MAMMALIAN SPECIES No. 694, pp. 1–5, 3 figs.

Indri indri.

By Aleta Quinn and Don E. Wilson

Published 5 July 2002 by the American Society of Mammalogists

Indri É. Geoffroy Saint-Hilaire, 1796

Indri É. Geoffroy Saint-Hilaire, 1796:46. Type species *Lemur indri* Gmelin, by tautonymy.
Indris Cuvier, 1805: table I. Emendation of *Indri* É. Geoffroy Saint-Hilaire.
Lichanotus Illiger, 1811:72. Type species *Lemur indri* Gmelin, by subsequent designation.
Indrium Rafinesque, 1815:54. New name for *Indri* É. Geoffroy Saint-Hilaire.
Lichanotes Temminck, 1827:xvi. Lapsus for *Lichanotus* Illiger.
Pithelemur Lesson, 1840:208. Type species *Lemur indri* Gmelin, by monotypy.

CONTEXT AND CONTENT. Order Primates, suborder Strepsirhini, family Indridae, genus *Indri*, which includes only the species *I. indri*.

Indri indri (Gmelin, 1788)

Indri

Lemur indri Gmelin, 1788:42. Type locality "Madagascar."
Indri brevicaudatus É. Geoffroy Saint-Hilaire, 1796:46. Based on "l'Indri," plate 88 of Sonnerat (1782:142).
Indri niger Lacépède, 1799:5. No locality given.
Indris ater I. Geoffroy Saint-Hilaire, 1825:534. Lapsus for *I. niger* Lacépède.
Pithelemur indri Lesson, 1840:208. Based on Gmelin's *L. indri*.
Lichanotus mitratus W. Peters, 1871:360. Type locality "northern Madagascar."
Indris variegatus Gray, 1872:474. No locality given.

CONTEXT AND CONTENT. Generic context as above. Two subspecies are recognized based on color (Groves 2001).

I. i. indri Gmelin, 1788:42, see above.
I. i. variegatus Gray, 1872:474, see above.

DIAGNOSIS. The indri (Fig. 1) is the largest extant lemur (mean body mass 6.5 kg). *Propithecus diadema diadema* males (6.4 kg) typically outweigh *I. indri* males (5.8 kg), but *I. indri* females are on average larger (7.1 kg—Glander and Powzyk 1998). *I. indri* possesses a vestigial tail (length < 50 mm) much shorter than that of *P. d. diadema*. Color pattern of *I. indri*, predominately black with whitish patches, is similar to *Propithecus diadema edwardsi*; where the ranges of the 2 species intersect, *I. indri* can be distinguished easily by its prominent tufted ears and vestigial tail. Although color pattern of *Varecia variegata variegata* is also similar, *I. indri* is much larger and assumes a vertical body posture at rest.

GENERAL CHARACTERS. Pelage color of *I. indri* is variable. Infants are extremely dark or completely black and develop whiter areas between 4 and 6 months of age. Face remains black but is encircled by a white ring. A white triangle occurs on the lower dorsal region including the vestigial tail. *I. i. variegatus* has white patches on back of head, collar, forelimbs, and hind limbs. White patches may be tinged with yellow, gray, or brown (Groves 2001; Mittermeier et al. 1994; Pollock 1975; Tattersall 1982; Thalmann et al. 1993). Eyes are yellow-green (Garbutt 1999).

Length of head and body ranges from 575 to 695 mm (Jenkins 1987). Length of tail ranges from 30 to 80 mm (Garbutt 1999; Jenkins 1987; Mittermeier et al. 1994; Petter et al. 1977). Length of hind limbs is equivalent to length of head and body (Garbutt 1999; Tattersall 1982).

Head is longer than broad, with nose moderately elongated and covered with short hairs. Digits are haired to their tips, and ears are rounded and covered with a bristly fringe. Arms are only about one-fourth as long as legs, and hands are elongated with digits 2–5 united by a membrane at the 1st knuckle. Toes are also united along their basal halves. Ears are large, with a tufted appearance, and tail is rudimentary (Elliot 1912; Hill 1953).

Mean skull length for a sample of 73 indri was 102.6 mm (range, 95.9–108.2 mm—Albrecht et al. 1990). Skull measurements (in mm) of 1 National Museum of Natural History male specimen (Fig. 2) are: postorbital width, 33.9; interorbital width, 18.4; zygomatic width, 58.5; mastoid width, 43.7; rostrum width, 32.9; length of bulla, 19.3; width of bulla, 15.0; palatal length, 30.7; mandible length, 75.9.

DISTRIBUTION. *Indri indri* is confined to the northeastern rainforests of Madagascar (Fig. 3) between sea level and 1,500 m (Garbutt 1999; Petter et al. 1977). Currently, *I. indri* occurs northward from the Mangoro River near Mahanoro (Mittermeier et al. 1994; Thalmann et al. 1993) to near Sambava (Mittermeier et al. 1994), although it may be extremely rare in the northern limits near the Andapa basin (Tattersall 1982). *I. indri* does not occur in the Masoala peninsula (Tattersall 1982). Historical evidence suggests that the range recently extended as far north as Vohemar (Schwarz 1931) and as far south as the Masora River (Grandidier and Petit 1932; Hill 1953) and Mananjary (Lamberton 1939).

FIG. 1. *Indri indri* mother and young. Photograph by Russel A. Mittermeier/Conservation International.

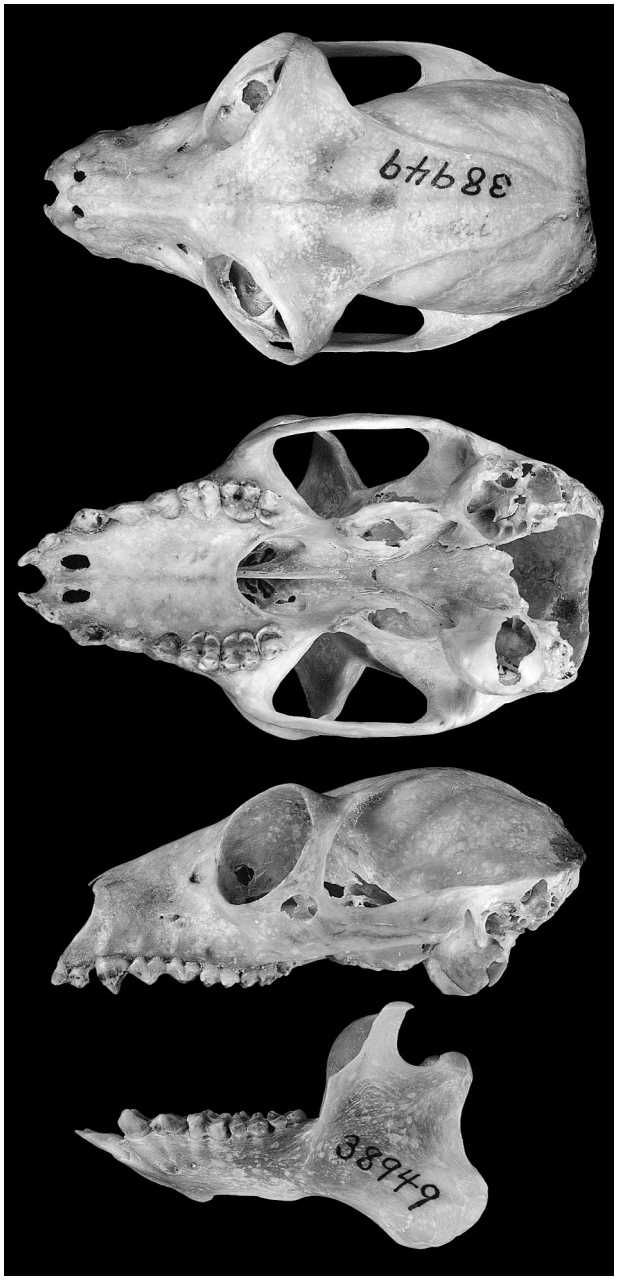

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Indri indri* (male, United States National Museum of Natural History 38949). Greatest length of skull is ca. 107 mm.

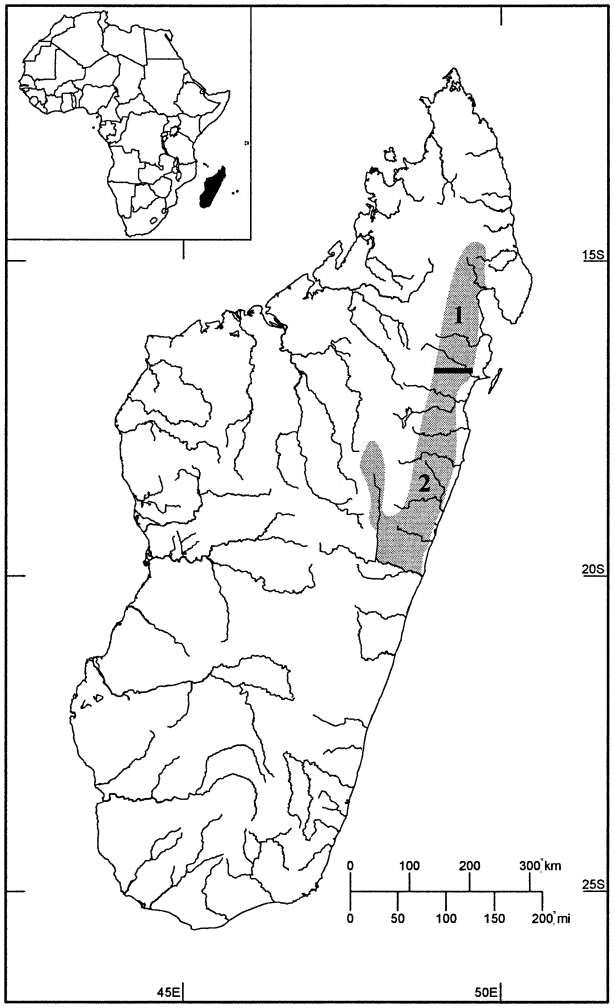

FIG. 3. Distribution of *Indri indri*. 1, *I. i. indri*; 2, *I. i. variegatus*; modified from Mittermeier et al. 1994.

FOSSIL RECORD. Late Quaternary subfossils of *I. indri* have been found in the caves of the Ankarana Massif 75 km south of Antisiranana at the northern tip of Madagascar. This region, now composed of pockets of dry forest, may once have been connected to the current range of the indri by corridors of rainforest. Alternatively, *I. indri* may once have included animals capable of occupying dry forest. Subfossils are also known from Ampasambazimba in central Madagascar (Godfrey et al. 1999; Jungers et al. 1995; Lamberton 1939). Also, Godfrey et al. (1999) illustrated a fragmentary subfossil humerus from Ampoza in western Madagascar that may have belonged to indri. Thus, subfossil indri have been identified positively from central and northern Madagascar and tentatively from the west. These subfossils are a bit more robust than recent animals (Albrecht et al. 1990; Godfrey et al. 1999; Jungers et al. 1995).

FORM AND FUNCTION. Dental formula is either i 2/2, c 1/0, p 2/2, m 3/3, total 30 (Gingerich 1977; Gingerich and Ryan 1979; Hill 1953) or i 2/1, c 1/1, p 2/2, m 3/3, total 30 (Schwartz 1974; Swindler 1976). The 2nd tooth in the lower tooth row is either a slightly enlarged incisor or a displaced lower canine. Although arguments in favor of the canine are cogent, Gingerich (1977) presented a compelling case for the more traditional view that the incisiform teeth are indeed incisors. Upper incisors are separated by a wide diastema and the long, closely spaced lower incisors form a tooth comb (Godfrey 1976). Primary function of the tooth comb is grooming, but it is also used in feeding (Pollock 1977). Both upper premolars are unicuspids, and molars have 4 cusps (Fig. 2). Canines are higher than premolars, and a diastema is not present. Incisors are slightly subequal in size (Elliot 1912).

Alimentary system is highly specialized and reflects the indri's folivorous and frugivorous diet. Salivary glands are hypertrophied, abdominal viscera and stomach are large, caecum is elongated, intestine is uniform and lengthy, and colon is capacious and compactly folded (Hill 1953; Pollock 1975). An ethmoid exposure occurs in some specimens, indicating the existence of a true os planum (Cartmill and Gingerich 1978). A large, membranous, laryngeal sac and mobile cheeks aid in vocalizations (Hill 1953; Jenkins 1987; Pariente 1979; Pollock 1986). The long thigh (mean femoral length, 240.2), elongated foot, and long manus with pseudo-opposable thumb are adaptations for vertical clinging and leaping (Demes et al. 1991; Jenkins 1987). The indri has a tapetum, indicating nocturnal ancestry. Vertebral formula is 7 C, 12 T, 8–9 L, 2–4 S, and 14 Ca, total 43–46.

ONTOGENY AND REPRODUCTION. *Indri indri* reaches sexual maturity between 7 and 9 years of age. Females give birth every 2–3 years after a gestation of 120–150 days. A single offspring is born and carried ventrally for 4 months. The infant is then carried dorsally and is capable of independent movement at 8 months (Garbutt 1999; Pollock 1975). Nursing decreases at 8 months and ceases at 1 year. Juveniles sleep with their mothers for the 1st year and remain spatially and behaviorally close for 2 years (Pollock 1975).

ECOLOGY. *Indri indri* inhabits lowland to midaltitude primary and secondary rainforest (Garbutt 1999). A series of parallel ridges, aligned roughly north–south, composes the southern part of the *I. indri* range (Petter and Peyriéras 1974; Pollock 1975, 1977). The ridges are ca. 400 m high, up to 2,000 m long, and separated by valleys not exceeding 200 m in depth (Petter and Peyriéras 1974). Each ridge supports a heterogeneous rainforest comprising tall, straight trees in the valley and short, thick trees at the highest point (Pollock 1977).

Indri indri lives in small family groups of 2–6 composed of an adult pair and their dependent offspring (Garbutt 1999; Harcourt and Thornback 1990; Oliver and O'Conner 1980; Pollock 1975). Pollock (1975) estimated indri density between 8 and 16 individuals/km^2, corresponding to 3–5 groups. Petter and Peyriéras (1974) estimated 1 group/km^2 and suggested Pollock's higher indri density was due to animals fleeing local agricultural development; however, the estimate of Petter and Peyriéras (1974) is based on vocalizations, which may not have been produced by all groups in the study area. This disparity in population density estimates increases the difficulty in determining the total population, but Mittermeier et al. (1992) estimated a total population of 1,000–10,000 indri.

The main diet comprises leaves, fruits, buds, and flowers from all levels of the canopy (Pollock 1975, 1977; Thalmann et al. 1993). Young leaves and leaf shoots are most often consumed unless fruit is available (Pollock 1977). Plant families most often consumed in the northern range include Guttiferae for fruits and Lauraceae for leaves and buds (Thalmann et al. 1993) and in the southern range Annonaceae, Euphorbiaceae, Guttiferae, Lauraceae, Monimiaceae, Moraceae, and Sapindaceae (Pollock 1975). *I. indri* descends to the ground on ca. 75% of days to consume soil exposed by fallen trees (Pollock 1977). Pollock (1977) gained the impression of an organized diet because *I. indri* consumes 5–12 species daily, often choosing 3–4 of these species selectively and bypassing other possible food sources.

In November and December, *I. indri* groups move downward in the canopy to avoid seasonally abundant horseflies (Thalmann et al. 1993). *I. indri* has been protected from human predation by local taboos, but recently nonnative tribes and foreigners have hunted indri (Garbutt 1999; Thalmann et al. 1993).

Indri indri has never successfully bred in captivity. Only 1 individual has survived longer than 1 year in captivity, in a Forest Station at Ivoloina (Petter et al. 1977; Thalmann et al. 1993).

BEHAVIOR. *Indri indri* is the most strictly diurnal lemur, with an activity period of 5–11 h depending on season, temperature, and atmospheric conditions (Garbutt 1999; Mittermeier et al. 1994; Pollock 1975, 1979b). Indri sleep alone or in pairs 10–30 m above the ground in nonspecific trees (Garbutt 1999; Mittermeier et al. 1994; Pollock 1975). Group members urinate and defecate in concert at 1 of several designated defecation areas. Feeding occurs throughout the day, including occasional progressions to change feeding location. The nocturnal rest period is preceded by a grooming session during which individuals may alternate with a grooming partner but do not form chains (Pollock 1975, 1979b). Young, and occasionally adult female, indri will play-wrestle silently, for a few seconds to 15 min. A well-defined social displacement procedure involves 1 individual inducing another to leave a resting or feeding location by vocalizations or attempts to bite, wrestle, or kick. Social activity increases during the summer months between November and March (Pollock 1975).

Social observations suggest that adult female indri dominate adult males (Pollock 1979b). Adult females were more often groomed and less often groomers; adult females frequently displaced males but were never displaced by adult males; adult males were generally forced to occupy lower positions and poorer feeding locations in the tree; and the adult male's sexual advances were aggressively resisted. When breeding, copulation occurs between December and March while hanging from a branch in a ventroventral position (Thalmann et al. 1993).

Indri defend their territories by singing and scent-marking using glands or saliva from cheek and genital regions (Pollock 1975). A narrow (50-m) band in which neighboring groups may range surrounds each territory (Pollock 1979a). Ranging behavior is dependent on food supply but may entail a progression to a threatened territorial boundary. Groups generally move 300–700 m daily, traveling the most distance in midsummer when visiting fruiting trees (Pollock 1977).

While feeding, the animals usually sit or use 3 or 4 limbs to hang. Resting posture is generally vertical, but *I. indri* may sit supported by a forked trunk or crouch on horizontal branches with legs extended beyond forelimbs. Powerful leaps are the main form of locomotion, although quadrupedal movements along horizontal branches and bipedal hopping on the ground have been observed (Walker 1979).

Indri indri communicates via several vocalizations. A soft, quiet hum indicates imminent movement. An exhaled hoot from the adult male or largest male offspring warns of ground predators or disturbances. Aerial predators are announced by a loud, barking roar. The aerial alarm bark is sometimes emitted to introduce the main vocalization, a complex series of calls that form a group song. The song may be spontaneous or a response to an airplane, thunder, disturbance, or another group's song (Pollock 1975). Cold and wet weather decrease singing. Groups most frequently sing in the morning and during the austral summer. Generally, the adult male begins the song with a long (up to 5.2 s) and low call (main frequency 750 Hz) and is almost immediately joined by the other group members. Two further call types are a short (1.2–2 s) call in ascending pitch (700–3,000 Hz) and a short (1.2–2 s), loud, high call (up to 9,000 Hz—Pollock 1986). Songs last 40–250 s and conclude with a duet, usually by the adult pair. The adult female and male sing in any part of the song, whereas younger individuals sing at the beginning for a duration directly proportional to age (Pollock 1986). Cooperation minimizes the length of pauses (Thalmann et al. 1993). Ca. 27–28% of songs are unanswered by other groups, although this may be inaccurate because humans can hear the songs 1,500–2,000 m away, but indri can perhaps detect songs up to 3,000 m away (Oliver and O'Conner 1980; Pollock 1975, 1986). The group does not climb higher in the tree to maximize carrying distance before singing, and no overt change in behavior occurs when the song has concluded (Pollock 1986). Eight rapid exchanges of song between groups occurred when 1 group approached or crossed the border of another group's territory, suggesting the songs function as territorial declaration (Pollock 1986). Other functions may include reuniting temporarily dispersed individuals and advertising the mating potential of a group via the individuals' characteristic contributions (Pollock 1975, 1986).

GENETICS. *Indri indri* has a diploid number of 40 chromosomes. Twelve autosomes and the X chromosome are metacentric, whereas 6 autosomes and the Y chromosome are acrocentric. The remaining 20 autosomes are submetacentric (Rumpler 1975).

CONSERVATION STATUS. *Indri indri* is endangered and has been given the Highest Priority rating for rarity, taxonomic uniqueness, and discontinuity of habitat in the IUCN/SSC Primate Specialist Group's *Lemurs of Madagascar: an action plan for their conservation* (Harcourt and Thornback 1990; Mittermeier et al. 1992, 1994; Thalmann et al. 1993). All Indridae species are listed in Appendix One of the 1973 Convention on International Trade in Endangered Species, and all Lemuroidea are in Class A of the African Convention 1969 (Harcourt and Thornback 1990).

Seven wildlife reserves contain indri: Ambatovaky, Verezanantsoro, Betampona, Zahamena, Anjanaharibe-Sud, Mantady, and Analamazaotra (Garbutt 1999; Mittermeier et al. 1992). These reserves are generally underfunded and often represent isolated habitat surrounded by agricultural development (Harcourt and Thornback 1990). Suggested conservation measures include additional trails around reserves, more guards, additional reserves, and population surveys (Harcourt and Thornback 1990; Petter et al. 1977).

REMARKS. According to Hill (1953), the name indri was given by Sonnerat, who mistook the Malagasy exclamation for "there he is," *indri* or *indri izy*, for the vernacular name. However, the actual Malagasy word is *iry*, suggesting that Sonnerat must have

not only misunderstood the meaning but also misheard or misrecorded the word itself. The Malagasy name for the indri, *babakoto,* means father of *koto* (*koto,* a little boy)—so given because the calls made by indri seem to be those of a wailing father calling his lost son. The common name for the indri was used in naming a recently discovered paleopropithecid, *Babakotia radofilai*, an extinct relative of the indri (Godfrey et al. 1990).

LITERATURE CITED

ALBRECHT, G. H., P. D. JENKINS, AND L. R. GODFREY. 1990. Ecogeographic size variation among the living and subfossil prosimians of Madagascar. American Journal of Primatology 22: 1–50.

CARTMILL, M., AND P. D. GINGERICH. 1978. An ethmoid exposure (os planum) in the orbit of *Indri indri* (Primates, Lemuriformes). American Journal of Physical Anthropology 48:535–538.

CUVIER, G. 1805. Leçons d'anatomie comparée de G. Cuvier. C. Duméril, Paris, France.

DEMES, B., W. L. JUNGERS, AND K. SELPIEN. 1991. Body size, locomotion, and long bone cross-sectional geometry in indriid primates. American Journal of Physical Anthropology 86:537–547.

ELLIOT, D. G. 1912. A review of the Primates. Monographs of the American Museum of Natural History 1:1–317.

GARBUTT, N. 1999. Mammals of Madagascar. Pica Press, Sussex, United Kingdom.

GEOFFROY SAINT-HILAIRE, É. 1796. Mémoire sur les rapports naturels des makis *Lemur*, L. et description d'une espèce nouvelle de mammifère. Magasin Encyclopedique, ou Journal des Sciences des Lettres et des Arts (2)1:20–50.

GEOFFROY SAINT-HILAIRE, I. 1825. Dictionnaire classique d'histoire naturelle. Bory de Saint-Vincent, Paris, France 8:1–260.

GINGERICH, P. D. 1977. Homologies of the anterior teeth in Indriidae and a functional basis for dental reduction in primates. American Journal of Physical Anthropology 47:387–394.

GINGERICH, P. D., AND A. S. RYAN. 1979. Dental and cranial variation in living Indriidae. Primates 20:141–159.

GLANDER, K. E., AND J. A. POWZYK. 1998. Morphometrics of wild *Indri indri* and *Propithecus diadema diadema*. Folia Primatologica 69(Suppl. 1):399.

GMELIN, J. F. 1788. Revision of 'Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis synonymis, locis' by C. Linneaus. G. E. Beir, Lipsiae, Germany 1:1–232.

GODFREY, L. 1976. Dental reduction in the Indriidae. Pp. 109–139 in The measures of man (E. Giles and J. S. Friedlaender, eds.). Peabody Museum Press, Cambridge, Massachusetts.

GODFREY, L. R., W. L. JUNGERS, E. L. SIMONS, P. S. CHATRATH, AND B. RAKOTOSAMIMANANA. 1999. Past and present distributions of lemurs in Madagascar. Pp. 19–23 in New directions in lemur studies (B. Rakotosamimanana, H. Rasamimanana, J. U. Ganzhorn, and S. M. Goodman, eds.). Kluwer Academic/Plenum Publishers, New York.

GODFREY, L. R., E. L. SIMONS, P. S. CHATRATH, AND B. RAKOTOSAMIMANANA. 1990. A new fossil lemur (Babakotia, Primates) from northern Madagascar. Comptes Rendus de l'Académie des Sciences Série II, 310:81–87.

GRANDIDIER, G., AND G. PETIT. 1932. Zoologie de Madagascar. Société d'Editions Géographiques Maritimes et Coloniales, Paris, France.

GRAY, J. E. 1872. On the varieties of *Indris* and *Propithecus*. Annals and Magazine of Natural History, Series 4, 10:474.

GROVES, C. 2001. Primate taxonomy. Smithsonian Institution Press, Washington, D.C.

HARCOURT, C. AND J. THORNBACK. 1990. Lemurs of Madagascar and the Comoros. The IUCN red data book. International Union for the Conservation of Nature and Natural Resources, Gland, Switzerland.

HILL, W. C. O. 1953. Primates: comparative anatomy and taxonomy. Edinburgh University Press, Edinburgh, United Kingdom 1:1–798.

ILLIGER, C. 1811. Prodromus systematis mammalicim et avium. Sumptibus C. Salfeld, Berlin, Germany.

JENKINS, P. D. 1987. Catalogue of primates in the British Museum (Natural History) and elsewhere in the British Isles. Part III: suborder Strepsirrhini, including the subfossil Madagascar lemurs and family Tarsiidae. British Museum (Natural History), London, United Kingdom.

JUNGERS, W. L., L. R. GODFREY, E. L. SIMONS, AND P. S. CHATRATH. 1995. Subfossil *Indri indri* from the Ankarana Massif of northern Madagascar. American Journal of Physical Anthropology 97:357–366.

LACÉPÈDE, B. G. E. 1799. Tableau des divisions et sous-divisions, ordres et genres des mammifères. P. Didot l'ainé et Firmin Didot, Paris, France 8:1–298.

LAMBERTON, C. 1939. Contribution à la connaissance de la faune subfossile de Madagascar: lémuriens et cryptoproctes. Note V. Lémuriens subfossiles. Mémoires de l'Académie Malgache 27:51–73.

LESSON, R. P. 1840. Species des mammifères bimanes et quadrumanes. J. B. Baillière, Paris, France (not seen, cited in Groves 2001).

MITTERMEIER, R. A., W. R. KONSTANT, M. E. NICOLL, AND O. LANGRAND. 1992. Lemurs of Madagascar: an action plan for their conservation. International Union for the Conservation of Nature and Natural Resources, Gland, Switzerland.

MITTERMEIER, R. A., I. TATTERSALL, W. R. KONSTANT, D. M. MEYERS, AND R. B. MAST. 1994. Lemurs of Madagascar. Conservation International, Washington, D.C.

OLIVER, W. L. R., AND S. M. O'CONNOR. 1980. Circadian distribution of *Indri indri* group vocalizations: a short period sampling at two study sites near Perinet, eastern Madagascar. Dodo Journal of the Jersey Wildlife Preservation Trust 17:19–27.

PARIENTE, G. 1979. The role of vision in prosimian behavior. Pp. 411–459 in The study of prosimian behavior (G. A. Doyle and R. D. Martin, eds.). Academic Press, New York.

PETERS, W. 1871. Über eine neue Art von Indris, *Lichanotus mitratus*, aus Madagascar. Monatsberichte der Köngilich Preussischen Akademie der Wissenschaften zu Berlin, 1872: 360–363.

PETTER, J. J., R. ALBIGNAC, AND Y. RUMPLER. 1977. Mammifères lémuriens (Primates prosimiens). Faune de Madagascar 44:1–513.

PETTER, J. J., AND A. PEYRIÉRAS. 1974. A study of population density and home ranges of *Indri indri* in Madagascar. Pp. 39–48 in Prosimian biology (R. D. Martin, G. A. Doyle, and A. C. Walker, eds.). Gerald Duckworth and Co. Ltd., London, United Kingdom.

POLLOCK, J. I. 1975. Field observations on *Indri indri*: a preliminary report. Pp. 287–311 in Lemur biology (I. Tattersall and R. W. Sussman, eds.). Plenum Press, New York.

POLLOCK, J. I. 1977. The ecology and sociology of feeding in *Indri indri*. Pp. 37–69 in Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys, and apes (T. H. Clutton-Brock, ed.). Academic Press, London, United Kingdom.

POLLOCK, J. I. 1979a. Spatial distribution and ranging behavior in lemurs. Pp. 359–409 in The study of prosimian behavior (G. A. Doyle and R. D. Martin, eds.). Academic Press, New York.

POLLOCK, J. I. 1979b. Female dominance in *Indri indri*. Folia Primatologica 31:143–164.

POLLOCK, J. I. 1986. The song of the indris (*Indri indri*; Primates: Lemuroidea): natural history, form, and function. International Journal of Primatology 7:225–264.

RAFINESQUE, C. S. 1815. Analyse de la nature ou tableau de l'univers et des corps organisés. Jean Barravecchia, Palermo, Italy.

RUMPLER, Y. 1975. The significance of chromosomal studies in the systematics of the malagasy lemurs. Pp. 25–40 in Lemur biology (I. Tattersall and R. W. Sussman, eds.). Plenum Press, New York.

SCHWARTZ, J. H. 1974. Observations on the dentition of the Indriidae. American Journal of Physical Anthropology 41:107–114.

SCHWARZ, E. 1931. A revision of the genera and species of Madagascar Lemuridae. Proceedings of the Zoological Society of London 1931:399–428.

SONNERAT, P. 1782. Voyage aux Indes Orientales et à la Chine. Self-published, Paris, France 2:1–298.

SWINDLER, D. R. 1976. Dentition of living primates. Academic Press, London, United Kingdom.

TATTERSALL, I. 1982. The primates of Madagascar. Columbia University Press, New York.

TEMMINCK, C. J. 1827. Monographies de mammalogie. G. Dufour et E. d'Ocagne, Paris, France.

THALMANN, U., T. GEISSMANN, A. SIMONA, AND T. MUTSCHLER. 1993. The indris of Anjanaharibe-Sud, northeastern Madagascar. International Journal of Primatology 14:357–381.

WALKER, A. 1979. Prosimian locomotor behavior. Pp. 543–565 in The study of prosimian behavior (G. A. Doyle and R. D. Martin, eds.). Academic Press, New York.

Associate editors of this account were ELAINE ANDERSON and SERGE LAVIÈRE. Editor was VIRGINIA HAYSSEN.

ALETA QUINN AND DON E. WILSON, NATIONAL MUSEUM OF NATURAL HISTORY, SMITHSONIAN INSTITUTION, WASHINGTON, D.C. 20560.