



## The Genus *Cheirogaleus*: Unrecognized Biodiversity in Dwarf Lemurs

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Two species of dwarf lemur (*Cheirogaleus*) of Madagascar are conventionally recognized. To investigate this taxonomy, I studied the samples in the London and other collections. I could distinguish 7 different morphs, differing by size and by features of pelage, ears (hairy or naked), ear size, tail length, skull shape and dentition. As multiple features differentiate each form, they cannot be simply morphs within the two conventional species: they are discrete genetic entities, hence distinct species. The *Cheirogaleus medius* species group is split into two closely related allopatric species, *C. medius* from the western dry forests and *C. adipicaudatus* from the southern spiny forest. The *Cheirogaleus* major group has two widespread and partially sympatric species: *C. major* from the lowland rain forest and *C. crossleyi* from the plateau margins. I describe a species previously known only from the type series, *Cheirogaleus sibreei*, and two new species, one sympatric with *C. major* and one, apparently allopatric to all others, from the central plateau. I also discuss problems of nomenclature, dating from the original description itself.

**KEY WORDS:** *Cheirogaleus*; dwarf lemur; Madagascar; new species; biodiversity.

### INTRODUCTION

Since the influential revision of Malagasy lemurs by Schwarz (1931), it has been customary to recognize two or three species of *Cheirogaleus*:

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*C. medius*, *C. major*, and until its removal to *Allocebus* (Petter-Rousseaux and Petter, 1967), *C. trichotis*. Ernst Schwarz, one of the leading mammalian taxonomists of his day, was not only a perceptive groundbreaker but also an extreme lumpner: evidently concerned that interrelationships be clearly brought out, he used the species as his category of choice for expressing these interrelationships, and so produced schemes in which related taxa were regarded as conspecific regardless of sympatry or diagnosability.

Schwarz published taxonomic revisions of almost all African primate groups; revisions which, whenever they have been carefully scrutinised, for example by Bearder and coworkers on the Bush babies (Honest and Bearder, 1996), have proved to be grossly oversimplified. Much of the biodiversity of primates would remain undetected if Schwarz's revisions were allowed to stand untested. It is time for a complete overhaul of all the primate groups revised by Schwarz, including—perhaps especially—the Malagasy lemurs.

### Taxonomic History

*Cheirogaleus* was described not from specimens but from three drawings sent to Paris from Madagascar by Dr. Philibert Commerçon and described by Geoffroy St. Hilaire (1812), who allocated them to a new genus, *Cheirogaleus*—hand-weasel. Each of Commerçon's three drawings he considered to represent a separate species: *Cheirogaleus major*, *C. medius* and *C. minor*. He insisted that the figures were fully accurate; he stated confidently that Commerçon made all his drawings life-size and with extreme exactitude.

No localities were given by Geoffroy (1812), but Schwarz (1931) listed the type localities of all these names without comment as Fort Dauphin. As a long-established French post, this may have been where Commerçon examined his specimens, but it is by no means guaranteed that it was their place of capture. If the specimen described as *Cheirogaleus major* really was the species to which that name is given today, a rainforest species, then Fort Dauphin (in the spiny desert) is most unlikely to have been its locality of origin.

The first commentator, Wolf (1822), rejected Geoffroy's genus, pointing out features in common with *Lemur*; and considered that all three species were one and the same: "da die Namen *minor*, *medius* und *minor* fehlerhaft sind" ("as these names are defective"), he renamed the one and only species *Lemur commersonii*. The plate accompanying Wolf's text is simply a reproduction of Geoffroy's plate of *Cheirogaleus major*, so it could be argued that *commersonii* is a junior objective synonym of *major*. To

preclude any doubts, Wolf's (1822) plate (derived from Geoffroy's) is designated lectotype of *Lemur commersonii*.

By late in that decade, an actual specimen of a dwarf lemur had reached Paris: a living specimen, which Geoffroy (1828) allocated to *Cheirogaleus* but not to any of his three previously described species, which he now regarded as having been named provisionally. The living animal he made the type of a new species, *Cheirogaleus millii* (Geoffroy St. Hilaire, 1828). The animal's skin and skeleton were preserved at death, and are in the Muséum National d'Histoire Naturelle.

Smith (1833) recognized *Cheirogaleus* as a valid genus, to include Geoffroy's *C. major* and *C. minor*, together with a new species, *Cheirogaleus typicus*; and he listed *C. commersonii*, ascribing it not to Wolf but to Vigors and Horsfield, but—even more curiously—stated that it "will probably be found to form the type of a new genus." The type of *Cheirogaleus typicus* is in the Natural History Museum, London; its locality is given on the label as "S.E. Central Madagascar."

Lesson (1840) divided dwarf lemurs between two genera, *Cebugale*, a renaming of Geoffroy's *Cheirogaleus* (uniting *C. major* and *C. medius* into a single species under the name *Cebugale commersonii* Wolf), and *Mioxicebus*, including Geoffroy's *C. millii*, which he renamed *Mioxicebus griseus*, and which he did not believe represented the same kind of animal, plus a mouse lemur.

Granddier (1867) described the small, fat-tailed *Cheirogaleus* [sic] *sannati* from the River Tsitibon, on the west coast of Madagascar; the following year Granddier (1868) described two further species, *Cheirogaleus* [sic] *glitroides* and *C. adipicaudatus*, both from Tulleat; and finally, 2 years later east of Antsianak, " *Cheirogaleus sannati* was the third species of dwarf lemur to be described using actual specimens, two of which are in the Muséum National d'Histoire Naturelle, Paris. The type of *Cheirogaleus glitroides* is also in the Paris collection, but it is a mouse lemur (*Microcebus*). I know of no type specimen of *adipicaudatus* or *crossleyi*."

Gray (1872) recognized both *millii* and *typicus* (including *sannati*), and even separated them generically, as *Opolemur* and *Cheirogaleus*, respectively; but his descriptions and figures are muddled and it is unclear which generic and specific names he meant to apply to which specimens.

Although probably not even closely related to previously described species of *Cheirogaleus*, Gunther's (1875) description of *C. trichotis* continued to be discussed in the present context until it was eventually made the type of a new genus, *Allocebus*, by Petter-Rousseaux and Petter (1967).

In a revision of all of what are now termed the Cheirogaleidae, Forsyth Major (1894) pointed out Gray's (1872) muddle, and while accepting divi-

sion of dwarf lemurs into two genera, switched their type species, so that *Opolemur*—fat lemur—now referred to the fat-tailed *sumati* and *Chirogale* (sic) to *militi*. In the group as a whole the only other valid genus which he recognized was *Microcebus*, which included not only mouse lemurs but also *M. jirefifer*, i.e. *Phaner jirefifer*. He also indicated that "*Chirogale trichotis*" should probably be placed in a separate genus, thereby anticipating Petter-Rousseaux and Petter by >70 years, and he thought that *crossleyi* would prove comparable to it. He recognized in *Opolemur* two species, *O. sumati* and a new species *O. thomasi* (type locality Fort Dauphin), and in *Chirogale* also two, *C. militi* (synonyms *typicus* Smith and *adipicandatus* Grandidier) and a new species *C. melanotis* (type locality Vohima). The types of Forsyth Major's two new species are still in the collection of the Natural History Museum, London, the type and paratype of *C. melanotis* being the specimens depicted by Gray (1872) as *Chetrogaleus typicus*. Two years later, Forsyth Major (1896) described another new species, *Chirogale sibretei* (type locality Ankeramadinka, "one day's journey to the east of Antananarivo"). No further new species of *Chetrogaleus* have been described since that date.

Elliott (1913) acknowledged Forsyth Major's criticisms of Gray, but argued that, nonetheless, Gray had made *militi* the type of *Opolemur* so that if the *militi* and *sumati* groups were to be separated generically, it is the latter that needs a new name. He therefore made *Opolemur* a synonym of *Chetrogaleus*, and described a new genus, *Altillemur*, for the fat-tailed species. Elliott (1913) was also the first author for a century to take Geoffrey St. Hilaire's names *Chetrogaleus major*, *melhis* and *minor* seriously. He relegated *minor* to the synonymy of *Microcebus murinus*, but used *major* as the senior synonym for what had hitherto been called *militi*, and *melhis* as senior synonym for *sumati*.

Schwarz (1931) recognized only two species (apart from *C. trichotis*) in a single genus: *Chetrogaleus melhis* (with *sumati* a subspecies) and *C. major* (with *crossleyi* a subspecies). Geoffrey's *Chetrogaleus minor* (and Grandidier's *C. glitroides*) he placed in the synonymy of *Microcebus murinus murinus*; Forsyth Major's *Opolemur thomasi* in the synonymy of *Chetrogaleus melhis melhis*; Wolf's *Lemur commersonii*, Geoffrey's *Chetrogaleus militi*, Smith's *C. typicus*, Lesson's *Microcebus griseus* and Grandidier's *adipicandatus* in the synonymy of *Chetrogaleus major major*; and Forsyth Major's *Chetrogaleus melanotis* and *C. sibretei* in the synonymy of *C. major crossleyi*.

Variants of this scheme have persisted with only minor variations through the 20th century. Tattersall (1982) transferred *Chetrogaleus minor* to the synonymy of *C. melhis*; he recognized *no subspecies in either C. major* or *C. melhis*. Ahbrecht et al. (1990) were puzzled by the extreme

variability in specimens attributed to *Chetrogaleus major*, and chose to exclude specimens from certain regions from their ecoreographic analysis. Most interesting, however, are the remarks of Petter et al. (1977), based on field observations: they recognized (p. 80) "au moins trois formes" (at least three forms) in *Chetrogaleus major*. The first (*Chetrogaleus major major*) lives all along the east coast, and inland as far as the central plateau; the second (*C. m. crossleyi*, synonym *melanotis*), north of Marossetra, but extending southward along the high crests at the edge of the plateau as far as Lake Alaotra (Stanaka Forest); the third (undescribed) was in the Bongolava Forest, northeast of Tsiranomandidy (see also Thalmann and Rakotoarison, 1994). In some regions, they state, the first two seem to occur sympatrically; thus, at Belalona on the Sambava–Andapa road, they captured *Chetrogaleus major major* in the high forest while *C. m. crossleyi* has been observed "en abondance" in plantations and "zones dégradées" (Petter et al., 1977, p. 83). On this basis, Groves (1989) suggested that *Chetrogaleus crossleyi* was most likely a distinct species.

#### MATERIAL AND METHODS

I studied specimens of *Chetrogaleus* in the collections of the Natural History Museum, London (BM); the Muséum National d'Histoire Naturelle, Paris (MNHN); the Zoologisches Museum A. Humboldt, Berlin (ZMB); and Naturalis (formerly the Rijksmuseum van Natuurlijke Historie), Leiden (RML). I made notes on skins, including color, color pattern, and hair disposition, and on skulls and teeth, including aspects of skull shape and cusp development. I noted any flesh measurements available from the labels. I took the following skull and tooth measurements: greatest skull length (GTL); condylobasal length (CBL), basal length (BASL), braincase height (basion to bregma, BRAINHT), facial height (nasion to palate, NASPAL), biorbital breadth (BIORB), bulla length (BULLAL), bulla breadth (BULLABR), maxillary premolar–molar row length (TEETH) and breadths of M<sup>1</sup> (MONE), M<sup>2</sup> (MTWO) and M<sup>3</sup> (MTHREE). Some of the skulls were in pieces and had to be partially reassembled in order to take measurements. I also examined the skulls for the characters deemed by Schwartz and Tattersall (1985) to distinguish *Chetrogaleus melhis* and *C. major*.

Most of the specimens ascribed to *Chetrogaleus melhis* are sexed, and there is no consistent size difference. Four female skulls from Beraboka all measure 40 mm in greatest length; 8 males from the same locality vary from 39 to 41 mm. Very few of the specimens ascribed to *Chetrogaleus major* are sexed, but again there is no evidence of sexual dimorphism: for

example, a male and a female of the grey-brown morph both have skulls 55 mm long. Albrecht *et al.* (1990) could find little or no sexual dimorphism in size in any Malagasy lemur.

## RESULTS

In what follows, I use the concepts *C. major* group and *C. medius* group informally and for convenience only. The literature typically refers to two species, and any taxonomic disentangling that has to be done must operate within the context of the current paradigm. Actually, as one may infer, there is no actual evidence that the two are real entities in any sense.

### Skins

#### *C. major* Group

Within this informal group, most specimens have pale digits, and pigmented ears. The general color tone is grey-brown (from wood-brown to much greyer), with a reddish tone mid-dorsally which forms a thick dorsal stripe of greater or lesser definition, and the tail is somewhat bushy. None has much white on the face; all have thick blackish eye-rings. Skins of the *C. major* group assort into four morphs:

1. Furry-eared. Color is a warm red-brown dorsally; grey below, very creamy toward midline. Yellow of midfacial zone invades the region above the eyes, and the eye-rings are clearly expressed and blackish. Feet not light. The ears are black, and well covered, inside and out, with black fur. The tail is about equal in length to the head and body. Six skins are of this morph: BM 1939.1289 (E. Imerina), 48, 160 (30 miles northeast of Lake Alaotra, 2500 feet), and 70.5.5.24 (Anisiana; type of *melanotis* Forsyth Major, 1894); MNHNP 1967.1653 (Périnet); ZMB 3787 (Vohima); and RML Kat.H (Malewo).
2. Grey-brown. Color a paler grey-brown above, somewhat darker and greyer below. Often a vaguely expressed red-brown dorsal stripe. Midfacial zone pale but not white or yellow, does not extend above eye level; eye-rings much less marked. Feet not white. Ears are less darkly pigmented, and naked. The tail is much longer than the head and body. Eleven skins belong to this morph: BM 48.159 (8 miles west of Rantabe, Antongil Bay), 35.1.8.169 (Maroansetra), and 37.9.26.77 (S.E. Central Madagascar; type of *typicus* Smith,

- 1833); MNHNP No.148 (type of *millii* Geoffroy St. Hilaire, 1828), 1871.231 (Bay of Antongil), 1882.1560 (Farafangana), and 1932.3362 (Maroansetra); ZMB 35352 (Stanaka); and RML cat.c (no locality), cat.f (Passumbée), and cat.g (Maroansetra).
3. Iron-grey. Color is iron-grey above and below (N.B. not as pure grey as in the *C. medius* group), but yellower towards the ventral midline; with a very vaguely expressed dorsal stripe. Feet (but not hands) white. Tail colored like body, or very slightly browner. Ears sparsely clothed with hair, inside and out, their skin noticeably pigmented. The tail, in the single specimen in which flesh measurements are recorded, is equal in length to the head and body, and it seems to be much the same in the other skins. There are 12 skins of this type: BM 88.2.18.3 (Tamatave), 11.6.21.1 (Amboisitra), and 82.6.3.4 (forest of Ancyai); MNHNP 1964.74 (Ambodivony) and 1964.72, -3 (both, Mahambo) [locality not found], and 71432 and 21664 (both, Tamatave); and RML cats. d and e (both, Mahambo). At least one of the skins (BM 88.2.18.3) has a white tail-tip, and probably so did 11.6.21.1, but the tail is broken. The ear rims of 11.6.21.1 are more noticeably furred; this specimen is also much smaller than the others (it is labelled "juvenile," but examination of the skull shows that it is not).
4. *Chirogaleus sibrezi* Forsyth Major, 1896. There are four skins of this morph, BM 97.9.1.160 (type of *C. sibrezi*, from Ankeramadinka, 1 day's journey east of Anatanarivo); ZMB 71434 (Imerina); and RML cats. a and b (both, Pasandava Bay). They are grey-fawn above, with more white tipping to the hairs than any others, and very creamy below; the creamy ventral zone advances further up the flanks and on the outside of the thighs than the others. The BM and ZMB skins have a dark dorsal stripe, which is absent in others. Ears are nearly naked.

#### *C. medius* Group

In skins of this group, the digits (and sometimes whole of extremities) tend to be white. Median facial strip is always white; eye-rings vary. They are paler and grayer, and the dorsal stripe is narrower, and usually sharper, than in *C. major* group; the tail is less bushy (and expands seasonally, acting as a nutrient store). There are two morphs:

1. Western. Color lighter, frosted fawn-grey above, with a brown dorsal

stripe: broadly creamy or yellowish below, yellow on the median strip; a partial white collar round throat, sharply marked, extending well up on sides of neck. A white median facial stripe; eye-rings dark brown, generally restricted to rims of eyes. Hands and feet white. The tail is about equal to the head and body; the ear is relatively short. Twenty-seven skins are referable to this morph: BM 48.161, -2, -3, -4, -5 and -6 (all from Beroboka, 40 miles north of Morondava, west coast); MNHN No. 136a (two specimens: Tsidibon River, west coast; syntypes of *C. samani* Grandidier, 1867), 1986.425, -6, -7, -8, -9, -30, -31 (Beroboka), and 1967.1654 and -5 (both, Ampijoroa); ZMB 4354 (Morondava); and RML cats. a, b, c, d, e, f, g, h, and I (all, Morondava).

2. Southern. Often noticeably darker above (but variable), dorsal stripe vaguer; more grey below, with traces of creamy-yellow more towards midline; white collar vaguer, much less sharp, on sides of neck. White median facial stripe shorter, not extending so far up beyond level of eyes; eye-rings black, thick, invading sides of nose. Only digits are white. The tail is much longer than the head and body; the ear is longer than in the Western morph. Seven skins belong to this morph: BM 35.1.8, 168 (Tabiky, west of Ankazobabo), 35.1.1, 166, -7 (both from 170 km east of Tuléar), and 91.11.30, 3 (Fort Dauphin; type of *C. thomasi* Forsyth Major, 1894); MNHN 1932.3363 (Tabiky, west of Ankazobabo), and 1932.3364 and -5 (both, 170 km east of Tuléar).

These two morphs are not as strikingly distinct in pelage as are the four in the *C. major* group.

### Skulls and Teeth

#### *C. major* Group

The skulls ( $n = 6$ ) of the furry-eared morph are remarkably low and flat, with a low facial skeleton and low crown; in the dentition,  $P^1$  is relatively low-crowned, not rising much above  $P^2$ . Those of the iron-grey morph ( $n = 6$ ) are not dissimilar in the skull, but the flattening is less marked;  $P^1$  is relatively higher-crowned, and the upper incisors project forward to a lesser degree. Skulls of the grey-brown morph ( $n = 9$ ) have a high braincase, which falls away steeply at the back, and a deeper facial skeleton; the dentition resembles that of the Iron-grey form. The type and a second skull of *C. sibreui* resembles the furry-eared morph both cranially and dentally.

Cranial and dental size and proportions differ between these morphs (Table 1). In greatest skull length the size series, from largest to smallest, is: iron-grey (large)—grey-brown—furry-eared—*C. sibreui*—iron-grey (small). Sample sizes are small, but consistent, with no overlap. Biorbital breadth does not follow this trend; skulls of the large iron-grey morph average narrower than those of the grey-brown.

The maxillary toothrows of the grey-brown and iron-grey (large) forms are consistently larger than those of the other three morphs, but dental proportions vary (Table 1). In general,  $M^2$  is slightly broader than  $M^1$ , but  $M^1$  is markedly smaller than either, but the reduction of the third molar is most marked on average in the iron-grey morph, least in the furry-eared, and in *C. sibreui* there is hardly any third molar reduction at all.

#### *C. medius* Group

The skulls of the western morph ( $n = 26$ , plus two others represented by facial skeletons only) have a noticeable diastema between anterior and middle maxillary premolars. In those of the southern form ( $n = 3$ ), this diastema is poorly developed or absent. The two are about the same size, but the bulla is much smaller (especially, it is anteroposteriorly shorter) in the southern morph.

#### Comparison between the *C. major* and *C. medius* Groups

In general size, as represented by first vs. second molar breadths (Fig. 1), dwarf lemurs fall into three groups: the grey-brown and iron-grey (large) morphs of the *C. major* group are largest, the furry-eared morph and *C. sibreui* are intermediate, and the two forms of *C. minor* plus the iron-grey (small) morph of the *C. major* group are smallest. There is thus no absolute size difference between the two conventionally recognized "species."

Schwartz and Tattersall (1985:35–42) detailed the differences between the two conventionally recognized species, figuring two skulls from the American Museum of Natural History collection. The skull selected by them to illustrate *C. major* AMNH 100640, has all the characteristics of the grey-brown form, but their skull of *C. medius* cannot be further identified, as it is incompletely macerated. Comparing their descriptions and figures and the material from the London, Paris, Berlin and Leiden collections, valid differences between *C. major* and *C. medius* groups appear to be as follows: in both members of the *C. medius* group, braincase is lower and flatter, though there are differences among the *C. major* group forms: the maxillary

Table I. External and craniodental measurements (in mm) of *Cheirogaleus major* group

		<i>crossleyi</i> Furry-eared	<i>major</i> Grey-brown	<i>rauus</i> Iron-grey (large)	<i>minusculus</i> Iron-gray (small)	<i>sibrexi</i>
Head + Body	Mean	247.0	251.0	240	—	—
	sd	22.52	15.19	—	—	—
	n	3	4	1	—	—
	Range	221–260	230–264	—	—	—
Tail % H + B	Mean	100.1	119.0	100.0	—	—
	sd	13.21	4.46	—	—	—
	n	3	3	—	—	—
	Range	85–110	116–124	—	—	—
Skull length	Mean	51.8	55.5	56.7	42.0	47.3
	sd	0.29	2.26	—	—	—
	n	3	8	2	1	2
	Range	51.5–52.0	53.7–60.7	56.4–57.0	—	46.6–48.0
Biorbital breadth	Mean	32.1	35.9	34.2	25.3	30.7
	sd	0.82	1.38	2.35	—	—
	n	3	8	3	1	2
	Range	31.4–33.0	34.0–37.4	31.6–36.1	—	30.6–30.8
Maxillary toothrow	Mean	18.5	21.2	20.0	16.3	17.4
	sd	0.43	0.53	1.42	—	—
	n	5	5	5	1	2
	Range	17.9–18.9	20.3–22.0	18.0–21.6	—	17.0–17.8
M <sup>1</sup> breadth	Mean	3.56	4.14	4.28	3.0	3.4
	sd	0.09	0.08	0.27	—	—
	n	5	7	5	1	2
	Range	3.5–3.7	4.1–4.3	4.0–4.6	—	3.4–3.4
M <sup>2</sup> breadth	Mean	3.70	4.30	4.38	3.2	3.4
	sd	0.01	0.14	0.22	—	—
	n	5	7	5	1	2
	Range	3.6–3.8	4.1–4.5	4.1–4.6	—	3.3–3.5
M <sup>3</sup> breadth	Mean	3.22	3.71	3.55	2.8	3.05
	sd	0.18	0.11	0.44	—	—
	n	5	7	4	1	2
	Range	3.0–3.4	3.6–3.9	3.0–4.0	—	2.8–3.3

The Genus *Cheirogaleus*: Unrecognized Biodiversity in Dwarf Lemurs

Table II. External and craniodental measurements (in mm) of *Cheirogaleus mehillis* group

		West	South
Head + Body	Mean	183.9	170.7
	sd	11.55	8.14
	n	16	3
Tail % H + B	Range	164–215	165–180
	Mean	95.6	113.2
	sd	5.40	—
Ear % H + B	Range	86–103	108–109
	Mean	9.4	12.7
	sd	0.89	—
Skull length	Range	7.9–10.6	12.2–13.2
	Mean	40.1	39.8
	sd	1.45	—
Biorbital breadth	Range	37.7–42.9	39.6–40.0
	Mean	26.0	24.8
	sd	1.00	—
Bulla length	Range	23.9–27.4	23.5–26.0
	Mean	8.8	7.40
	sd	0.42	—
Bulla breadth	Range	8.1–9.7	7.2–7.6
	Mean	5.7	5.45
	sd	0.38	—
	Range	5.0–6.5	5.4–5.5

incisors, especially the central incisor, are even less forwardly projecting, though again there are differences among the *C. major* group forms: the palate is less extended behind the third molars: the auditory bullae are larger (more so in the western than in the southern morph) and the mastoid region is more convex; the maxillary canine is less back-curved and has less development of the lingual talon; P<sup>2</sup> is higher-crowned—Petter-Roussaux and Petter (1967) speak of a caniniform tendency—though there are differences among the *C. major* group morphs: P<sup>3</sup> is only barely larger in mesiodistal and buccolingual dimensions than P<sup>2</sup>, and is more triangular in occlusal view, due to the much bigger lingual pillar; P<sup>3</sup> is more triangular, less oblong in occlusal view: the molar cusps are higher, more pointed; the upper molars are more rounded lingually, with a relatively larger protocone; and M<sup>3</sup> is less reduced distally, but again, there are differences among the *C. major* morphs. Therefore, there are differences between the two groups,

## Cheirogaleus medius group

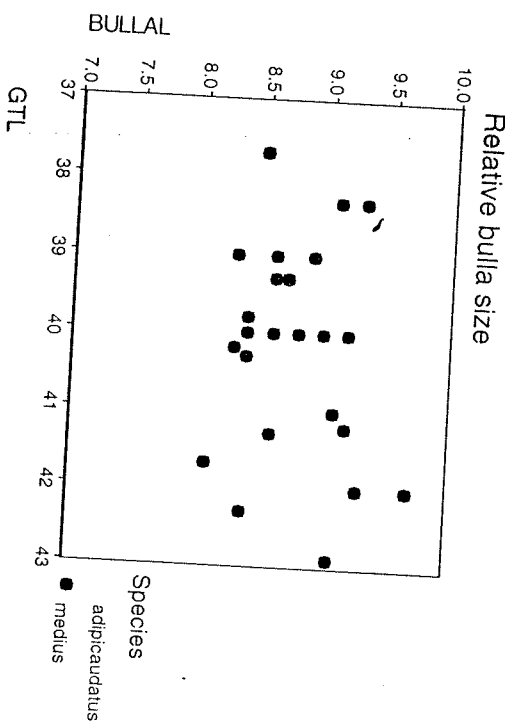


Fig. 1. Relative bulla size in species of the *Cheirogaleus medius* group. Abscissa, GTL. Ordinate, BULLAL.

but they are in many cases only exaggerations of the variations among the morphs within each group.

### DISCUSSION

There seems little doubt that the five morphs in the *C. major* group and the two in the *C. medius* group are of taxonomic significance. There are numerous congruent differences in both craniodental and external characters between the furry-eared, grey-brown and iron-grey (large) morphs in the *C. major* group; the tiny iron-grey (small) specimen is greatly different from the iron-grey (large) morph, and not merely in size; and the type of *C. sibreai* and the other specimens resembling it cannot be fitted into any of the other four morphs. The three large forms, at least, overlap in distribution, so they cannot be simply subspecifically different, and it is evident that they are not merely polymorphic variants within a single species. This means that they must be distinct species. Field observations of

Groves

The Genus *Cheirogaleus*: Unrecognized Biodiversity in Dwarf Lemurs

955

## Cheirogaleus

### First and second molar size

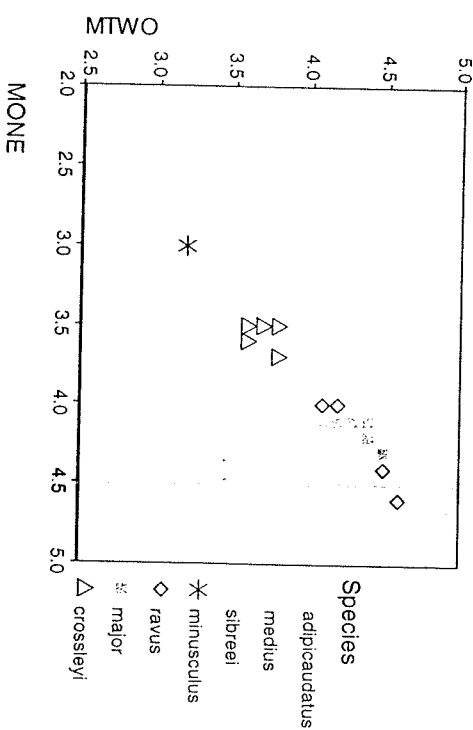


Fig. 2. Depiction of tooth size in genus *Cheirogaleus*. Abscissa, MONE; ordinate, MTWO.

two of them, the furry-eared and grey-brown ones, confirm that they are either sympatric or closely parapatric, and indicate different ecological preferences (Petter *et al.*, 1977). The single specimen that forms the iron-grey (small) form is likewise verified by field observations (Petter *et al.*, 1977; Thalmann and Rakotoarison, 1994), and is sharply distinct, especially in size, from its presumed relative, the iron-grey (large) form: it inhabits remnant forests on the central plateau of Madagascar. Finally *Cheirogaleus sibreai*, which cannot be aligned with any of these four, must stand as a fifth species.

In mammalogy, recognition of distinct species on the basis of single specimens is common, but the criteria are rarely made explicit. For example, Musser and Holden (1991, p. 389), described a new species of *Rattus* from Indonesia, stating only that the single known specimen is "so unlike" its nearest relative, "so distinctive in fact that we hypothesize it represents a species until now without a name." The nature of this uniqueness has been explored by Kimbel and Rak (1993:471, 476-477), who argue that it is when a particular specimen varies from the rest of the sample in many congruent but unrelated characters that we may conclude that the null

hypothesis of a single species is refuted. Such is the case with the iron-grey (small) specimen of dwarf lemur: so many congruent character states of it fall apart from those of every other species of the *C. major* group that the single-species hypothesis is clearly untenable.

The two forms of the *C. medius* group are less different from each other, but still diagnosably distinct. In this case, the two are geographically separated, one apparently living in the western dry forests, the other in the southern xerophytic bush zone; an adherent of the biological species concept might well recommend that they be recognized only as subspecies within a single species, though in phenetics the distinction between specific and geographic (especially ecogeographic) variation is in fact problematic (Albrecht and Miller, 1993). One cannot, however, combine species on a hypothesis that they might interbreed where their ranges meet, and I urge that both be awarded specific rank.

Are there names available for any or all of these 7 species of dwarf lemur? Within the contorted history of taxonomy and nomenclature of the group, it appears that there are plenty of names, but few are clearcut—least of all the names first given by Geoffroy St. Hilaire (1812). The type of *Cheirogaleus major* was described as 11 inches long; dark in color, especially on the forehead; that of *C. medius*, 8½ inches long, and less dark, with a black ring round the eyes, and the forehead light; that of *C. minor* was of length 7 inches, light in color, again with a black eye-ring and light forehead. While Geoffroy (1812) was confident in the drawings' accuracy, we must demur: in particular, they were all depicted with claws, and no *Cheirogaleus* has a wholly dark nose and interorbital region as is depicted for *C. major*. It is evident that they were, after all, drawn from memory (albeit a good memory), and this may affect our interpretation of the quoted body sizes as well. Eleven inches is about 280 mm, just slightly—probably not significantly—above the maximum head and body length of the *Cheirogaleus major* group; 8½ inches is about 215 mm, at the top end of the range for the *C. medius* group. Seven inches, the length of Geoffroy's *Cheirogaleus minor*, is about 175 mm, which is in fact well above the range for *Microcebus murinus*, the species with which Geoffroy himself at one point compared it (and with which Schwarz [1931] synonymized it), but within the range of the *C. medius* group (with which Tattersall [1982] synonymized it); like the other two figures, that of *C. minor* has a wide, short *Cheirogaleus*-like snout, and this too—if the draftsmanship is to be trusted—supports Tattersall's allocation.

The type of Geoffroy's (1828) *Cheirogaleus miltii* (of which Lesson's [1840] *Moxicebus griseus* is a simple renaming) is an example of what I have called the grey-brown form of the *C. major* group. So is the type of Smith's (1833) *Cheirogaleus typicus*, of which the type is in the Natural

History Museum, London. The syntypes of *Cheirogaleus* [sic] *samanii* Grandidier (1867) are what I have called the western form of the *C. medius* group.

It might be argued that, as Geoffroy's (1812) three species are little more than hypothetical concepts, the best course of action would be to reject them in favor of those supported by type specimens. But the names are now dignified by nearly a century of use; and, of course, *C. major* is the type species of *Cheirogaleus* itself (Elliot, 1913). As long as only two species, easily distinguished by size, were recognized in the genus, there was nothing wrong with using the names *major* and *medius* in a rather generalized sense; the recognition of further species, however, makes it mandatory to fix the names. I therefore designate Neotypes, as follows:

- *Cheirogaleus major*: Neotype, Paris Museum type gallery No. 148 (the holotype of *Cheirogaleus miltii*: E. Geoffroy St. Hilaire, 1828), mounted skin and separate skull.

- *Cheirogaleus medius*: Neotype, Paris Museum type gallery No. 162 (the holotype of *Cheirogaleus samani* Grandidier, 1867), mounted skin with skull inside, from R. Tsidisbon, western Madagascar. (Note that the allotype is part of the same mount and has the same number).

This fixes the names *miltii* and *samanii* as junior objective synonyms of *major* and *medius*, respectively. Accordingly the grey-brown member of the *C. major* group and the western member of the *C. medius* group take the names *Cheirogaleus major* and *C. medius*, respectively.

*Cheirogaleus* [sic] *adipicandulus* Grandidier, 1868 was described as the size of *Lepilemur ruficaudatus*: light grey, and with a very fatty tail; no measurement was given. Although no type specimen is known to exist, the type locality, Tuléar (now Toliary), is within the range of the southern member of the *C. medius* group, which accordingly takes the name *Cheirogaleus adipicandulus*. Schwarz (1931) inexplicably placed it as a synonym of *Cheirogaleus major major*, which occurs nowhere near Toliary and apparently does not have a grossly fattened tail.

*Cheirogaleus* [sic] *crossleyi* Grandidier, 1870 was reddish above, especially on the head, and whiter below; with black eye-rings. The head was enormous and rounded; the inside of the ears covered with dark brown hairs, and their rims bordered with black. The tail was short; the ears small. Body length 20 cm, tail 12 cm, ears 1 cm. These descriptive features, except for the short (broken?) tail, are those of the furry-eared member of the *C. major* group (*pace* Forsyth Major [1894], who thought it might refer to what is now called *Allocebus trichotis*), and the type locality is the forests east of Antsianak, where only the furry-eared form appears to be known. This species therefore takes the name *Cheirogaleus crossleyi*.

Of Forsyth Major's (1894) two new species, *Opolemur thomasi* (type

locality Fort Dauphin) is an example of the southern form of the *C. medius* group, and *C. melanotis* (type locality Vohima) is an example of the furry-eared form; the names are therefore junior subjective synonyms of *C. adipicaudatus* and *C. crossleyi*, respectively. Schwarz (1931) recognized the synonymy of *C. melanotis* with what he called *Cheirogaleus major crossleyi*. The type specimen of Forsyth Major's (1896) third new species, *Chirogale sibrezi* (type locality Ankeramadinika, one day's journey to the east of Antananarivo), is unlike any of these species, and its status as a separate species is corroborated by the existence of similar specimens in the Berlin and Leiden collections.

The two iron-grey forms of the *C. major* group are described below as new species.

## CONCLUSION: A NEW CLASSIFICATION OF CHEIROGALEUS

### Genus *Cheirogaleus* E. Geoffroy St. Hilaire, 1812

Synonyms: *Cebugale* and *Mioicebus* Lesson, 1840; *Chirogale* Gloger, 1841; *Myspithacus* F. Cuvier, 1842; *Opolemur* Gray, 1873; *Altillemur* Elliot, 1913. The distinctions between the two species groups are given above in Results.

#### *Cheirogaleus medius* Group

*Cheirogaleus medius* E. Geoffroy St. Hilaire, 1812  
 Synonym: *C. sannai* Grandidier, 1867.  
 Western form.

Diagnosis: Light frosted fawn-grey above, with a brown dorsal stripe; broadly creamy or yellowish below, yellow on the median strip; a partial white collar round throat, sharply marked, extending well up on sides of neck. A white median facial stripe; eye-rings dark brown, generally restricted to rims of eyes. Hands and feet white. Tail length 86–103 percent of head and body; ear short, 7.9–10.6% of head and head length. A noticeable diastema between anterior and middle maxillary premolars. Auditory bulla length 8.3–9.7 mm. Distribution: I have seen specimens from Berahoka, 40 miles north of Morondava; Tsidsibon River, west coast; and Ampijoroa. The range would seem to be the dry forests of western Madagascar.

*Cheirogaleus adipicaudatus* Grandidier, 1868  
 Synonym: *Opolemur thomasi* Forsyth Major, 1894.  
 Southern form

The Genus *Cheirogaleus*: Unrecognized Biodiversity in Dwarf Lemurs

Diagnosis: Usually darker above; dorsal stripe more vaguely expressed; more grey below, with traces of creamy-yellow more towards midline; white collar much less sharply expressed on sides of neck. White median facial stripe shorter, not extending so far up beyond level of eyes; eye-rings black, thick, invading sides of nose. Only digits are white. The tail is much longer than the head and body; the ear longer. Diastema poorly developed or absent. Auditory bulla length only 7.2–7.6 mm. Distribution: I have seen specimens from Tabiky, west of Ankarazabo; 170 km east of Tuléar, and Fort Dauphin.

#### *Cheirogaleus major* Group

*Cheirogaleus major* E. Geoffroy St. Hilaire, 1812  
 Synonyms: *Lemur commersonii* Wolf, 1822; *C. millii* E. Geoffroy St. Hilaire, 1828; *C. rypicus* Smith, 1833; *Mioicebus griseus* Lesson, 1840; *Myspithacus typus* F. Cuvier, 1842.  
 Grey-brown form.

Diagnosis: Grey-brown above, somewhat darker and greyer below. Dorsal stripe, where present, vaguely expressed and red brown. Midfacial zone pale but not white or yellow, does not extend above eye level; eye-rings relatively poorly marked. Feet not white. Ears poorly pigmented, naked. The tail is much longer ( $\geq 116\%$ ) than the head and body. Skull has a high braincase, which falls away steeply at the back, and a deeper facial skeleton. M<sup>1</sup> tends to be much reduced compared to other molars.

Distribution: I have seen specimens from Antongil Bay, Passumbee, Siakanaka, Maroansetra, Mahambo and Farafangana; the distribution would seem to extend down the east coast of Madagascar from (the western shore of?) Antongil Bay to nearly 23°S.

Notes: Peltier *et al.* (1977), based on field observations, described them as large with grey-brown pelage and rounded muzzle, and say that they live all along the east coast; where they are sympatric with *Cheirogaleus crossleyi*; they are characteristic of the high forest.

*Cheirogaleus crossleyi* Grandidier, 1870  
 Synonym: *Chirogale melanotis* Forsyth Major, 1894.  
 Furry-eared form.

Diagnosis: Warm red-brown dorsally; grey below, becoming creamy toward midline. Yellow of midfacial zone invades the region above the eyes; eye-rings blackish. Feet not light. Ears heavily pigmented, with black fur inside and out. The tail length is 85–110% of head and body. Skull slightly smaller but much narrower than *Cheirogaleus major*; facial skeleton and crown low.

teeth smaller than *C. major*, P<sup>2</sup> lower-crowned, M<sup>3</sup> less reduced, maxillary incisors project more forward.

**Distribution:** I have seen specimens from (south to north) Imerima, Lake Alaotra (30 miles northeast, at 2500 feet), Périnet, Malewo, Antisanaka, and Vohima. This range is mainly inland of that of *C. major*, and extends further north.

**Notes:** Petter *et al.* (1977) distinguish this dwarf lemur from *C. major* by its slightly smaller size, reddish color and pointed nose, and its very marked black rings round the eyes. They recorded them along the edge of the plateau, inland from the coast, from north of Maransetra south to Lake Alaotra, and wrote that they are abundant in plantations and "zones dégradées."

*Cheirogaleus sibrexi* Forsyth Major, 1896

**Diagnosis:** Grey-fawn above, with abundant white frosting; creamy below, this zone advancing further up the flanks and on the outside of the thighs than other species. A well-marked dark dorsal stripe. Ears are dark, nearly naked. Skull and teeth similar to those of *C. crossleyi* but smaller, and M<sup>3</sup> still less reduced.

**Distribution:** known from the type locality, Ankeraminika, not found on the map but described as "1 day's journey east of Anananarivo"; from Imerima, and from Pasandava.

*Cheirogaleus riuus* new species

Iron-grey (large) form.

**Type:** BM(NH) 88.2.18.3, young adult skin and skull, sex not recorded, from Tamatave (about 18°S, 14°E).

**Diagnosis:** Iron-grey, with brownish tones, similarly grey below, but yellower towards the ventral midline; a very vaguely expressed dorsal stripe. Feet white. Tail colored like body, often with a white tip; about equal in length to head and body. Ears dark, nearly naked or only sparsely haired. Skull resembling that of *C. crossleyi*, but larger, and flattening less extreme; toothrow longer, molars broader even than those of *C. major*, P<sup>2</sup> relatively higher-crowned, M<sup>3</sup> extremely reduced, and upper incisors less projecting forward.

**Etymology:** Latin, greyish.

**Distribution:** I have seen specimens from Tamatave, including Tampira, Mahambo, Ancaya, Ambodivangy, and Fesi Malendo. The last three localities have not been found in a gazetteer. Tamatave is about 18°S, Mahambo about 17°S, giving this species a small coastal range within that of *C. major*.

*Cheirogaleus minusculus* new species

Iron-grey (small) form.

**Type:** BM(NH) 11.6.21.1, young adult skin and skull, of unrecorded sex, from Ambosira, on the central plateau at about 20°S, 47°E.

**Diagnosis:** Color similar to *C. riuus* n.sp.; tail probably white-tipped; ears furred, but not as thickly as in *C. crossleyi*. Size extremely small, at the upper end of the range of *C. medius*; teeth small but M<sup>3</sup> less reduced compared to other molars.

**Etymology:** Latin, fairly small.

**Distribution:** known only from the type locality, Ambosira.

**Notes:** This is certainly the species seen by Petter *et al.* (1977) and Thalmann and Rakotoarison (1994) in the forests of the Bongolava massif, about 18°30'S, 45°30'E and not far southwest of the type locality. Petter *et al.* (1977) noted that the Bongolava form is smaller and lighter in color than others of the *C. major* group, with a pointed muzzle and sometimes with a white tail-tip; while Thalmann and Rakotoarison (1994) expected to find *C. medius* at that locality, and found instead this larger and browner *C. major*-like form. Despite its more or less equivalent size, it is distinguishable from *C. medius* by its much darker grey color, darker underside, more bushy tail, and lack of white collar, and by skull characters.

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## Taxonomic Revision of Mouse Lemurs (*Microcebus*) in the Western Portions of Madagascar

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The genus *Microcebus* (mouse lemurs) are the smallest extant primates. Until recently, they were considered to comprise two different species: *Microcebus murinus*, confined largely to dry forests on the western portion of Madagascar, and *M. rufus*, occurring in humid forest formations of eastern Madagascar. Specimens and recent field observations document rufous individuals in the west. However, the current taxonomy is entangled due to a lack of comparative material to quantify intrapopulation and intraspecific morphological variation. On the basis of recently collected specimens of *Microcebus* from 12 localities in portions of western Madagascar, from Ankarana in the north to Beza Mahafaly in the south, we present a revision using external, cranial, and dental characters. We recognize seven species of *Microcebus* from western Madagascar. We name and describe 3 spp., resurrect a previously synonymized species, and amend diagnoses for *Microcebus murinus* (J. F. Miller, 1777), *M. myoxinus Peters, 1852*, and *M. ravelobensis Zimmerman et al., 1998*.

**KEY WORDS:** mouse lemur; *Microcebus*; taxonomy; revision; new species.

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