. 4, Fig. 1). Individuals from Sambava were excluded from C. sp. nov. 4, and were referred to as Confirmed

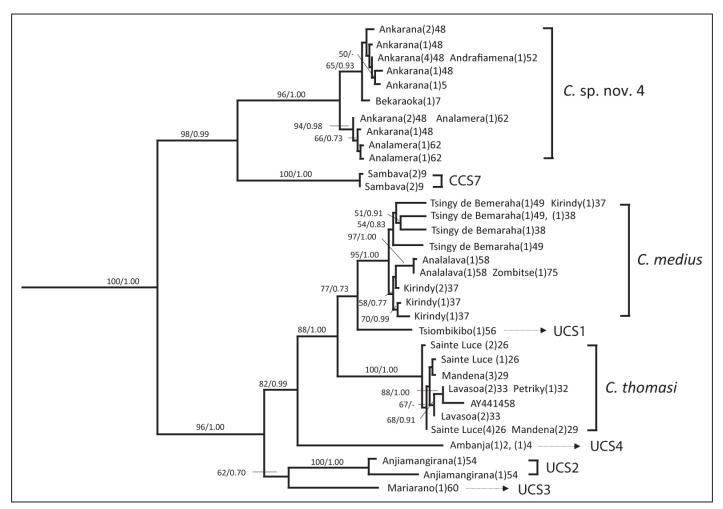


Figure 1. Subtree of the phylogenetic relationships between taxa within the *Cheirogaleus medius* group based on cytb sequence data as presented in Lei *et al.* (2014; Fig. 2). Numbers on branches represent maximum likelihood values followed by posterior probability support. Tip labels include locality, followed by number of individuals carrying the haplotype in brackets, then the locality numbers.

Candidate Species (CCS) 7, but more information is required to confidently describe the CCS7 lineage (Lei *et al.* 2014).

The Ankarana SR covers more than 18,000 ha in northern Madagascar and is about 108 km southwest of the large port city of Antsiranana. Ankarana was established in 1956, and first explored widely in the 1960s (Wilson et al. 1988). A plateau of limestone dating to the Jurassic Period, caves and underground rivers, and deciduous tropical forests are the most notable geographic features of the reserve (Rossi 1974a; Fowler 1989). The cave systems of Ankarana have been featured in popular writings and documentaries as a wonder of the natural world (Wilson 1990). Ankarana displays great diversity in birds (Fowler et al. 1989) and cave-dwelling marine life (Gurney 1984; Palacios-Vargas and Wilson 1990; Banister 1994; Wilson 1996), as well as primates (Wilson et al. 1995). In addition to Cheirogaleus, Ankarana SR is home to populations of the lemur genera Avahi, Daubentonia, Eulemur, Hapalemur, Lepilemur, Microcebus, Phaner, and Propithecus (Wilson et al. 1988, 1989, 1995). Subfossil remains of several extinct lemur species (Archaeolemur, Babakotia, Megaladapis, Mesopropithecus, Pachylemur, Paleopropithecus), as well as two genera still extant elsewhere in Madagascar but now extinct locally (Indri indri, Prolemur simus), have also been found in the caves of Ankarana (Wilson et al. 1995; Godfrey et al. 1996).

The limestone massif extends east through the Andrafiamena forest to the Analamerana SR (Du Puy and Moat 1996), which has nearly 35,000 ha ranging from sea level to 650 m (Mittermeier et al. 2010). Analamerana SR is located to the north and east of Ankarana and about 100 km southwest of Antsiranana (Mittermeier et al. 2010). In the 1970s this area was referred to as uninhabited by humans (Rossi 1974b), and the lemur diversity found there reflects the historically low pressure from humans. Lemur species with distributions from Ankarana to Analamerana, similar to that of C. sp. nov. 4, include the Critically Endangered Perrier's sifaka (Propithecus perrieri) and the Endangered Lepilemur ankaranensis (Mittermeier et al. 2010; Salmona et al. 2013, 2015a, 2015b); both of which are threatened due to human activities elsewhere within their very small geographic ranges. Fortunately, much of the area from Ankarana east to Analamerana is now protected either as special reserves or as an IUCN Category V protected area, which strives to maintain a balance between wildlife and habitation by people.

To the south of the Ankarana-Analamerana massif, the Loky River has eroded away the sandstone, creating an expansive low area prone to flooding, which has been used extensively for agriculture (Rossi 1974b). On the other side of this highly anthropogenically modified area is the Bekaraoka Forest near Daraina. This area is flanked by the Loky and Manambato rivers and is within the Loky-Manambato Category V Protected Area. Although rivers have been cited as possible barriers to dispersal, the geographic range of *Lep-ilmur milanoii* straddles the Loky River similar to that of *C*. sp nov. 4; *L. milanoii* is found in numerous forests of the

Loky-Manambato region and the Andrafiamena Classified Forest (Mittermeier *et al.* 2010; Salmona *et al.* 2014).

Genetic samples, measurements and photographs of several *Cheirogaleus* individuals captured along the Ankarana-Andrafiamena-Analamerana corridor were obtained prior to their release (Fig. 2). The genetic samples were analyzed as part of a larger phylogenetic study of the genus *Cheirogaleus* conducted by Lei *et al.* (2014) including pre-existing data from Bekaraoka (Groeneveld *et al.* 2009). Together, they were determined to be consistently distinct from all other samples of the *C. medius* group and designated as *C.* sp. nov. 4 (Lei *et al.* 2014). Here, we describe this new species of dwarf lemur endemic to the Ankarana-Andrafiamena-Analamerana corridor and the Loky-Manambato region in northern Madagascar.

Methods

Sampling and morphology

See Lei *et al.* (2014) for a comprehensive list of localities and numbers of individuals that were represented in the most recent genus-wide study of *Cheirogaleus*. Here, we enumerate only those belonging to the *C. medius* group along with individuals used as outgroups from other *Cheirogaleus* species (Table 1). From the focal lineage, *C.* sp. nov. 4, ten individuals from Ankarana SR, two individuals from Andrafiamena-Andavakoera protected area, and three individuals from Analamerana SR were immobilized by the field team from the Madagascar Biodiversity Partnership (MBP; Table 2, Fig. 2). An additional individual from Ankarana was immobilized in 2015 and was incorporated into this work.

Immobilization was carried out as reported in Louis *et al.* (2006a), and genetic samples were acquired as described by Lei *et al.* (2014). Morphometric measurements taken on sedated lemurs using bone anatomical landmarks were recorded as in Louis *et al.* (2006a) and standardized according to the guidelines of Smith and Jungers (1997). All lemurs were released at their point of capture within 24 hours. Interactions with the study subjects abided by Omaha's Henry Doorly Zoo and Aquarium's IACUC (97-001, 12-101) and all collection and export permits were obtained from the appropriate authorities in Madagascar and the United States respecting the Convention for International Trade in Endangered Species.

Data generation and phylogenetic analyses

Methods used to identify this new species were presented in Lei *et al.* (2014). In addition, a Bayesian species delimitation analysis was performed using the bPTP webserver (http:// species.h-its.org; Zhang *et al.* 2013) with 100,000 Markov Chain Monte Carlo generations as in Lei *et al.* (2015). The cytb tree was used as the starting tree as it was the most inclusive dataset allowing for the incorporation of previously published sequence data from Bekaraoka (EU825327; Groeneveld *et al.* 2009) and Ankarana SR (AY605904; Hapke *et al.* 2005). All haplotypes recovered in Lei *et al.* (2014) of *C.* sp. nov. 4 that were sampled by MBP from Ankarana SR east

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ID	Species designation	Location	Latitude	Longitude
ANK5.12	<i>C</i> . sp. nov. 4	Ankarana	-12.96631	49.13808
ANK5.13	C. sp. nov. 4	Ankarana	-12.96631	49.13808
ANK5.14	<i>C</i> . sp. nov. 4	Ankarana	-12.96631	49.13808
ANK5.15	C. sp. nov. 4	Ankarana	-12.96631	49.13808
ANK5.16	C. sp. nov. 4	Ankarana	-12.96631	49.13808
ANK5.17	C. sp. nov. 4	Ankarana	-12.96631	49.13808
ANK5.18	C. sp. nov. 4	Ankarana	-12.96631	49.13808
ANK5.19	C. sp. nov. 4	Ankarana	-12.96631	49.13808
ANK5.20	C. sp. nov. 4	Ankarana	-12.96631	49.13808
ANK5.21	C. sp. nov. 4	Ankarana	-12.96631	49.13808
KAR15.1	C. sp. nov. 4	Ankarana	-12.95636	49.12969
FIA5.19	C. sp. nov. 4	Andrafiamena (Anjakely)	-12.91539	49.31956
FIA5.22	<i>C</i> . sp. nov. 4	Andrafiamena (Anjakely)	-12.91539	49.31956
MATY5.31	<i>C</i> . sp. nov. 4	Analamerana (Ampasimaty)	-12.76556	49.48358
MATY5.40	C. sp. nov. 4	Analamerana (Ampasimaty)	-12.76703	49.48358
MATY5.42	C. sp. nov. 4	Analamerana (Ampasimaty)	-12.77136	49.48303
BEMA7.19	C. medius	Tsingy de Bemaraha	-19.04525	44.77772
BEMA7.21	C. medius	Tsingy de Bemaraha	-19.04581	44.78119
BEMA7.22	C. medius	Tsingy de Bemaraha	-19.05383	44.78075
LAVA1	C. medius	Analalava	-22.59242	45.13333
LAVA45	C. medius	Analalava	-22.58778	45.12803
ZOM6.2	C. medius	Zombitse	-22.88631	44.69375
KIBO7.9	UCS1*	Tsiombikibo	-16.04886	45.81067
HIH7.3	UCS2*	Anjiamangirana	-15.21642	47.75189
HIH9	UCS2*	Anjiamangirana (Antsohihy)	-15.15692	47.73311
MAR30	UCS3*	Mariarano	-15.47992	46.69333
AMB5.27	C. andysabini	Montagne d'Ambre	-12.51722	49.1795
GAR8	CCS2*	Manongarivo	-14.02369	48.27233
KAL7.7	C. lavasoensis	Kalambatritra (Sahalava)	-23.53672	46.5335
MIZA16	C. crossleyi	Maromizaha	-18.97375	48.46461
TRA8.81	<i>C.</i> sp. nov. 2	Andringitra (Ambarongy)	-22.22269	47.01889
POLO5.2	C. major	Tampolo	-17.28989	49.40753
JOZO4.17	C. sibreei	Anjozorobe	-18.46789	47.94131
Roos <i>et al.</i> (2004), Hap	ke <i>et al.</i> (2005), Groeneveld <i>et al.</i>	(2009) and Thiele <i>et al.</i> (2013)		
AY605904	<i>C</i> . sp. nov. 4	Ankarana	-12.9250	49.1250
EU825327	<i>C</i> . sp. nov. 4	Bekaraoka	-13.1047	49.7074
EU825333	C. medius	Bemaraha	-19.1036	44.7675
EU825325	C. medius	Kirindy	-20.0737	44.6757
EU825326	C. medius	Kirindy	-20.0737	44.6757
EU825328	CCS7*	Sambava	-14.3994	50.1739
EU825329	CCS7*	Sambava	-14.3994	50.1739
EU825323	UCS4*	Ambanja/Ambato	-13.3958	48.4705

Table 1. Free-ranging *Cheirogaleus* samples used in this study. IDs correspond to Table 1 (Lei *et al.* 2014), with the exception of previously published samples denoted at the bottom of this table.

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Table 1. continued

ID	Species designation	Location	Latitude	Longitude
AY605905	C. thomasi	Ste. Luce	-24.7730	47.1710
AY605906	C. thomasi	Ste. Luce	-24.7730	47.1710
AY605907	C. thomasi	Ste. Luce	-24.7730	47.1710
AY605908	C. thomasi	Mandena	-24.9530	46.9920
AY605909	C. thomasi	Petriky	-25.0610	46.8730
AY605910	C. thomasi	Lavasoa	-25.0840	46.7660
AY441458	C. thomasi	n/a	n/a	n/a

* CCS and UCS designations are from Lei et al. (2014).

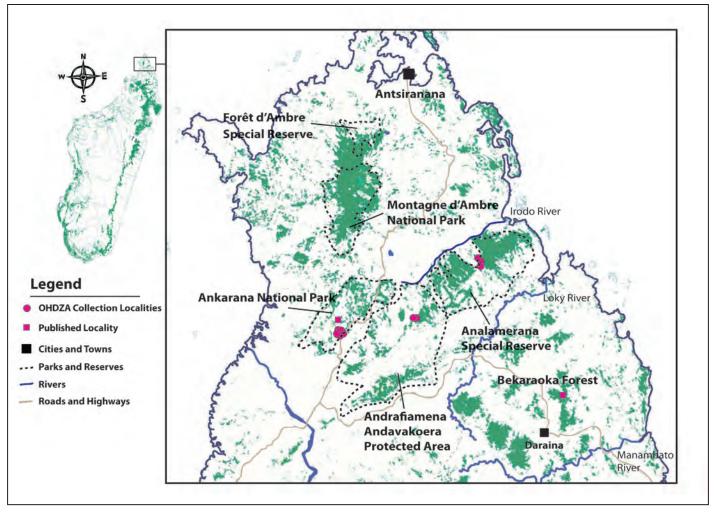


Figure 2. Map of the study locality in northern Madagascar. Circles represent collection localities of *Cheirogaleus* sp. nov. 4 individuals listed in Table 1. Pink squares represent the localities of two additional samples from other research groups.

to Analamerana SR and Bekaraoka Forest were included plus other individuals in the *C. medius* group (*C. thomasi*, UCS1-4, and CCS7). Representatives from the remaining *Cheirogaleus* species groups (*C. crossleyi*, *C. major*, and *C. sibreei*), plus *Microcebus berthae* as an outgroup, were also included in the bPTP analyses.

Additionally, a D-loop sequence was generated from a fecal sample collected in March 2015 from Ankarana SR

(KAR15.1), which was identical to those from blood and tissue samples. Because of the identical nature of this sample, it was not used in the genetic analyses, but was included in the morphological analyses.

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Table 2. List of dwarf lemurs, *Cheirogaleus* sp. nov. 4, from Ankarana, Andrafiamena and Analamerana examined during this study using acronyms ANK, KAR, FIA and MATY to designate sites (see Table. 1). Catalog and tissue accession numbers from the Museum of Texas Tech University (TTU-M).

ID No.	Catalog No.	Tissue No.	Sex	Microchip ID	Weight (kg)	GPS		Sampling Date	
ANK5.12			n/a	n/a	n/a	-12.96631	49.13808	12/04/2005	
ANK5.13			n/a	n/a	n/a	-12.96631	49.13808	12/04/2005	
ANK5.14			n/a	n/a	n/a	-12.96631	49.13808	12/04/2005	
ANK5.15			n/a	n/a	n/a	-12.96631	49.13808	12/05/2005	
ANK5.16			n/a	n/a	n/a	-12.96631	49.13808	12/05/2005	
ANK5.17			n/a	n/a	n/a	-12.96631	49.13808	12/05/2005	
ANK5.18			n/a	n/a	n/a	-12.96631	49.13808	12/05/2005	
ANK5.19			n/a	n/a	n/a	-12.96631	49.13808	12/06/2005	
ANK5.20			n/a	n/a	n/a	-12.96631	49.13808	12/07/2005	
ANK5.21			n/a	n/a	n/a	-12.96631	49.13808	12/07/2005	
KAR15.1			Male	480447362B	0.125	-12.95636	49.12969	03/06/2015	
FIA5.19	TTU-M 122795	TK 128750	Female	442720357C	0.123	-12.91539	49.31956	12/03/2005	
FIA5.22			Male	442A535373	n/a	-12.91539	49.31956	12/04/2005	
MATY5.31	TTU-M 118805	TK 129243	Male	n/a	0.112	-12.76556	49.48358	11/16/2005	
MATY5.40	TTU-M 118804	TK 129242	Female	n/a	0.080	-12.76703	49.48358	11/18/2005	
MATY5.42	TTU-M 118806	TK 129244	Male	n/a	0.101	-12.77136	49.48303	11/18/2005	

Results

Morphology

Morphological data were available for three males and two females of C. sp. nov. 4. One of the females (MATY5.40) was likely immature due to her lower weight and smaller linear measurements; she was excluded from the morphological analysis. In a study by Blanco and Godfrey (2013), juvenile and subadult male dwarf lemurs generally did not show visible signs of testicular development. As two of the three C. sp. nov. 4 males had developed testes, they are expected to be adults. The third male (KAR15.1) had small testes, but comparable linear measurements to the other adult males, so was included in the morphological analysis. This individual was caught in March, which is after the breeding season (Blanco and Godfrey 2013) and when testes are reduced in size in the closely related mouse lemurs (Perret and Aujard 2001; Wrogemann et al. 2001). Although the sample size was small, the combined head and body length of C. sp. nov. 4 was shorter than the minimum for other species of the C. medius group. One individual from Tsiombikibo, currently the only representative of UCS1 (Lei et al. 2014), was similar in length. See Table 3 for morphometric measurements.

Phylogenetic analyses

The Bayesian species delimitation analysis using the bPTP webserver provided posterior delimitation probabilities in support of our elevation of the Ankarana *Cheirogaleus* group as an independent species. We obtained a Bayesian PTP support value of 0.92 indicating a high probability that this lineage is an independent species based on the given dataset (Fig. 3). We acknowledge the limitations of any species delimitation methodology when used independent of other corroborating methods (Carstens *et al.* 2013). In the case of this *Cheirogaleus* group the bPTP species delimitation is presented as additional evidence of our assertion that this group constitutes a new species.

Discussion

Previous genetic studies by Lei *et al.* (2014) identified a new *Cheirogaleus* species using the following mitochondrial regions: cytb (Irwin *et al.* 1991); Cytochrome oxidase subunit II (COII) (Adkins and Honeycutt 1994); the displacement loop or control region (D-loop) (Baker *et al.* 1993; Wyner *et al.* 1999); as well as the Pastorini fragment (PAST) that includes a fragment of the Cytochrome oxidase subunit III gene, NADH-dehydrogenase subunits 3, 4L, and 4 and five tRNAs (Pastorini *et al.* 2000). Three nuclear loci were also sequenced in Lei *et al.* (2014): alpha fibrinogen intron 4 (FIBA), von Willebrand Factor intron 11 (vWF) and Cystic Fibrosis Transmembrane conductance (CFTR-PAIRB) (Heckman *et al.* 2007; Horvath *et al.* 2008). See Table 4 for GenBank accession numbers.

In the cytb sequence fragments, C. sp. nov. 4 differs from its closest genetic relatives, the other members of the medius group (C. medius, CCS7, CCS8, UCS 1-4), in genetic distance by 7.2%±0.7% (C. medius), 4.7%±0.6% (CCS7), 7.7%±0.7% (CCS8), 7.7%±0.8% (UCS10), 7.3%±0.7% (UCS2), 7.4%±0.7% (UCS3), and 8.0%±0.7% (UCS4), respectively (Lei et al. 2014, Appendix II(g) for cytb genetic distance data). Additional analyses using D-loop, COII, and PAST mitochondrial gene regions resulted in C. sp. nov. 4 segregating as a distinct lineage with a high degree of confidence (posterior probabilities equal to 1.00; Lei et al. 2014, Figs. 2-4). This was also supported by a Bayesian analysis based on three nuclear loci (CFTR-PAIRB, FIBA, vWF), but with less robust support (posterior probabilities ranging from 0.87 to 0.89; Lei et al. 2014, Figs. 5-6). The population aggregation analysis (PAA) results are congruent with those presented in Appendix II (n, q, s and t; Lei et al. 2014).

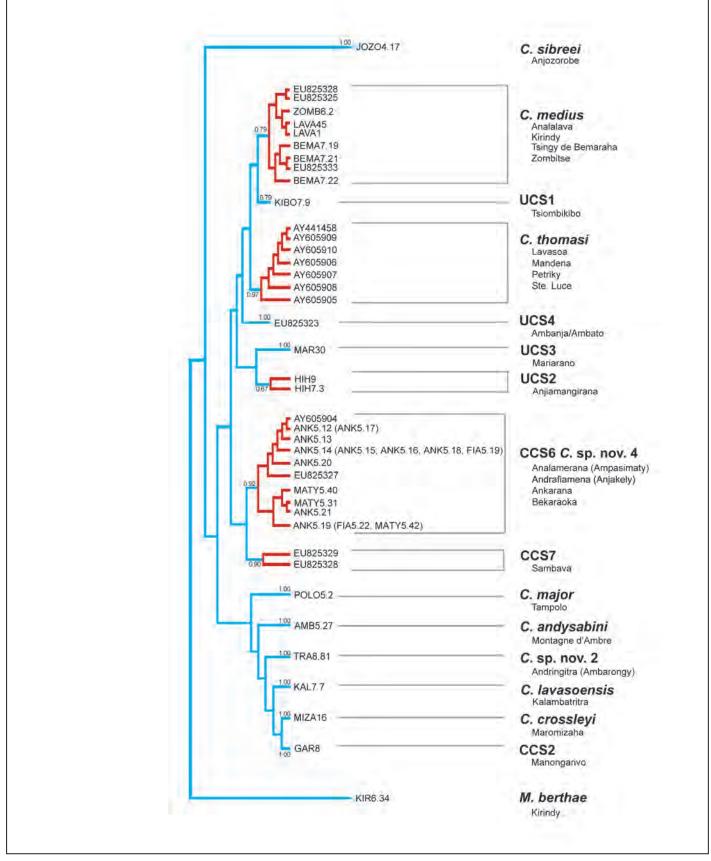


Figure 3. The Bayesian species delimitation analysis of the cytb dataset for the *Cheirogaleus medius* group using the bPTP webserver (Zhang *et al.* 2013). Maximum Likelihood phylogeny with Bayesian support values presented for all lineages recognized as species by the PTP analysis. Monophyletic groups in red indicate a single putative species as well as terminal branches in blue. Names of terminals coincide with sample IDs in Table 1; IDs in parentheses have equivalent haplotypes to their associated terminals.

Table 3. Morphological data for adult Cheirogaleus shethi individuals from Ankarana, Andrafiamena and Analamerana.

	N.	W	HC	BL	TL	EL	EW	ML	F-Tb	F-LD	F-Hd
Class	No.	(kg)	(cm)	(cm)	(cm)	(mm)	(mm)	(mm)	(cm)	(cm)	(cm)
Male	3	0.113±0.012	4.9±1.2	12.1±1.1	16.5±1.0	15.9±1.4	10.9±1.2	10.8±2.4	0.6±0.0	1.2±0.0	2.6±0.0
Female	1	0.123±0.000	4.1±0.0	12.4±0.0	15.5±0.0	14.5±0.0	9.6±0.0	8.2±0.0	0.9±0.0	1.2±0.0	2.4±0.0
Total	4	0.115±0.011	4.7±1.0	12.2±0.9	16.3±0.9	15.5±1.4	10.6±1.2	9.9±2.3	0.7±0.2	1.2±0.0	2.5±0.1

W: weight, HC: head crown, BL: body length, TL: tail length, EL: ear length, EW: ear width, ML: muzzle length, F-Tb: thumb length (forelimb), F-LD: longest digit length (forelimb), F-Hd: hand length (forelimb).

Table 3. continued

Class	F-UR	F-H	H-Tb	H-LD	H-Ft	H-T	H-F	UC	LC (mm)	TeL-R	TeW-R	TeL-L	TeW-L
	(cm)	(cm)	(cm)	(cm)	(cm)	(cm)	(cm)	(mm)	(mm)	(mm)	(mm)	(mm)	(mm)
Male	3.1±0.0	3.4±0.0	$1.0{\pm}0.0$	1.5±0.2	4.3±0.0	4.7±0.0	4.3±0.0	2.3±0.4	2.2±0.5	8.8±1.7	5.85±1.2	8.2±0.0	4.35±0.4
Female	2.8±0.0	2.5±0.0	1.4±0.0	1.2±0.0	3.5±0.0	3.4±0.0	2.9±0.0	3.1±0.0	2.9±0.0	NA	NA	NA	NA
Total	3.0±0.2	3.0±0.6	1.2±0.3	1.4±0.2	3.9±0.6	4.1±0.9	3.6±1.0	2.6±0.6	2.4±0.6	NA	NA	NA	NA

F-UR: ulna/radius length, F-H: humerus length, H-Tb: thumb length (hindlimb), H-LD: longest digit length (hindlimb), H-Ft: foot ength (hindlimb), H-T: tibia length, H-F: femur length, UC: upper canine length, LC: lower canine length, TeL-R: right testis length, TeW-R: right testis width, TeL-L: left testis length, TeW-L: left testis width.

Cheirogaleus. sp. nov. 4 harbored five diagnostic sites for cytb, one for COII and none for both FIBA and vWF.

The small size coupled with geographic distance to other known populations of C. medius groups and mitochondrial genetic divergence demonstrate that this lineage is diagnosably distinct. The first factors taken alone, size or geography, provide questionable evidence of speciation. A combination of these factors with the observed genetic divergence, however, provides stronger justification for this elevation. Cheirogaleus sp. nov. 4 is separated from other Cheirogaleus populations by a significant geographical distance with the exception of the recently described Montagne d'Ambre dwarf lemur, C. andysabini (Fig. 4). However, C. andysabini is a member of the C. crosslevi group (Lei et al. 2015), while C. sp. nov. 4 is in the C. medius group. Phenotypically C. sp. nov. 4 individuals have less pronounced eye rings than other individuals in the C. medius group (Lei et al. 2014; Fig. 8). In addition, C. sp. nov. 4 individuals have a lower body weight $(0.115\pm0.011 \text{ kg})$ and a shorter tail $(16.3\pm0.9 \text{ cm})$ than individuals identified as C. medius (0.23±0.06 kg; 20.2±2.4 cm).

The species status of another possible *C. medius* population identified at Sambava (approximately 175 km from Ankarana SR) and described as CCS7 in Lei *et al.* (2014) has yet to be confirmed. This population, grouped by Thiele *et al.* (2013) into the proposed *C.* sp. Bekaraoka Sambava lineage, is sister to *C.* sp. nov. 4 (Lei *et al.* 2014).

Conservation status

Much of the corridor that includes Ankarana, Andrafiamena, and Analamerana is within Madagascar's system of protected areas. The bookends of this corridor are restrictive special reserves that afford a greater degree of protection to wildlife than the Category V protected areas (Fig. 2). Gardner (2011) acknowledged that Category V protected areas in Madagascar function differently than in Europe making it difficult to apply the same criteria globally. In Madagascar, communities rely on forests for their daily needs, and the extraction of resources at this intensity negatively affects biodiversity, contradicting one of the main tenants of IUCN's Category V definitions (Gardner 2011). Refining the objectives of Category V to reflect the reality in Madagascar was suggested (Gardner 2011).

Effective management of both the Andrafiamena-Andavakoera and Loky-Manambato Category V Protected Areas is vital to maintaining connectivity between populations of *C.* sp. nov. 4. Effective support of organizations striving to manage these sustainable use protected areas is recommended, such as FANAMBY, a Malagasy NGO that is managing both the aforementioned Category V protected areas. Additional fieldwork is necessary to establish baseline data on population density and the extent of the range to determine to which IUCN Red List category this species belongs.

Cheirogaleus shethi sp. nov.

Formerly *Cheirogaleus* sp. nov. 4, also CCS6 (Lei *et al.* 2014); in part *C*. sp. Bekaraoka Sambava (Thiele *et al.* 2013). See Table 3.

Holotype: FIA5.19; adult female; Permit number 181; 4×2.0 mm biopsies from ear pinna and 0.02 cc of whole blood; stored and curated at the Museum of Texas Tech University (MTTU, catalog number: TTU-M 122795/TK 128750) Genetic Resources Collection, Natural Sciences Research Laboratory (NSRL). We placed a microchip subcutaneously between the scapulae and recorded it as 442720357C; Collected by Nirina Jean de Dieu Andriamadison, Jean Aimé Andriamihaja, Jean Claude Randriamanana, Joseph Désiré Rabekinaja, François Randrianasolo, Philbert Randrianarinjaka, and Rambinintsoa Andriantompohavana on 3 December 2005.

Paratypes: ANK5.12-21, KAR15.1, FIA5.22; MATY5.31, MATY5.40, MATY5.42.

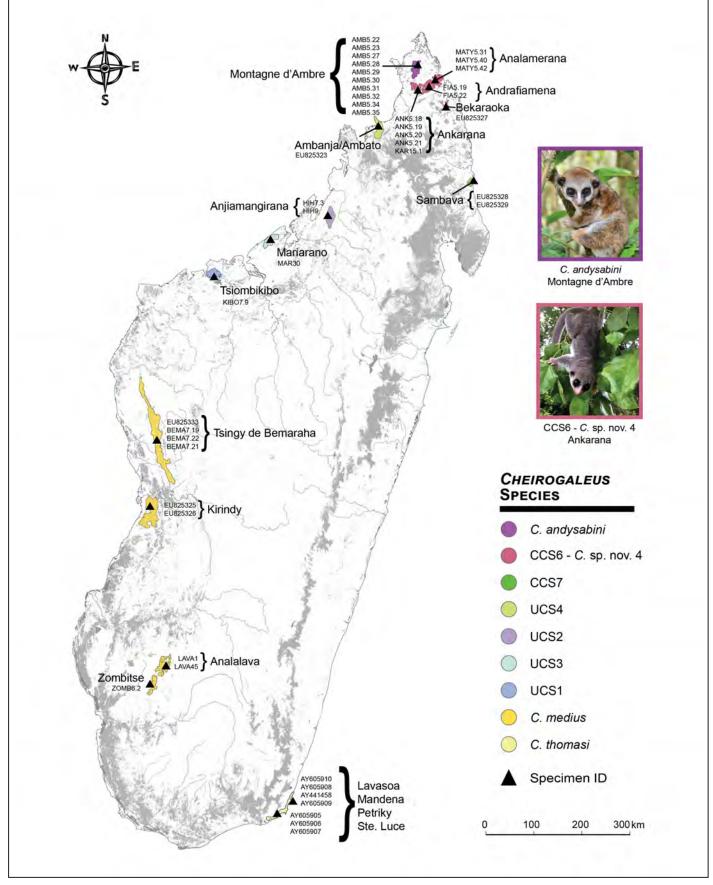


Figure 4. Map of Madagascar with the ranges of *Cheirogaleus*. sp. nov. 4 and closely related *Cheirogaleus* species highlighted to show the geographic distance between lineages. Identification numbers on the map correspond to ID numbers of animals listed in Table 1. Photographs of *C. andysabini* and *C.* sp. nov. 4 are provided to show a clear difference in pelage and the distance between the ranges of the two lineages from different species groups.

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ID	COII	Cytb	D-loop	PAST	vWF	FIBA	CFTR
AMB5.27	KM872108	KM872197	KM872288	KM872377	KM872557	KM872466	KM872648
ANK5.12	KM872119	KM872208	KM872299	KM872388	KM872568	KM872477	KM872659
ANK5.13	KM872120	KM872209	KM872300	KM872389	KM872569	KM872478	KM872660
ANK5.14	KM872121	KM872210	KM872301	KM872390	KM872570	KM872479	KM872661
ANK5.15	KM872122	KM872211	KM872302	KM872391	KM872571	KM872480	KM872662
ANK5.16	KM872123	KM872212	KM872303	KM872392	KM872572	KM872481	KM872663
ANK5.17	KM872124	KM872213	KM872304	KM872393	KM872573	KM872482	KM872664
ANK5.18	KM872125	KM872214	KM872305	KM872394	KM872574	KM872483	KM872665
ANK5.19	KM872126	KM872215	KM872306	KM872395	KM872575	KM872484	KM872666
ANK5.20	KM872127	KM872216	KM872307	KM872396	KM872576	KM872485	KM872667
ANK5.21	KM872128	KM872217	KM872308	KM872397	KM872577	KM872486	KM872668
BEMA7.19	KM872129	KM872218	KM872309	KM872398	KM872578	KM872487	KM872669
BEMA7.21	KM872130	KM872219	KM872310	KM872399	KM872579	KM872488	KM872670
BEMA7.22	KM872131	KM872220	KM872311	KM872400	KM872580	KM872489	KM872671
FIA5.19	KM872139	KM872228	KM872319	KM872408	KM872588	KM872497	KM872679
FIA5.22	KM872140	KM872229	KM872320	KM872409	KM872589	KM872498	KM872680
GAR8	AY584486	KM872230	AY584498	AY582562	KM872590	KM872499	KM872681
HIH9	KM872141	KM872231	KM872321	KM872410	KM872591	KM872500	KM872682
HIH7.3	KM872142	KM872232	KM872322	KM872411	KM872592	KM872501	KM872683
KAL7.7	KM872148	KM872238	KM872328	KM872417	KM872598	KM872507	KM872689
KIBO7.9	KM872149	KM872239	KM872329	KM872418	KM872599	KM872508	KM872690
LAVA1	KM872153	KM872243	KM872333	KM872422	KM872603	KM872512	KM872694
LAVA45	KM872154	KM872244	KM872334	KM872423	KM872604	KM872513	KM872695
MAR30	KM872156	KM872246	KM872336	KM872425	KM872606	KM872515	KM872697
MATY5.31	KM872160	KM872250	KM872340	KM872429	KM872610	KM872519	KM872701
MATY5.40	KM872161	KM872251	KM872341	KM872430	KM872611	KM872520	KM872702
MATY5.42	KM872162	KM872252	KM872342	KM872431	KM872612	KM872521	KM872703
MIZA16	KM872163	KM872253	KM872343	KM872432	KM872613	KM872522	KM872704
POLO5.2	KM872170	KM872260	KM872350	KM872439	KM872620	KM872529	KM872711
TRA8.81	KM872181	KM872272	KM872361	KM872450	KM872632	KM872541	KM872723
ZOMB6.2	KM872194	KM872285	KM872374	KM872463	KM872645	KM872554	KM872736

Table 4. A subset of GenBank accession numbers from Lei *et al.* (2014) for sequence data of *Cheirogaleus* individuals represented in the Bayesian species delimitation analysis.

Other specimens: *Cheirogaleus* collected by George R. Albinac in January, 1969, in the Collection des specimens morts, Parc Botanique et Zoologique Tsimbazaza in Antananarivo (Hapke *et al.* 2005); E1055 collected from Bekaraoka (Groeneveld *et al.* 2009).

Type locality: Madagascar: Antsiranana Province, Diana Region, District Antsiranana II, Andrafiamena (Anjakely), 12°54'55"S, 49°19'10"E (S12.91539, E49.31956) at 316 m above sea level.

Measurements of holotype: Measurements recorded in field catalog: body length, 124 mm; tail length, 155 mm; head crown, 41 mm; mass, 0.123 kg.

Description: The dorsum, limbs and head are gray, with no dorsal stripe. Underside white, from interramal area to base of tail. Facial mask poorly expressed; the area around the orbits is narrowly brownish and dorsally bleeding into the gray of the forehead and crown; median strip between them is paler than rest of face. The ears are sparsely furred. Hands and feet are light colored (Fig. 5).

Diagnosis: *Cheirogaleus shethi* can be distinguished from *C. medius*, UCS1, UCS2, UCS3, CCS7, *C. thomasi* and UCS4 by eight, six, nine, nine, 11, nine and 13 diagnostic characters in the cytochrome b gene, respectively (Appendix II(k); Lei *et al.* 2014). *C. shethi* has five diagnostic sites in cytb sequence fragment (G, T, T, T and C at the positions of 387, 468, 675,



Figure 5. Illustration of Cheirogaleus shethi (Stephen D. Nash © Conservation International) and photographs of KAR15.1 taken at Ankarana Special Reserve (photos by Richard Randriamampionona).

886 and 1101, respectively), which differentiate Cheirogaleus shethi from all other species in the C. medius group. Furthermore, although geographically close to CCS7 from Sambava, C. shethi can be distinguished from CCS7 by five diagnostic characters in the COII gene (Appendix II (q); Lei et al. 2014). Morphometrically, C. shethi can be distinguished by its very small size. Head plus body length is 164–175 mm in four specimens, whereas all other members of the C. medius group measure >177 mm, with one individual from western Madagascar being comparable to C. shethi. Adult weight is 101-125 g; all other members of the C. medius group are >165 g. Despite being geographically close to C. andysabini, with the Irodo River as a barrier, C. shethi is distinct from C. andysabini, which is clustered in the C. crossleyi group, by nine diagnostic characters, and distinguished by differences in pelage and size.

Distribution: Known from northern Madagascar, from Ankarana east to Bekaraoka in dry and transitional forests. Found in the Ankarana Special Reserve, Andrafiamena-Andavakoera Protected Area, Analamerana Special Reserve, and Loky-Manambato Protected Area.

Etymology: This new species is named after Brian Sheth, the Chair of the Board of the NGO Global Wildlife Conservation. Brian is deeply committed to biodiversity conservation worldwide, and is a leading philanthropist for species and ecosystem conservation. He has supported many projects in Madagascar, including research and the establishment and management of nature reserves. His passion and drive to help save the diversity of life on our planet has been an inspiration to all around him.

Vernacular names: Ankarana or Sheth's dwarf lemur.

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