MAMMALIAN SPECIES No. 740, pp. 1–6, 3 figs.

Daubentonia madagascariensis.

By Aleta Quinn and Don E. Wilson

Published 13 July 2004 by the American Society of Mammalogists

Daubentonia É. Geoffroy Saint-Hilaire, 1795

Sciurus Gmelin, 1788:152. Part.

Daubentonia É. Geoffroy Saint-Hilaire, 1795:195. Type species *Sciurus madagascariensis* Gmelin, by tautonymy.

Scoleophagus É. Geoffroy Saint-Hilaire, 1795:196. Alternate name for *Daubentonia* É. Geoffroy Saint-Hilaire.

Aye-aye Lacépède, 1799:6. Unavailable name, non Linnaean. Based on Sonnerat 1782.

Lemur Shaw, 1800:109. Type species *Lemur psilodactylus* Shaw.

Cheyromis É. Geoffroy Saint-Hilaire, 1803:180. Based on Sonnerat (1782).

Chiromys Illiger, 1811:75. Replacement name for *Daubentonia* É. Geoffroy Saint-Hilaire.

Psilodactylus Oken, 1816:xi, 1164. Unavailable name (ICZN 1956, Opinion 417).

Cheiromys G. Cuvier, 1817:207. Replacement name for *Daubentonia* É. Geoffroy Saint-Hilaire.

Myspithecus Blainville, 1839:34. Replacement name for *Cheiromys* G. Cuvier.

Myslemur Blainville, 1846:559. Replacement name for *Myspithecus* Blainville.

CONTEXT AND CONTENT. Order Primates, suborder Strepsirhini, family Daubentoniidae, genus *Daubentonia*, which includes the extant *D. madagascariensis* and the extinct *D. robusta* Lamberton, 1934. Morphological studies (Groves 1989; Jablonski 1986) and cytochrome-*c* mitochondrial DNA analysis (Adkins and Honeycutt 1994) suggest that *Daubentonia* may be the sister group to both lemuriformes and loriformes. Immunodiffusion data (Dene et al. 1980), chromosomal banding patterns (Rumpler et al. 1988), cytochrome-*b* mitochondrial DNA analysis (Del Pero et al. 1995), and ϵ-globin gene sequencing (Porter et al. 1995) indicate that *Daubentonia* is the sister group to all other lemuriformes. A monotypic superfamily or infraorder (Chiromyiformes—Groves 1989) has been proposed.

Daubentonia madagascariensis (Gmelin, 1788)

Aye-aye

Sciurus madagascariensis Gmelin, 1788:152. Type locality "Occidentali parte insulae Madagascar."

Lemur psilodactylus Shaw, 1800:109. No type locality; based on Sonnerat (1782).

Cheiromys madagascariensis var. *laniger* G. Grandidier, 1929: 106. No type locality.

CONTEXT AND CONTENT. Generic context given above. The designation of *D. madagascariensis* var. *laniger* was proposed for a specimen of similar size but with longer ears, milky-brown pelage, and less marked white tips to the hairs (Grandidier 1929). Suggestions that the specimen was molting and did not justify separate taxonomic status were met by arguments that other differences, such as length of tail, were present (Sterling 1994c).

DIAGNOSIS. The aye-aye is the largest nocturnal lemur (mean body mass, 2.5 kg—Feistner and Sterling 1995) and the only extant member of the family Daubentoniidae (Oxnard 1981). *D. madagascariensis* (Fig. 1) can be distinguished from other lemurs by its long (365–445 mm—Feistner and Sterling 1995), bushy tail; prominent, triangular, naked ears; and elongated digits with curved claws (Soligo and Möller 1999).

GENERAL CHARACTERS. Mean length of head and body is 319.5 mm for males (n = 6, SD = 25.2) and 305.0 mm for females (n = 2, SD = 7.1—Feistner and Sterling 1995). Despite reports that males are generally larger than females, a study of 20 wild-caught individuals revealed no significant sexual dimorphism in body mass. Eight individuals were monomorphic for the following characters ($\bar{X}$, in mm): cranial length (148.3), length of body (319.5), length of tail (480.8), circumference of neck (199.2), length of ear (96.8), and width of ear (70.0—Feistner and Sterling 1995).

Pelage is long, coarse, and dark brown to black with scattered white-tipped guard hairs. Eyes are yellow-orange or sandy-brown and surrounded by dark rings (Feistner and Ashbourne 1994; Garbutt 1999). Nictitating membrane is present. Face and throat are pale gray. Snout is short and blunt and nose is pink (Garbutt 1999). Legs are longer than arms, claws are compressed and pointed, and thumb and hallux are opposable (Elliot 1912). A single pair of mammae is inguinal. Third digit is elongated and extremely narrow.

Skull measurements (in mm) of 1 specimen are: occipitonasal length, 83; zygomatic width, 61; intertemporal width, 35; palatal length, 28; breadth of braincase, 45; median length of nasals, 15; length of upper molar series, 13; length of mandible, 38; length of lower molar series, 12 (Elliot 1912). Incisors are large and continuously growing (Fig. 2).

DISTRIBUTION. Distribution of *D. madagascariensis* is wide in Madagascar (Fig. 3), but population density remains low in all areas. Range extends in the north to Montagne d'Ambre and Sambava, in the northwest to Sambirano, and in the south to Ran-

FIG. 1. *Daubentonia madagascariensis*. Photograph courtesy Duke University Primate Center.

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Daubentonia madagascariensis* (male, United States National Museum of Natural History 199694). Greatest length of skull is 92 mm.

omafana and Bemaraha (Ankel-Simons 1990; Garbutt 1999; Harcourt and Thornback 1990).

FOSSIL RECORD. The late-Holocene species *Daubentonia robusta* represents an extinct congener of *D. madagascariensis*. Remains of *D. robusta* include 4 incisors, a tibia, and postcranial material from 5 sites spanning central and southwest Madagascar (Godfrey et al. 1999; Simons 1994). *D. robusta* is considerably more robust than extant aye-ayes (mean robusticity index 24.5 for *D. robusta*, 16.5 for *D. madagascariensis*—Simons 1994) and 30% larger in linear dimensions (Tattersall 1982). Estimated body mass of *D. robusta* is 6.7–13.5 kg (Simons 1994). Holes drilled in *D. robusta* incisors indicate human modification and suggest the species was hunted by humans (MacPhee and Raholimavo 1988; Simons 1994, 1995).

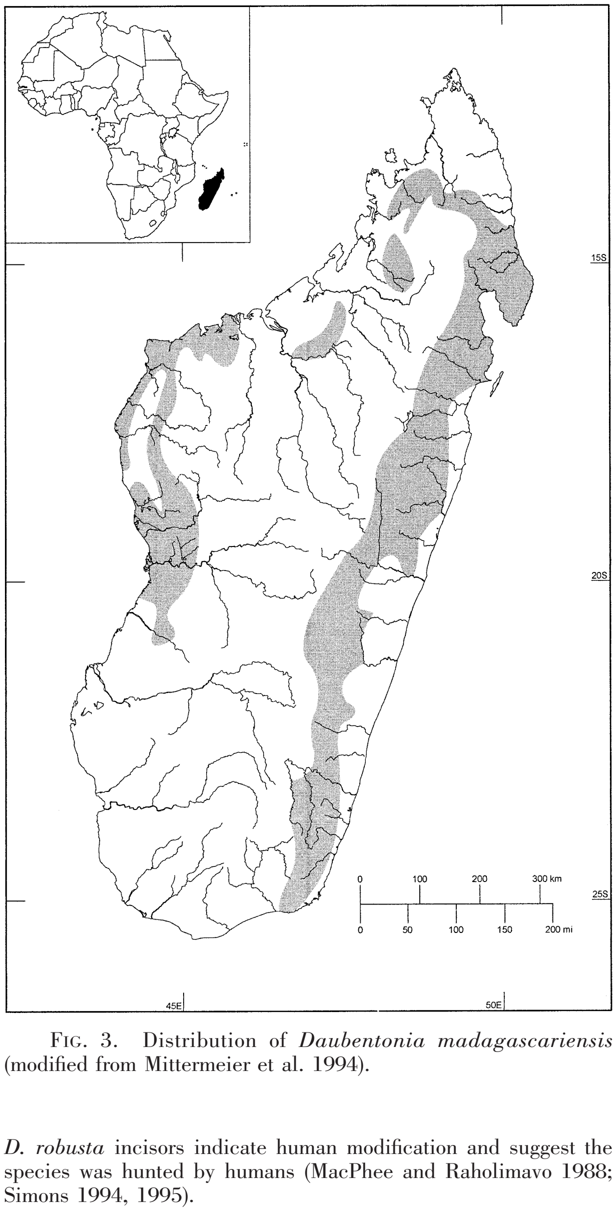

FIG. 3. Distribution of *Daubentonia madagascariensis* (modified from Mittermeier et al. 1994).

FORM AND FUNCTION. Dental formula is i 1/1, c 0/0, p 1/0, m 3/3, total 18 (Hill 1953). Deciduous dentition is polymorphic: i 1–2/1, c 1/1, p 2/2 (Ankel-Simons 1996; Luckett and Maier 1986). Incisors are ever-growing. Permanent upper incisors are large, form a quarter-circle, and are coated with enamel on anterior surfaces. Lower incisors are larger, describe a half-circle, and have a more extensive enamel coating. Postincisor diastemata occur on upper and lower jaws (Hill 1953). Molars are small with indistinct cusps (Hill 1953).

Skull and braincase are smaller in anterioposterior length and larger in dorso-ventral height compared to other prosimians. Brain is large and klinorhynchy (downward bending of the facial skeleton with respect to the cranial base) is marked (Cartmill 1974).

Musculature and skeletal anatomy have been described (Hill 1953). Vertebral formula is 7 C, 13 T, 6 L, 3 S, and 18–24 Ca, total 47–53. Auricular, masticatory, and caudal muscles are strongly developed. Stomach is simple and subglobular. Seminal vesicles are absent, a condition unique among lemurs (Hill 1953). Oogenesis is persistent in adult females (Petter-Rousseaux and Bourlière 1965).

Claws on all digits except hallux enable the use of small-diameter supports (Ancrenaz et al. 1994). A toilet claw is present on the 2nd digit of the foot (Soligo and Möller 1999). Digits are elongated (4th digit = 104.6 mm, n = 2—Iwano 1991b) and the 3rd digit is extremely narrow, exceptionally flexible, and independently controlled (Milliken et al. 1991). Powerful opposable hallux, robust shoulder girdle, and high humeral compressive and bend strengths enable head-first descent (Curtis and Feistner 1994).

ONTOGENY AND REPRODUCTION. Matings and births observed or inferred in the wild indicate mating and reproduction are not seasonal (Sterling 1994b). Female estrous cycle length ranges from 21 to 65 days ($\bar{X}$, 47 days—Feistner and Taylor 1998). Cycles are characterized by changes in size and color of vulva from small (ca. 5 mm in diameter) and gray during anestrus to large (ca. 25 mm) and red during estrus (Carroll and Beattie 1993; Winn 1994b). The period of maximum swelling is ca. 2–10 days (Feistner and Taylor 1998). Copulation occurs at peak swelling; male mounting attempts at other times are aggressively rebuffed (Carroll and Haring 1994; Feistner and Taylor 1998). Copulation occurs in the dorsoventral position while hanging from an obliquely positioned branch (Beattie et al. 1992; Winn 1994b). Mating lasts 55–65 min (Beattie et al. 1992; Carroll and Haring 1994; Feistner and Taylor 1998). Females mate with >1 male per estrus, exhibiting a multimale–multifemale mating system (Sterling 1993). One infant is born after 158–172 days (Glander 1994) with a 2–3-year interval between births (Garbutt 1999).

Neonatal mass is ca. 90–140 g (Glander 1994). Infant eyes are green, ears are floppy, and pelage is similar to adult (Feistner and Ashbourne 1994; Winn 1994a).

Infant development is slow. Deciduous dentition is shed at ca. 20 weeks (Winn 1994a) and weaning is complete by ca. week 28 (Feistner and Ashbourne 1994). Full adult locomotor range is attained by ca. 9 months (Feistner and Ashbourne 1994; Winn 1994a). Sexual maturity is attained at ca. 2.5 years (Winn 1994a).

BEHAVIOR. *Daubentonia madagascariensis* is strictly nocturnal. Activity begins from 30 min before to 3 h after sunset; males are generally active before females (Ancrenaz et al. 1994; Garbutt 1999). The day is spent in an ovular nest constructed of leaves and twigs high (10–15 m) in the canopy (Haring et al. 1994). Nests have been found in coconut palms (*Cocos nucifera*), clove trees, (*Eugenia caryophyllus*), hintzy (*Intsia bijuga*), lychees (*Litchi chinensis*), mango trees (*Mangifera*), badamiers (*Terminalia catappa*), and copaliers (*Trachylobium verrucosum*—Ancrenaz et al. 1994; Petter 1977; Petter and Petter 1967; Petter and Peyriéras 1970; Petter et al. 1977). A particular nest might be used for several consecutive days or remain unoccupied for several weeks (Ancrenaz et al. 1994). Different individuals may use the same nest on different days. Individuals typically sleep singly in the wild although individuals sometimes share a nest (Coffman et al. 1993).

Individuals may rest up to 7 h each night between bouts of feeding and self-grooming. Activity declines after ca. 0200 h with frequent resting (Iwano 1991a). The 3rd finger and tongue are used to groom for up to 30 min (Ancrenaz et al. 1994; Haring et al. 1994). Allogrooming has been observed in captivity but not in the wild (Rendall 1993; Sterling 1993).

Substrate use is diverse, including horizontal, oblique, and vertical branches (Curtis 1992). Aye-ayes use both narrow (Ancrenaz et al. 1994) and wide branches (Petter et al. 1977) preferentially. Ca. 82% of the time is spent in the highest 2 levels of the canopy (Ancrenaz et al. 1994).

Daubentonia madagascariensis frequently clings upside down and may rest in a horizontal or vertical posture. Quadrupedal walking and leaping between vertical supports occur. Individuals may climb downward either head or tail first (Ancrenaz et al. 1994).

The 3rd digit is used in feeding and delicate grooming (Goix 1993; Iwano 1991b; Petter and Peyriéras 1970). Fruits are pierced with the 3rd or 4th digit and the contents scooped out by rapidly (ca. 3.3 strokes/s) inserting and withdrawing the 3rd digit (Iwano and Iwakawa 1988). The 3rd digit is also used to find and extract larvae from within branches (Erickson 1994, 1995a). The aye-aye taps its 3rd digit against the wood, ears bent forward, apparently interpreting acoustical reverberations to detect prey. This percussive foraging reveals the location of empty cavities, but cavities containing prey were more often excavated (Erickson 1991, 1998). Cavities filled with frass, acoustical foam, gelatin, or wood also were excavated, suggesting that any break in the integrity of the wood stimulates excavation (Erickson 1995b; Erickson et al. 1998).

Lateralization in hand preference and performance exists but is not consistent among individuals (Ancrenaz et al. 1994; Feistner et al. 1994; Goix 1993; Milliken 1995). A tendency for female dominance in priority of access to food resources may extend to other contexts such as grooming and agonistic interactions (Rendall 1993).

Daubentonia madagascariensis scent-marks by rubbing anogenital, neck, or cheek region against branches (Ancrenaz et al. 1994). Urine marking occurs on oblique branches and on the ground (Andriamasimanana 1994). Individuals can discriminate between scents of different age–sex classes (Price and Feistner 1994). A characteristic mark is left by biting bark hard with the incisors (Ancrenaz et al. 1994).

Vocalizations include numerous variations of the primary contact call and a sonorous screech lasting 2–3 s. These serve affiliative, aggressive, and informative functions (Ancrenaz et al. 1994; Andriamasimanana 1994; Stanger and Macedonia 1994). A sneezelike sound ("ron-tsit") is emitted in response to the appearance of conspecifics, other lemurs, or humans. A high-amplitude, harmonically rich scream accompanies aggressive interactions. Protest is indicated by a lower-arousal closed-mouth version of the scream. A brief, descending whimper, often in 3–4 call sequences, corresponds to competition for resources or females seeking to terminate copulation. The "hai-hai" vocalization from which the aye-aye possibly derives its name is emitted while fleeing the nest during capture attempts (Stanger and Macedonia 1994).

ECOLOGY. *Daubentonia madagascariensis* individuals may be captured in their nests. Primary and secondary low- to mid-altitude rainforest, deciduous forest, some cultivated areas (coconut and lychee plantations), and possibly dry scrub forests and mangrove swamps are inhabited (Garbutt 1999; Tattersall 1982).

The main diet comprises xylophagous insect larvae, fruits, nuts, and plant exudates. *D. madagascariensis* consumes flesh and seeds of the breadfruit (*Arctocarpus*), *Chrysalidocarpus*, *Ficus*, *Howmarea distichy*, banana fruit (*Musa*), barbibanjina fruit (*Passiflora quadrangularis*), and *Terminalia catappa* (Andriamasimanana 1994). Unripened coconuts (*Cocos nucifera*) and the hard interior of the ramy nut (*Canarium madagascariensis*) are favored (Iwano and Iwakawa 1988; Sterling et al. 1994). Bamboo (*Bambusa vulgaris*), lychees (*Litchi chinensis*), and ripe mangoes (*Mangifera*) are consumed (Constable et al. 1985; Petter and Peyriéras 1970; Petter et al. 1977; Pollock et al. 1985). Feeding damage in some bamboo stalks (*Ochlandra capitata*) may be attributed to aye-ayes searching for insect larvae (Duckworth 1993). Nectar from the traveler's tree (*Ravenela madagascariensis*) and the banana flower (*Musa*) are consumed (Ancrenaz et al. 1994; Andriamasimanana 1994; Sterling 1994a). Cankers (either galls or fungus) on the hintzy (*Intsia bijuga*) are consumed, including sap, fibrous bark, cambium, and possible concealed insects and vertebrates (Andriamasimanana 1994; Constable et al. 1985; Petter 1977; Pollock et al. 1985; Sterling 1994a; Sterling et al. 1994). Organisms found in hintzy cankers include frogs (*Anodonthyla rouxae*, Microhylidae, Cophylinae), *Cercyon grandis* (Coleoptera, Hydrophilidae, Sphaeridiinae), *Chaetospania* (Dermaptera, Labiidae, Labiinae), click-beetles (Coleoptera, Elateridae, Agrypninae), moths (Lepidoptera, Noctuidae), and *Technomyrmex* (Hymenoptera, Formicidae, Dolichoderinae—Pollock et al. 1985).

The fossa (*Cryptoprocta ferox*) may prey on *D. madagascariensis* (Garbutt 1999; Petter 1977).

Aye-ayes are generally solitary, although foraging associations of 2 or 3 individuals form (Ancrenaz et al. 1994; Sterling and Richard 1995). Female ranges (30–50 ha) are smaller than male ranges (100–200 ha). Male ranges may overlap 40–75%. (Andriamasimanana 1994; Garbutt 1999; Sterling 1993).

ANIMAL HUSBANDRY. Typically *D. madagascariensis* is housed in dyads although experimentation with different pairings may be necessary (Carroll and Haring 1994; Feistner and Carrol 1993a, 1993b, 1995). Individuals are maintained on reversed local photoperiods to facilitate research, except at the Duke University Primate Center where individuals are maintained on Madagascar photoperiod. Supplementary "twilight" lessens the shock of light changes (Carroll and Beattie 1993; Carroll and Haring 1994).

Diet in captivity is subject to individual preference, but fruits and vegetables high in fat, nuts, eggs, and larval insects are favored (Ashbourne 1994; Carroll and Haring 1994; Haring et al. 1994; Winn 1989). Ripeness and variation in diet are important (Carroll and Beattie 1993).

Manipulating food is successful as a means of enrichment;

mealworms can be hidden in bamboo and rotten logs may be provided to tear apart (Carroll and Beattie 1993; Carroll and Haring 1994; Grossi and Dill 1998). Hard substances are provided to enable the aye-ayes to sharpen their continuously growing incisors (Grossi and Dill 1998). A wide variety of substrates and travel routes, nest boxes, and nesting material are ideally provided (Carroll and Beattie 1993). Structural components such as bolts must be steel to prevent chewing damage (Grossi and Dill 1998).

The first captive-conceived aye-aye was born in 1992 (Beattie et al. 1992). Removal of the male prior to and for 6 months following parturition reduces stress on the female (Coffman et al. 1993). Infants should be housed with their mothers at least 12 months and preferably until 2 years old (Feistner and Ashbourne 1994).

GENETICS. *Daubentonia madagascariensis* has 2n = 30 chromosomes. Karyotype consists of 14 autosomal metacentrics, 10 autosomal submetacentrics, and 4 autosomal acrocentrics. The X and Y chromosomes are metacentric (Poormann-Allen and Izard 1990; Rumpler et al. 1988).

CONSERVATION STATUS. *Daubentonia madagascariensis* is endangered and has been given the "Highest Priority" rating for rarity, taxonomic uniqueness, and discontinuity of habitat by the IUCN/SSC Primate Specialist Group (Harcourt and Thornback 1990; Mittermeier et al. 1992). *D. madagascariensis* is listed in Appendix One of the 1973 Convention on International Trade in Endangered Species and in Class A of the African Convention 1969 (Harcourt and Thornback 1990). An order of magnitude estimate of the total population is 1,000–10,000 individuals (Mittermeier et al. 1992).

Habitat destruction is the main threat to *D. madagascariensis*. Individuals may be killed on sight as crop pests or harbingers of evil (Albignac 1987). Due to its evil reputation the aye-aye is never eaten (Garbutt 1999; Petter 1977).

At least 16 protected areas contain aye-ayes: Mantady, Montagne d'Ambre, Ranomafana, and Verezanantsoro National Parks; Andohahela, Bemaraha, Betampona, Marojejy, and Zahamena Nature Reserves; and Ambatovaky, Analamazaotra, Analamera, Ankarana, Foret d'Ambre, Manangarivo, and Manombo Special Reserves (Harcourt and Thornback 1990; Mittermeier et al. 1992, 1994). A population in Nosy Mangabe Special Reserve resulted from the introduction of 9 individuals in 1966 (Mittermeier et al. 1992). Captive breeding colonies exist at the Duke University Primate Center and the Jersey Wildlife Preservation Trust.

REMARKS. The generic name honors Louis Jean Marie d'Aubenton (Daubenton), a naturalist and Étienne Geoffroy Saint-Hilaire's mentor (Sterling 1994c). Sonnerat's (1782) claim that he coined the common name in reference to cries of alarm uttered by Malagasy villagers when they saw the aye-aye is unlikely because the name is common throughout Madagascar. Possibly the common name is onomatopoeic, referring to the "hai hai" call. In some dialects "heh heh," possibly the root of "aye-aye," means "I don't know," supposedly the recourse of villagers that have no name for the animal or who do not wish to speak its name because it is "fady" (Simons 1995). Other common names include "hay-hay," "ahay," and "aiay" in Malagasy (Tattersall 1982) and "fingertier" in German (Mittermeier et al. 1992).

LITERATURE CITED

Adkins, R. M., and R. L. Honeycutt. 1994. Evolution of the primate cytochrome *c* oxidase subunit II gene. Journal of Molecular Evolution 38:215–231.

Albignac, R. 1987. Status of the aye-aye in Madagascar. Primate Conservation 8:44–45.

Ancrenaz, M., I. Lackman-Ancrenaz, and N. Mundy. 1994. Field observations of aye-ayes (*Daubentonia madagascariensis*) in Madagascar. Folia Primatologica 62:22–36.

Andriamasimanana, M. 1994. Ecoethological study of free-ranging aye-ayes (*Daubentonia madagascariensis*) in Madagascar. Folia Primatologica 62:37–45.

Ankel-Simons, F. 1990. The aye-aye. American Association of Zoological Parks and Aquariums Regional Proceedings 1990: 421–426.

Ankel-Simons, F. 1996. Deciduous dentition of the aye-aye, *Daubentonia madagascariensis*. American Journal of Primatology 39:87–97.

Ashbourne, C. J. 1994. Nutritional analysis of the diet of captive aye-ayes *Daubentonia madagascariensis* at the Jersey Wildlife Preservation Trust. Dodo Journal of the Jersey Wildlife Preservation Trust 30:32–47.

Beattie, J. C., A. T. C. Feistner, N. M. O. Adams, P. Barker, and J. B. Carroll. 1992. First captive breeding of the aye-aye *Daubentonia madagascariensis*. Dodo Journal of the Jersey Wildlife Preservation Trust 28:23–30.

Blainville, H. M. D. 1839. Ostéographie ou déscription iconographique comparée du squelette et du système dentaire des mammifères recents et fossiles pour servir de base à la zoologie et à la géologie. J. B. Baillère et Fils, Paris, France.

Blainville, H. M. D. 1846. Dictionnaire universel d'histoire naturelle (C. D'Oribigny, ed.). Renard, Martinet, et Cie, Paris, France.

Carroll, J. B., and J. C. Beattie. 1993. Maintenance and breeding of the aye-aye *Daubentonia madagascariensis* at the Jersey Wildlife Preservation Trust. Dodo Journal of the Jersey Wildlife Preservation Trust 29:45–54.

Carroll, J. B., and D. M. Haring. 1994. Maintenance and breeding of aye-ayes (*Daubentonia madagascariensis*) in captivity: a review. Folia Primatologica 62:54–62.

Cartmill, M. 1974. *Daubentonia*, *Dactylopsila*, woodpeckers, and klinorhynchy. Pp. 655–670 in Prosimian biology (R. D. Martin, G. A. Doyle, and A. C. Walker, eds.). Gerald Duckworth and Co. Ltd., London, United Kingdom.

Coffman, B. S., W. R. Hess, K. E. Glander, P. E. Feeser, and E. L. Simons. 1993. Management of a breeding colony of aye-ayes (*Daubentonia madagascariensis*) at the Duke University Primate Center. American Association of Zoological Parks and Aquariums Regional Proceedings 1993:161–167.

Constable, I. D., J. I. Pollock, J. Ratsirarson, and H. Simons. 1985. Sightings of aye-ayes and red ruffed lemurs on Nosy Mangabe and the Maosola Peninsula. Primate Conservation 5: 59–62.

Curtis, D. J. 1992. Substrate use in captive aye-ayes *Daubentonia madagascariensis*. Dodo Journal of the Jersey Wildlife Preservation Trust 28:30–44.

Curtis, D. J., and A. T. C. Feistner. 1994. Positional behaviour in captive aye-ayes (*Daubentonia madagascariensis*). Folia Primatologica 62:155–159.

Cuvier, G. 1817. Le règne animal distribué d'après son organisation. Deterville, Paris, France 1:1–540.

Del Pero, M., S. Crovella, P. Cervella, G. Arditor, and Y. Rumpler. 1995. Phylogenetic relationships among Malagasy lemurs as revealed by mitochondrial DNA sequence analysis. Primates 36:431–440.

Dene, H., M. Goodman, and W. Prychodko. 1980. Immunodiffusion systematics of the primates. Mammalia 44:211–223.

Duckworth, J. W. 1993. Feeding damage left in bamboos, probably by aye-ayes (*Daubentonia madagascariensis*). International Journal of Primatology 14:27–31.

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

Erickson, C. J. 1991. Percussive foraging in the aye-aye, *Daubentonia madagascariensis*. Animal Behaviour 41:793–801.

Erickson, C. J. 1994. Tap-scanning and extractive foraging in aye-ayes, *Daubentonia madagascariensis*. Folia Primatologica 62:125–135.

Erickson, C. J. 1995a. Feeding sites for extractive foraging by the aye-aye, *Daubentonia madagascariensis*. American Journal of Primatology 35:235–240.

Erickson, C. J. 1995b. Perspectives on percussive foraging in the aye-aye (*Daubentonia madagascariensis*). Pp. 251–259 in Creatures of the dark: the nocturnal prosimians (L. Alterman, G. A. Doyle, and M. K. Izard, eds.). Plenum Press, New York.

Erickson, C. J. 1998. Cues for prey location by aye-ayes (*Daubentonia madagascariensis*). Folia Primatologica 69(supplement 1):35–40.

Erickson, C. J., S. Nowicki, L. Dollar, and N. Goehring. 1998. Percussive foraging: stimuli for prey location by aye-ayes (*Daubentonia madagascariensis*). International Journal of Primatology 19:111–122.

Feistner, A. T. C., and C. J. Ashbourne. 1994. Infant development in a captive-bred aye-aye (*Daubentonia madagascariensis*) over the first year of life. Folia Primatologica 62: 74–92.

Feistner, A. T. C., and J. B. Carroll. 1993a. Breeding aye-ayes: an aide to preserving biodiversity. Biodiversity and Conservation 2:283–289.

Feistner, A. T. C., and J. B. Carroll. 1993b. Captive breeding of the aye-aye (*Daubentonia madagascariensis*). Primate Eye 49:16–18.

Feistner, A. T. C., and J. B. Carroll. 1995. Aye-aye conservation: the role of the Jersey Wildlife Preservation Trust. Pp. 519–525 in Creatures of the dark: the nocturnal prosimians (L. Alterman, G. A. Doyle, and M. K. Izard, eds.). Plenum Press, New York.

Feistner, A. T. C., and E. J. Sterling. 1995. Body mass and sexual dimorphism in the aye-aye *Daubentonia madagascariensis*. Dodo Journal of the Jersey Wildlife Preservation Trust 31:73–76.

Feistner, A. T. C., and T. Taylor. 1998. Sexual cycles and mating behaviour of captive aye-ayes, *Daubentonia madagascariensis*. Folia Primatologica 69(supplement 1):406–416.

Feistner, A. T. C., E. C. Price, and G. W. Milliken. 1994. Preliminary observations on hand preference for tapping, digit-feeding and food-holding in captive aye-ayes (*Daubentonia madagascariensis*). Folia Primatologica 62:136–141.

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

Geoffroy Saint-Hilaire, É. 1795. La décade philosophique, litteraire, et politique. Memoires d'Histoire Naturelle 4(28):193–206.

Geoffroy Saint-Hilaire, É. 1803. Catalogue des mammifères du muséum national d'histoire naturelle. (Printed draft, but not published), Paris, France.

Glander, K. E. 1994. Morphometrics and growth in captive aye-ayes (*Daubentonia madagascariensis*). Folia Primatologica 62:108–114.

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

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.

Goix, E. 1993. L'utilisation de la main chez le aye-aye en captivité. Mammalia 57:71–188.

Grandidier, G. 1929. Une variété du *Cheiromys madagascariensis* actuel et un nouveau *Cheiromys* subfossile. Bulletin de l'Académie Malgache 11:101–107.

Grossi, B., and E. Dill. 1998. Rethinking captive management practices for the aye-aye (*Daubentonia madagascariensis*). American Zoo and Aquarium Association Regional Conference Proceedings 1998:444–446.

Groves, C. 1989. A theory of human and primate evolution. Clarendon Press, Oxford, United Kingdom.

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.

Haring, D. M., W. R. Hess, B. S. Coffman, E. L. Simons, and T. M. Owens. 1994. Natural history and captive management of the aye-aye at the Duke University Primate Center, Durham. International Zoo Yearbook 33:201–219.

Hill, W. C. O. 1953. Primates, comparative anatomy and taxonomy. Edinburgh University Press, Edinburgh, Scotland 1:1–798.

ICZN. 1956. Opinion 417. Rejection for nomenclatural purposes of volume 3 (Zoologie) of the work by Lorenz Oken entitled Okens Lehrbuch der Naturgeschichte published in 1815 1816. Opinions and declarations rendered by the International Commission on Zoological Nomenclature, London, United Kingdom 14(1):1–42.

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

Iwano, T. 1991a. Nocturnal activity of a captive aye-aye (*Daubentonia madagascariensis*). African Study Monographs 12: 99–118.

Iwano, T. 1991b. The usage of the digits in a captive aye-aye (*Daubentonia madagascariensis*). African Study Monographs 12:87–98.

Iwano, T., and C. Iwakawa. 1988. Feeding behaviour of the aye-aye (*Daubentonia madagascariensis*) on nuts of ramy (*Canarium madagascariensis*). Folia Primatologica 50:136–142.

Jablonski, N. G. 1986. A history of form and function in the primate masticatory apparatus from the ancestral primate through the strepsirhines. Pp. 537–558 in Comparative primate biology: systematics, evolution, and anatomy (D. R. Swindler and J. Erwin, eds.). Alan R. Liss, Inc., New York 1:1–820.

Lacépède, B. G. E. 1799. Tableau des divisions et sous-divisions, orders et genres des mammifères. Plassan, Paris, France.

Lamberton, C. 1934. Contribution à la connaissance de la faune subfossile de Madagascar. Lémuriens et ratites. Mémoires de l'Académie Malgache 17:40–46.

Luckett, W. P., and W. Maier. 1986. Developmental evidence for anterior tooth homologies in the aye aye, *Daubentonia*. American Journal of Physical Anthropology 69:233.

MacPhee, R. D. E., and E. M. Raholimavo. 1988. Modified subfossil aye-aye incisors from southwestern Madagascar: species allocation and paleoecological significance. Folia Primatologica 51:126–142.

Milliken, G. W. 1995. Right hand preference and performance biases in the foraging behavior of the aye-aye. Pp. 261–292 in Creatures of the dark: the nocturnal prosimians (L. Alterman, G. A. Doyle, and M. K. Izard, eds.). Plenum Press, New York.

Milliken, G. W., J. P. Ward, and C. J. Erickson. 1991. Independent digit control in foraging by the aye-aye (*Daubentonia madagascariensis*). Folia Primatologica 56:219–224.

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.

Oken, L. 1816. Lehrbuch der naturgeschichte. August Schmid und Companie, Jena, Germany 3:1–1270.

Oxnard, C. E. 1981. The uniqueness of *Daubentonia*. American Journal of Physical Anthropology 54:1–21.

Petter, J. J. 1977. The aye-aye. Pp. 37–57 in Primate conservation (Prince Rainier III and G. H. Bourne, eds.). Academic Press, New York.

Petter, J. J., and A. Petter. 1967. The aye-aye of Madagascar. Pp. 195–205 in Social communication among primates (S. A. Altmann, ed.). University of Chicago Press, Illinois.

Petter, J. J., and A. Peyriéras. 1970. Nouvelle contribution à l'étude d'un lemurien malgache, le aye-aye (*Daubentonia madagascariensis* É. Geoffroy). Mammalia 34:167–191.

Petter, J. J., R. Albignac, and Y. Rumpler. 1977. Mammifères lémuriens (Primates prosimiens). Faune de Madagascar 44:1–513.

Petter-Rousseaux, A., and F. Bourlière. 1965. Persistence des phénomènes d'ovogénèse chez l'adulte de *Daubentonia madagascariensis* (Prosimii, Lemuriformes). Folia Primatologica 3:241–244.

Pollock, J. I., I. D. Constable, R. A. Mittermeier, J. Ratsirarson, and H. Simons. 1985. A note on the the diet and feeding behavior of the aye-aye *Daubentonia madagascariensis*. International Journal of Primatology 6:435–447.

Poormann Allen, P., and M. K. Izard. 1990. Chromosome banding patterns of the aye-aye, *Daubentonia madagascariensis* (Primates, Daubentoniidae). International Journal of Primatology 11:401–410.

Porter, C. A., I. Sampaio, H. Schneider, M. P. C. Schneider, J. Czelusniak, and M. Goodman. 1995. Evidence on primate phylogeny from ϵ-globin gene sequences and flanking regions. Journal of Molecular Evolution 40:30–55.

Price, E. C., and A. T. C. Feistner. 1994. Responses of captive aye-ayes (*Daubentonia madagascariensis*) to the scent of conspecifics: a preliminary investigation. Folia Primatologica 62:170–174.

Rendall, D. 1993. Does female social precedence characterize captive aye-ayes (*Daubentonia madagascariensis*)? International Journal of Primatology 14:125–130.

RUMPLER, Y., S. WARTER, J. J. PETTER, R. ALBIGNAC, AND B. DUTRILLAUX. 1988. Chromosomal evolution of Malagasy lemurs. Folia Primatologica 50:124–129.

SHAW, G. 1800. General zoology, or systematic natural history: Mammalia. G. Kearsley, London, United Kingdom, 1:1–552.

SIMONS, E. L. 1994. The giant aye-aye *Daubentonia robusta*. Folia Primatologica 62:14–21.

SIMONS, E. L. 1995. History, anatomy, subfossil record and management of *Daubentonia madagascariensis*. Pp. 133–140 in Creatures of the dark: the nocturnal prosimians (L. Alterman, G. A. Doyle, and M. K. Izard, eds.). Plenum Press, New York.

SOLIGO, C., AND A. E. MÖLLER. 1999. Nails and claws in primate evolution. Journal of Human Evolution 36:97–114.

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

STANGER, K. F., AND J. M. MACEDONIA. 1994. Vocalizations of aye-ayes (*Daubentonia madagascariensis*) in captivity. Folia Primatologica 62:160–169.

STERLING, E. J. 1993. Patterns of range use and social organization in aye-ayes (*Daubentonia madagascariensis*) on Nosy Mangabe. Pp. 1–10 in Lemur social systems and their ecological basis (P. M. Kappeler and J. U. Ganzhorn, eds.). Plenum Press, New York.

STERLING, E. J. 1994a. Aye-ayes: specialists on structurally defended resources. Folia Primatologica 62:142–154.

STERLING, E. J. 1994b. Evidence for nonseasonal reproduction in wild aye-ayes (*Daubentonia madagascariensis*). Folia Primatologica 62:46–53.

STERLING, E. J. 1994c. Taxonomy and distribution of *Daubentonia*: a historical perspective. Folia Primatologica 62:8–13.

STERLING, E. J., AND A. F. RICHARD. 1995. Social organization of the aye-aye (*Daubentonia madagascariensis*) and the perceived distinctiveness of nocturnal primates. Pp. 439–451 in Creatures of the dark: the nocturnal prosimians (L. Alterman, G. A. Doyle, and M. K. Izard, eds.). Plenum Press, New York.

STERLING, E. J., E. S. DIERENFELD, C. J. ASHBOURNE, AND A. T. C. FEISTNER. 1994. Dietary intake, food composition, and nutrient intake in wild and captive populations of *Daubentonia madagascariensis*. Folia Primatologica 62:115–124.

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

WINN, R. M. 1989. The aye-ayes, *Daubentonia madagascariensis*, at the Paris Zoological Garden: maintenance and preliminary behavioral observations. Folia Primatologica 52:109–123.

WINN, R. M. 1994a. Development of behavior in a young aye-aye (*Daubentonia madagascariensis*) in captivity. Folia Primatologica 62:93–107.

WINN, R. M. 1994b. Preliminary study of the sexual behaviour of three aye-ayes (*Daubentonia madagascariensis*) in captivity. Folia Primatologica 62:63–73.

Associate editors of this account were ELAINE ANDERSON, LUI MARINELLI, and KAREN MCBEE. Editor was VIRGINIA HAYSSEN.

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