

Subfossil Lemurs of Madagascar

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Madagascar's living lemurs (order Primates) belong to a radiation recently ravaged by extirpation and extinction. There are three extinct and five extant families (two with extinct members) of lemurs on an island of less than 600,000 km². This level of familial diversity characterizes no other primate radiation. The remains of up to 17 species of recently extinct (or subfossil lemurs) have been found alongside those of still extant lemurs at numerous Holocene and late Pleistocene sites in Madagascar (figure 21.1, table 21.1). The closest relatives of the lemurs are the loriform primates of continental Africa and Asia; together with the lemurs, these comprise the suborder Strepsirrhini.

Most researchers have defended an ancient Gondwanan (African or Indo-Madagascan) origin for lemurs. On the basis of molecular data, some posit an origin of primates between 85 and 90 Ma (e.g., Martin, 2000; Eizirik et al., 2001; Springer et al., 2003; Yoder and Yang, 2004; Miller et al., 2005), and of lemurs on Madagascar by ~80 Ma (e.g., Yoder and Yang, 2004). Using nuclear genes only, Poux et al. (2005) place the origin of primates at ~80 Ma and the colonization of Madagascar at between 60 and 50 Ma, with a 95% credibility interval of 70–41 Ma. There is general agreement that lemurs must have been established on Madagascar by the middle Eocene (Roos et al., 2004). Actual putative fossil primates (e.g., *Altiatlasius*, plesiadapiforms) first appear ~60 Ma in Algeria (Hooker et al., 1999; Tabuce et al., 2004). Seiffert et al. (2003, 2005) identify the earliest definitive strepsirrhines (*Karanisia*, *Saharagalago*, and *Wadilemur*) as primitive loriforms; they do not appear in the fossil record until after ~40 Ma (in northern Egypt, alongside definitive anthropoids). On the basis of limited dental evidence, Marivaux et al. (2001) have described a possible fossil lemur (*Bugtilemur*)—the only one found outside Madagascar—in 30-million-year-old deposits in Pakistan (see Seiffert et al., 2003, and Godinot, 2006, for critiques).

If primates originated 80–90 million years ago, then the first quarter or third of the primate evolutionary record is missing entirely. An early primate origin can be defended on the basis of the fossil record if existing fossils are used to model the tempo of primate diversification (Tavaré et al., 2004), and 2.5 million years is used as an average species lifespan. An alternative explanation is that the early evolution of the Primates was more explosive than a model based

on steady, gradual diversification would suggest. We believe that the latter scenario is more consistent with the fossil record.

The question of how lemurs got to Madagascar is still far from resolved (Godinot, 2006; Masters et al., 2006; Stevens and Heesy, 2006; Tattersall, 2006a, 2006b). It is clear that Madagascar (with the Indian plate) separated from Africa long before primates evolved and that it arrived at its present position relative to Africa by 120–130 Ma (Krause et al., 1997; Roos et al., 2004; Masters et al., 2006; Rabinowitz and Woods, 2006). Most scholars favor chance rafting of an ancestral lemur from continental Africa to Madagascar (Krause et al., 1997; Kappeler, 2000; Roos et al., 2004; Rabinowitz and Woods, 2006), with prior divergence of lemurs and lorises. Reports of floating islands at sea (such as one observed in 1902 some 30 miles off the coast of San Salvador supporting a troop of monkeys and plentiful vegetation including coconut trees) are intriguing in this regard (Van Duzer, 2004). Others are skeptical of long-distance water rafting for terrestrial mammals (Lawlor, 1986; Hedges et al., 1996; de Wit and Masters, 2004; Stankiewicz et al., 2006; Masters et al., 2006) and urge consideration of other models. For example, an early Indo-Madagascan origin for primates might account for the presence of lemurs on Madagascar and a possible cheirogaleid, *Bugtilemur*, in Pakistan 30 million years ago.

But if primates originated on the Indo-Madagascan plate, or if they colonized Madagascar during the Cretaceous, then primates of some sort might be expected to occur in the Cretaceous deposits of Madagascar. The rich Gondwanan fossil record of Madagascar provides no such corroboration (Krause et al., 1997); there were apparently no proto-lemurs on Madagascar during the Cretaceous. Furthermore, if primates originated on Indo-Madagascar instead of Asia or Africa, some sweepstakes mechanism (long-distance water rafting or dispersal over a land bridge or stepping-stones) is still needed to explain their presence in northern Africa 60 million years ago. The breakup of India and Madagascar was underway around 90 million years ago (Storey, 1995), but India did not collide with continental Asia until much later—glancingly at 57 million years ago and fully at 35 million years ago (Ali and Aitchison, 2008). During the critical time period (90–60 million years ago), Madagascar, the Indian plate, and the

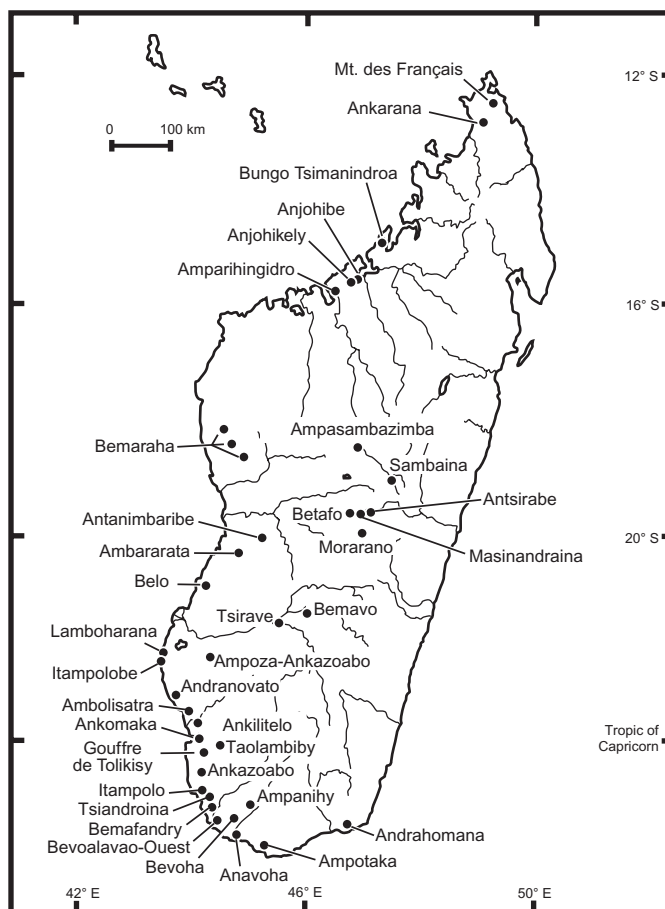


FIGURE 21.1 Map showing subfossil sites.

continental African and Asian plates functioned as isolated landmasses, although passage between southern India and Madagascar may have been facilitated by the Seychelles-Mascarene Plateau and nearby areas of elevated seafloor prior to the K/T catastrophic extinction event (65 million years ago; Ali and Aitchison, 2008). The Kerguelen Plateau, which formed ~118 million years ago and connected the Indo-Malagasy plate to what is now Australia and Antarctica during the mid-Cretaceous, had drowned by ~90 million years ago (Ali and Aitchison, 2008). During the early Cenozoic, there may have been intermittent stepping-stone islands south-southwest of India (along the Deccan-Réunion hot-spot ridge), but by this time, huge stretches of ocean separated India and Madagascar (Ali and Aitchison, 2008). A putative land “bridge” connecting Africa to Madagascar (45–26 Ma; see McCall, 1997) cannot explain the introduction of primates from Madagascar to Africa or the colonization of Madagascar by African primates because it is too recent (Poux et al., 2005); the Mozambique Channel seems to have been sufficiently narrow to allow sporadic independent crossings from the early Cenozoic onward.

Relationships among families of lemurs are also problematic. There is strong evidence that the Daubentoniidae were the first to diverge (~60 Ma, perhaps earlier; see Yoder et al., 1996; Yoder, 1997; DelPero et al., 2001, 2006; Pastorini et al., 2001; Poux and Douzery, 2004; Yoder and Yang, 2004; Roos et al., 2004, 2008), but the ages of divergence and relationships among the remaining four extant families (Cheirogaleidae, Lepilemuridae, Indriidae, and Lemuridae)

are poorly understood; alternative molecular data sets favor different topologies. There is some molecular support for a sister taxon relationship between Indriidae and Lemuridae (DelPero et al., 2001; Roos et al., 2004), with an age of divergence between 32 and 52 Ma (Roos et al., 2004). Poux et al. (2005) support a sister taxon relationship for the Cheirogaleidae and Lepilemuridae, with the Indriidae as the sister to that group, and the Lemuridae diverging from a cheirogaleid-lepilemurid-indriid clade just over 30 Ma. The latter topology was also supported by Horvath et al. (2008) using 11 novel markers from 9 chromosomes for 18 extant lemur species, but Orlando et al. (2008), using a taxonomically broader data set (35 lemur species, including 6 extinct ones) but relying on a smaller set of genes (12S and Cytb), found support for the former (i.e., a sister taxon relationship between the Indriidae plus their extinct relatives and the Lemuridae plus their extinct relatives), with the Lepilemuridae as the first family to diverge after the Daubentoniidae, followed by the Cheirogaleidae, and then the Indriidae and Lemuridae. Using a large, composite data set and a variety of analytical methods, DelPero et al. (2006) found equally strong support for two topologies—one identical to that found by Orlando et al. (2008), and the other with the Indriidae first to diverge after the Daubentoniidae, followed by the Lemuridae, and finally, the Lepilemuridae and Cheirogaleidae. In each of these topologies, the Cheirogaleidae are nested well within the lemur clade. The formerly favored notion (grounded in some remarkable morphological and developmental similarities; Szalay and Katz, 1973; Cartmill, 1975; Schwartz and Tattersall,



TABLE 21.1
Major occurrences and ages of extinct lemurs of Madagascar

Taxon	Occurrence (Site, Region)	Calibrated Range of Dated Specimens at 2 σ	Key References
PALAEOPROPITHECIDAE			
<i>Palaeopropithecus maximus</i>	Ampasambazimba, Itasy, possibly Ankarana	BP 2350–2160	Standing, 1903, 1905; Grandidier, 1899, 1901
<i>P. ingens</i>	Ambolisatra, Ampoza, Anavoaha, Andranovato, Ankazoabo-Grotte, Ankilitelo, Ankomaka, Beavoha, Belo-sur-mer, Betioky-Toliara, Itampolobe, Lower Menarandra, Manombo-Toliara, Taolambiby, Tsiandroina, Tsivonohy	BP 2366–2315, AD 640–946, AD 1300–1620	Filhol, 1895; Godfrey and Jungers, 2003
<i>Palaeopropithecus</i> sp. nov.	Amparihingidro, Anjohibe, perhaps Ampoza		[Description in progress] MacPhee et al., 1984
<i>Archaeoindris fontoyontii</i>	Ampasambazimba	BP 2362–2149, BP 2711–2338	Standing, 1909, 1910; Lamberton, 1934a; Vuillaume-Randriamanantena, 1988
<i>Babakotia radofilai</i>	Ankarana, Anjohibe	BP 5290–4840	Godfrey et al., 1990; Jungers et al., 1991; Simons et al., 1992
<i>Mesopropithecus globiceps</i>	Anavoaha, Ankazoabo-Grotte, Belo-sur-mer, Manombo-Toliara, Taolambiby, Tsiandroina, Tsirave	BC 354–60, AD 58–247, AD 245–429	Lamberton, 1936; Tattersall, 1971
<i>M. pithecoides</i>	Ampasambazimba	AD 570–679	Standing, 1905; Tattersall, 1971
<i>M. dolichobrachion</i>	Ankarana		Simons et al., 1995
ARCHAEOLEMURIDAE			
<i>Archaeolemur majori</i>	Ambararata-Mahabo, Amvolisatra, Anavoaha, Andrahomana, Ankazoabo-Grotte, Ankilitelo, Beavoha, Belo-sur-mer, Bemafandry, Betioky-Toliara, Itampolobe, Lamboharana, Manombo-Toliara, Nosy-Ve, Taolambiby, Tsiandroina, Tsirave. Possibly Ampasambazimba, Ampoza-Ankazoabo, Ankarana, Bungo-Tsimanindroa.	AD 260–530, AD 410–620, AD 620–700	Filhol, 1895; Forsyth-Major, 1896; Tattersall, 1973; Hamrick et al., 2000; Godfrey et al., 2005
<i>A. edwardsi</i>	Ampasambazimba, Ampoza-Ankazoabo, Ankarana, Belo-sur-mer, Masinandrana, Morarano-Betafo, Sambaina, Vakinanakaratra. Possibly Ambolisatra, Amparihingidro, Anjohibe, Anjohikely	BP 870–8410, BC 350–AD 80, AD 910–1150	Filhol, 1895; Standing, 1905; Tattersall, 1973; Hamrick et al., 2000; Godfrey et al., 2005
<i>Hadropithecus stenognathus</i>	Southern, southwestern, and central Madagascar: Ambovombe, Ampasambazimba, Anavoaha, Andrahomana, Belo-sur-Mer, Tsirave	BP 7660–7490, BP 2344–1998, AD 444–772	Lorenz von Liburnau, 1902; Lamberton, 1938; Godfrey et al., 1997b; Godfrey et al., 2006a
MEGALADAPIDAE			
<i>Megaladapis edwardsi</i>	Ambolisatra, Ampanihy, Ampoza-Ankazoabo, Anavoaha, Andrahomana, Andranovato, Ankomaka, Beavoha, Betioky-Toliara, Itampolobe, Lamboharana, Taolambiby, Tsiandroina	BP 5436–5059, AD 27–412, AD 666–816, AD 1280–1420	Grandidier, 1899; Lorenz von Liburnau, 1905; Jungers, 1977, 1978; Lamberton, 1934c; Vuillaume-Randriamanantena, et al., 1992



TABLE 21.1
(CONTINUED)

Taxon	Occurrence (Site, Region)	Calibrated Range of Dated Specimens at 2σ	Key References
<i>M. madagascariensis</i>	Ambararata-Mahabo, Ambolisatra, Amparihingidro, Ampoza-Ankazoabo, Anavoaha, Andrahomana, Anjohibe, Ankarana, Ankilitelo, Beavoaha, Belo-sur-mer, Bemafandry, Itampolobe, Mt. des Français, Taolambiby, Tsiandroina, Tsirave, Tsivonohy.	BP 15670–14380, BP 2870–2760	Forsyth-Major 1893, 1894; Jungers 1977, 1978; Vuillaume-Randriamanantena, et al., 1992
<i>M. grandidieri</i>	Ampasambazimba, Antsirabe, Itasy, Morarano-Betafo	AD 900–1040	Standing, 1903; Lamberton, 1934c; Jungers, 1977, 1978; Vuillaume-Randriamanantena, et al. 1992
LEMURIDAE			
<i>Pachylemur insignis</i>	Ambararata-Mahabo, Ambolisatra, Anavoaha, Andrahomana, Ampoza-Ankazoabo, Belo-sur-mer, Bemafandry, Lamboharana, Manombo-Toliara, Taolambiby, Tsiandroina, Tsirave, perhaps Amparihingidro	AD 680–960, BC 110–AD 100	Filhol, 1895; Lamberton, 1948
<i>P. jullyi</i>	Ampasambazimba, Antsirabe, Morarano-Betafo, possibly Ankarana	—	Grandidier 1899 Lamberton 1948
DAUBENTONIIDAE			
<i>Daubentonia robusta</i>	Anavoaha, Lamboharana, Tsirave	AD 891–1027	Grandidier 1929 Lamberton 1934b MacPhee and Raholimavo 1988 Simons 1994

NOTE: Source for dates Burney et al., 2004.

1985; Yoder, 1994), that the cheirogaleids are actually primitive lorisiforms invading Madagascar independently of lemurs, is countered by consistent and mounting molecular evidence to the contrary (Yoder, 1994, 1997; Yoder et al. 1996; Yoder and Yang, 2004; Roos et al., 2004; Poux et al., 2005; DelPero et al., 2006).

With regard to extinct lemurs, morphological, developmental and molecular data support a sister taxon relationship for the Palaeopropithecidae (four genera) and the Indriidae (Tattersall and Schwartz, 1974; Godfrey, 1988; Godfrey et al., 2002; Schwartz et al., 2002; Karanth et al., 2005). Morphological data (postcranial characters in particular) suggest that, within the Palaeopropithecidae, *Mesopropithecus* diverged first, then *Babakotia*; *Palaeopropithecus* and *Archaeoindris* share the most recent ancestor (Godfrey, 1988; Godfrey et al., 1990; Jungers et al., 1991; Simons et al., 1992, 1995; Godfrey and Jungers, 2002). Morphological and molecular evidence also favors a sister taxon relationship for the extinct *Pachylemur* and still extant *Varecia*, and their status as the sister to a *Eulemur-Lemur-Hapalemur* clade (Seligsohn and Szalay 1974; Crovella et al. 1994; Wyner et al., 2000; Pastorini et al., 2002). Relationships of the Archaeolemuridae and the Megaladapidae to extant lemurs have been more

controversial. Morphological data support affinity of *Megaladapis* and *Lepilemur* (Tattersall and Schwartz, 1974; Wall, 1997); most existing molecular data fail to support this connection (Yoder et al., 1999; Yoder, 2001; Karanth et al., 2005; Orlando et al., 2008). The latter instead affirm a close relationship of the Megaladapidae to the Lemuridae and suggest that Montagnon et al.'s (2001a, 2001b) molecular support for a link between the megaladapids and *Lepilemur* results from polymerase chain reaction (PCR) contamination. Within the genus *Megaladapis*, two species (*M. madagascariensis* and *M. grandidieri*) are clear sister taxa (Vuillaume-Randriamanantena et al., 1992). The Archaeolemuridae have long been considered the sister to the palaeopropithecid-indriid clade, largely on the basis of molar morphology and the number of teeth in the (modified) tooth comb (Tattersall and Schwartz, 1974; Godfrey, 1988; Godfrey and Jungers, 2002). Other morphological as well as developmental characters suggest closer affinity to the Lemuridae (King et al., 2001; Godfrey et al., 2006a; Lemelin et al., 2008), but recent molecular analysis has accorded support for the former scenario. Orlando et al. (2008) found strong molecular support for a close relationship among the Archaeolemuridae, Palaeopropithecidae, and Indriidae, but their data could not

resolve phylogenetic relationships within this group. A sister taxon relationship of *Archaeolemur* and *Hadropithecus*, long supported by morphological evidence (e.g., Tattersall, 1973; Godfrey, 1988; Godfrey and Jungers, 2002), has now received strong molecular support, however (Orlando et al., 2008).

Systematic Paleontology

Family PALAEOPROPITHECIDAE Tattersall, 1973

This is the most speciose of extinct lemur families, with four genera (*Palaeopropithecus*, *Archaeoindris*, *Babakotia*, *Mesopropithecus*) and seven recognized species (and an eighth in the process of being described); future revisions might collapse some of these species. All have the same adult dental formula (2.1.2.3/2.0.2.3) as in extant indriids, with only two pairs of premolars and four teeth in the tooth comb. *Mesopropithecus*, like *Babakotia* (and unlike *Palaeopropithecus* and *Archaeoindris*), retains a number of primitive craniodental features, including an inflated auditory bulla with intrabulbar ectotympanic ring, and a conventional tooth comb of indriid type, with four teeth. Palaeopropithecids share with indriids accelerated dental crown formation (Schwartz et al., 2002; Godfrey et al., 2006c), but the largest taxa (*Palaeopropithecus* and *Archaeoindris*) differ from indriids in details of the nasal aperture (e.g., paired protuberances) and the petrosal bone (e.g., deflated bulla). The namesake of the family, *Palaeopropithecus*, exhibits the most derived postcranial specializations for hind- and forelimb suspension—inferred behaviors that are correlated with greatly curved proximal phalanges (Jungers et al., 1997) and with high intermembral indices (Jungers, 1980; Jungers et al., 2002). The palaeopropithecids have been dubbed the “sloth lemurs” due to their remarkable postcranial convergences to sloths (Godfrey and Jungers, 2003), and recent research on the semicircular canals of giant lemurs lend support to this argument (Walker et al., 2008).

Genus PALAEOPROPITHECUS G. Grandidier, 1899
PALAEOPROPITHECUS MAXIMUS Standing, 1903

Partial Synonymy *Palaeopropithecus raybaudii*, Standing, 1903.

Age and Occurrence Late Quaternary, central, possibly northern Madagascar.

Diagnosis Largest species of genus; skull length averages 191 mm; orbits small; orbital margin raised to form a bony rim; petrosal elongated to form a tube; bulla not inflated; neurocranium small, frontal region of skull depressed; postorbital constriction strong; large frontal sinuses; facial retroflexion strong; sagittal crest often present; mandible deep (particularly in gonial region) but mandibular corpus thin; dental rows nearly parallel; paraoccipital processes large; dorsal portions of the premaxillae (as well as, to a far lesser extent, the lateral termini of the nasals) inflated and bulbous; “tooth comb” with four short, blunt, and slightly separated incisors; molars with low cusps; the hypocone on M1 and M2 is extremely reduced in height, almost shelflike; diastema present between anterior and posterior mandibular premolars; anterior mandibular dentition has been modified from a true tooth comb into four short and stubby procumbent teeth.

Description Body mass estimated at ~46 kg (Jungers et al., 2008); intermembral index 144–145 (Godfrey and Jungers,

2002). This species is about twice the size of the new species from the northwest, but only minimally larger than *P. ingens*. The cheek teeth resemble those of the indriids (especially *Propithecus*) in cusp configuration and styler development, but the first and second molars of both upper and lower jaws are more buccolingually compressed and mesiodistally elongated, and the third molars are smaller in relative size. The occlusal enamel tends to be crenulated. The lingual borders of the anterior maxillary molars are elongated so that they roughly equal the lengths of the buccal borders. As in indriids, the lower molars have accentuated trigonid and talonid basins, a strong protoconid, and a low hypoconid. Crests connect the protoconid and metaconid, as well as the hypoconid and entoconid. A paraconid is present on m1 and m2, separated from the metaconid by a moderately deep groove.

The hands and feet bear long, strongly curved metapodials and phalanges with deep flexor grooves; the metacarpo- and metatarsophalangeal joints are “notched” in a tongue-and-groove manner. The vertebral spinous processes are short and blunt throughout the entire thoracosacral vertebral column, and the transverse processes of the thoracic and lumbar vertebrae arise from the vertebral arches (Shapiro et al., 2005). The os coxae have a prominent ischial spine, but only a rudimentary anterior inferior iliac spine. The iliac blades flare laterally, and the pubis is long and flattened superoinferiorly. The small sacral hiatus suggests a reduced, if not vestigial, tail. By comparison, the pectoral girdle is poorly known. The humerus is long and robust and carries an entepicondylar foramen; the olecranon process of the ulna is reduced and its styloid process projects distally well beyond the head. The femur is short and anteroposteriorly flattened, with a shallow patellar groove and a reduced greater trochanter; the collodiaphyseal angle approaches 180 degrees, and the large, ball-like femoral head lacks a fovea capitis. The tibia and fibulae have very reduced (essentially absent) medial and lateral malleoli.

PALAEOPROPITHECUS INGENS G. Grandidier, 1899
Figure 21.2A

Partial Synonymy *Thaumastolemur grandidieri* Filhol, 1895; *Bradytherium madagascariense*, G. Grandidier, 1901.

Age and Occurrence Late Quaternary, southern and western Madagascar.

Diagnosis Skull (at ~184 mm in length) and teeth similar to *P. maximus* but slightly smaller; mandibular symphysis shorter.

Description Body mass estimated at approximately 42 kg (Jungers et al., 2008); intermembral index 135–138 (Godfrey and Jungers, 2002). Because the jaws of *P. ingens* are smaller than *P. maximus*, full adults from the south may lack diastemata separating the mandibular premolars. The length and development of the diastema between the anterior and posterior lower premolars in *Palaeopropithecus* depends on biological age and adult body size; diastemata are absent in all individuals when the premolars first erupt, but they may form and lengthen as the jaw grows. The dental microstructure of an individual belonging to this species was used to derive dental developmental data for *Palaeopropithecus* (Schwartz et al., 2002; Godfrey et al., 2006c); the permanent teeth show extremely accelerated crown formation, and they appear to have erupted when the jaws were still small, very like the condition in extant indriids. Postcrania largely similar to *P. maximus*, but carpal and tarsal bones are also known

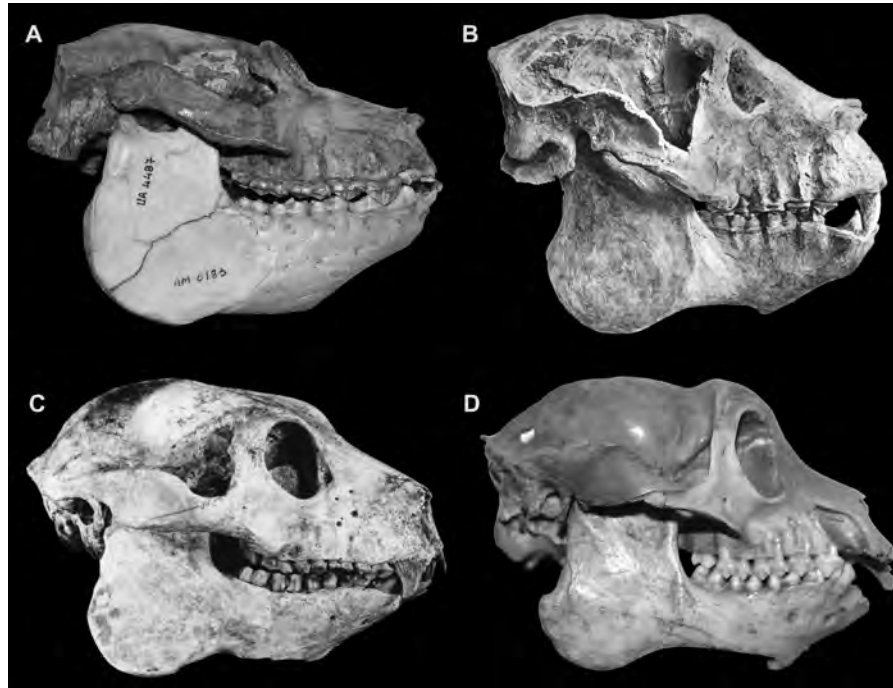


FIGURE 21.2 Lateral views of skulls of palaeopropithecids: A) *Palaeopropithecus ingens* (composite skull and mandible from southern Madagascar, collection of the Université d'Antananarivo); B) *Archaeoindris fontoyntii* (from Ampasambazimba, collection of the Académie Malgache); C) *Babakotia radofilai* (from the Ankarana Massif, collection of the Duke Primate Center); D) *Mesopropithecus globiceps* (from southern Madagascar, collection of the Université d'Antananarivo). Not to scale. The photograph of *Archaeoindris* was reproduced from Lamberton, 1934a: Plate I, and mirror-imaged.

for *P. ingens* (e.g., Hamrick et al., 2000; Jungers and Godfrey, 2003). The long ulnar styloid is excluded from the pisiform and articulates like a “mortar in pestle” with the triquetrum; the overall carpus has a flexed set. The hindfoot is reduced, especially the calcaneus, and the talar trochlea is globular; the plantar-flexed talar head articulates uniquely with both the navicular and cuboid.

Remarks on the Genus *Palaeopropithecus* Of all palaeopropithecids, *Palaeopropithecus* is most specialized for suspension, bearing long, curved phalanges, a very reduced hindfoot, the highest intermembral index (exceeding all living primates except orangutans), and extremely reduced spinous processes on thoracolumbar and sacral vertebrae. The sloth lemurs exhibit suspensory adaptations that imply a life almost entirely in the trees, even in areas that pollen evidence shows were not primarily dense forest, but rather a mosaic of woodland and grassland environments (e.g., Burney, 1987a, 1987b; Matsumoto and Burney, 1994). It is likely that *Palaeopropithecus* is the animal described by Etienne de Flacourt (1658) as the “tretretre” and represented in Malagasy folklore as an ogre incapable of moving on smooth rocky surfaces (Godfrey and Jungers, 2003). The smallest and most gracile of the *Palaeopropithecus* species, known from two fossil localities in the northwest (Amparihingidro and Anjohibe/Anjohikely), has yet to be formally described but is outside the observed ranges of the other two species in most respects (see MacPhee et al., 1984, for a description of the discovery of a skeleton belonging to this variant). A small but distinct hypocone is manifested on the first and second molars of the new species from the northwest, and its proximal phalanges are extremely curved. Further analysis may make it difficult to maintain the specific distinction between *P. maximus* and *P. ingens*.

Genus *ARCHAEOINDRIS* Standing, 1909
ARCHAEOINDRIS FONTOYNONTII Standing, 1909
 Figure 21.2B

Partial Synonymy Lemuridotherium Standing, 1910

Age and Occurrence Late Quaternary, central Madagascar.

Diagnosis Largest of extinct lemurs; length of single known skull 269 mm—shorter (but wider) than that of *Megaladapis*; neurocranium small; sagittal and nuchal crests strong; as in *Palaeopropithecus*: anterior molars buccolingually compressed; upper third molars reduced; postorbital constriction marked, external auditory meatus tubular (probably petrosal in origin); auditory bulla deflated; lower incisors stubby and blunt; diastema separates p2 and p4; palate rectangular; cheek tooth enamel crenulated; paired protuberances over the nasal aperture. The limited postcrania recall those of *Palaeopropithecus* but are much larger; large femoral head lacks fovea capitis; collodiaphyseal angle high; greater trochanter reduced; differs from *Palaeopropithecus* in having: much more massive and extremely robust postcranial bones; relatively deeper skull; orbits less dorsally oriented, and lacking the distinctly thickened rimming that characterizes those of *Palaeopropithecus*; cheek teeth are less wrinkled and slightly higher-crowned.

Description Body mass estimated at ~160 kg (Jungers et al., 2008). Knowledge of this species is based on one complete skull, additional fragmentary jaws, a fragmentary humerus and femur of an adult, and four long bone diaphyses of an immature individual. These bones are sufficient to demonstrate that the intermembral index well exceeded 100 but was probably lower than that of *Palaeopropithecus*.

Remarks on Genus Archaeoindris Adaptations for scansoriality are interesting in light of the massive size of *Archaeoindris*, which has been interpreted as convergent on ground sloths (Lamberton, 1934a; Jungers, 1980). This genus is only known from one site, Ampasambazimba, in the western highlands. Additional details on the postcranial anatomy of *Archaeoindris* are given by Vuillaume-Randriamanantena (1988).

Genus *BABAKOTIA* Godfrey et al., 1990
BABAKOTIA RADOFILAI Godfrey et al., 1990
Figure 21.2C

Age and Occurrence Late Quaternary, northern and northwestern Madagascar.

Diagnosis Skull length averages 114 mm; dentition similar to that of *Propithecus* but with greater mesiodistal elongation of premolars; cheek tooth enamel heavily crenulated; shearing crests well developed; face long as in *Indri*; differs from latter in greater postorbital constriction and more robust mandible. As in extant indriids, tooth comb is of the conventional indriid type, with four elongated teeth (Jungers et al., 2002).

Description Body mass estimated at ~21 kg (Jungers et al., 2008). The auditory bulla is inflated and possesses an intrabullar, ringlike ectotympanic. The postorbital bar is robust. There are no orbital tori or circumorbital protuberances.

Postcranially, *Babakotia* is more specialized for suspension than *Mesopropithecus*, but less so than *Palaeopropithecus*. The intermembral index is 118. There is a moderate degree of spinous process reduction in the thoracolumbar region. The innominate sports an incipient ischial spine, reduced rectus femoris process, and long pubis with some degree of superoinferior flattening. The femoral head is globular and somewhat cranially directed (but not to the extent seen in *Palaeopropithecus* and *Archaeoindris*); the collodiaphyseal angle is high; the femoral shaft is anteroposteriorly compressed; the patellar groove is shallow; the tibial malleolus is reduced; the calcaneus is quite reduced. There is also some reduction in relative lengths of the pollex and hallux; the proximal phalanges are long and curved with marked flexor ridges.

Remarks on the Genus Babakotia Geographically restricted to the north and northwest. First specimens discovered in the late 1980s and described in 1990. *Babakotia* was morphologically intermediate in the morphocline between *Mesopropithecus* and *Palaeopropithecus*. Many features of its axial and appendicular skeleton ally it functionally and phylogenetically with *Palaeopropithecus* (Jungers et al. 1991; Simons et al. 1992).

Genus *MESOPROPITHECUS* Standing, 1905
MESOPROPITHECUS GLOBICEPS Lamberton, 1936
Figure 21.2D

Partial Synonymy *Neopropithecus globiceps* Lamberton, 1936; *Neopropithecus platyfrons* Lamberton, 1936.

Age and Occurrence Late Quaternary, southern, southwestern, and southeastern Madagascar.

Diagnosis Skull length averages 94 mm; very similar to but slightly smaller than *M. pithecoides*; differs from latter in skull more gracile; snout narrows anteriorly to a greater degree; teeth very like (though slightly larger than) those of *Propithecus*, except: upper and lower premolars relatively shorter; M3 moderately buccolingually constricted. Tooth comb is that

typical of living indriids. Auditory bulla remains inflated. Both *M. globiceps* and *M. pithecoides* differ from *M. dolichobrachion* in limb proportions: relatively shorter forelimb.

Description Body mass estimated at ~11 kg (Jungers et al., 2008); intermembral index 97. Forelimb relatively conservative (indriid-like); hindlimb and axial skeleton more specialized for suspension (more like *Palaeopropithecus* and *Babakotia*). Forelimbs and hindlimbs approximately equal in length.

MESOPROPITHECUS PITHECOIDES Standing, 1905

Age and Occurrence Late Quaternary, central Madagascar.

Diagnosis Skull length averages 98 mm; very like *M. globiceps*; skull with well-developed sagittal and nuchal cresting; massive zygomatic arches; muzzle broader anteriorly than in *M. globiceps*.

Description Intermembral index 99. Limb proportions are virtually identical to those of *M. globiceps*. Marked craniodental similarities to *M. globiceps*.

MESOPROPITHECUS DOLICHOBRACHION Simons et al., 1995

Age and Occurrence Late Quaternary, northern Madagascar.

Diagnosis Skull length averages 102 mm; *M. dolichobrachion* differs little from congeners craniodentally, except in having a third upper molar with relatively wider trigon and smaller talon. Chief distinctions postcranial: humerofemoral (~104) and intermembral (~113) indices relatively high (hence its specific nomen); humerus substantially longer and more robust than that of either congener; humerus unique among congeners in exceeding length of femur.

Description Largest of the *Mesopropithecus* species at ~14 kg (Jungers et al., 2008). As in other *Mesopropithecus*, the central upper incisor is larger than the lateral, and there is a small gap separating them at prosthion; the upper premolars are short mesiodistally. Tooth comb is present. Sagittal and nuchal crests are evident, orbits are small, postorbital constriction is marked, and the muzzle is wide and squared anteriorly.

M. dolichobrachion has an indriid-like carpus but strongly curved proximal phalanges. Moderately reduced neural spines of lumbar vertebrae, and reduced rectus femoris process. The fovea capitis is reduced, the femoral condyles anteroposteriorly compressed. The value for the brachial index of *M. dolichobrachion* (also ~104) also deviates from those of its congeners (~101). Of all its congeners, *M. dolichobrachion* is most similar to *Babakotia*, *Archaeoindris*, and *Palaeopropithecus*, suggesting greater specializations for suspension.

Remarks on Genus Mesopropithecus Tattersall (1971) considered *Mesopropithecus* the sister taxon to *Propithecus*, but Godfrey (1988) defended a closer relationship to *Palaeopropithecus* and *Archaeoindris*. New discoveries have added evidence in favor of the latter. Two of the three species, *M. globiceps* and *M. pithecoides*, are very alike and allopatric. The latter may be a slightly larger-bodied, geographic variant of the former that should not be accorded separate species status. In comparison to *Propithecus*, *Mesopropithecus* has relatively smaller and more convergent orbits, a steeper facial angle, greater postorbital constriction, a more robust postorbital bar, a relatively wider and anteriorly squared muzzle, and zygoma that are more robust and cranially convex in outline. The temporal lines are anteriorly confluent and may

form a sagittal crest; the nuchal ridge is confluent with posterior root of the zygoma. *Mesopropithecus dolichbrachion* is the most distinct, and is geographically restricted to the extreme north.

Family ARCHAEOLEMURIDAE G. Grandidier, 1905

This family, dubbed the “monkey lemurs,” includes three recognized species in two genera: *Archaeolemur majori* (southern and western Madagascar), *A. edwardsi* (central Madagascar), and *Hadropithecus stenognathus* (largely southern and western Madagascar). Variants of *A. majori* and *A. edwardsi* exist in other parts of Madagascar, and a full review of this variation is warranted. The archaeolemurids have a dental formula of 2.1.3.3/2.0.3.3; they possess a highly modified tooth comb with four instead of six teeth, likely missing the lower canine. The lower incisors are procumbent but occlude directly with the uppers. The central upper incisors are considerably larger than the lateral, and there is substantial contact of the mesial edges of the two central incisors; they thus lack the typical strepsirrhine interincisal gap. The premolar series is modified into a continuous shearing blade in all species, and P4 is molariform (greatly buccolingually expanded with a distally emplaced and distinct protocone). As in most extant lemurs (except cheirogaleids), there is an inflated petrosal bulla with a free intrabullar tympanic ring, and the carotid foramen is located on the posterior wall of the bulla. The neurocranium of archaeolemurids is relatively large (at least by strepsirrhine standards) (see Tattersall, 1973, for detailed descriptions of the craniodental morphology of the archaeolemurids). A number of postcranial features suggest that the archaeolemurids spent considerable time on the ground (Walker, 1974; Godfrey, 1988). These include a posteriorly directed humeral head with greater tubercle projecting above it, a relatively deep olecranon fossa, a reduced and dorsomedially reflected medial epicondyle, and a greater trochanter projecting above the femoral head. In comparison to like-sized cercopithecids, the archaeolemurids have limb bones that are relatively short and robust, and very short metapodials. Hamrick et al. (2000) and Jungers et al. (2005) document newly discovered cheirideal elements of *Archaeolemur*, and the first known cheirideal elements of

Hadropithecus have recently also been described (Wunderlich et al., 1996; Godfrey et al., 1997b, 2006a; Lemelin et al., 2008).

Genus ARCHAEOLEMUR Filhol, 1895
 ARCHAEOLEMUR MAJORI Filhol, 1895
 Figure 21.3

Partial Synonymy *Nesopropithecus australis* Forsyth-Major, 1900a; *Protoindris globiceps* Lorenz von Liburnau, 1900; *Globilemur flacourti* Forsyth-Major, 1897; *Bradylemur bastardi*, G. Grandidier, 1900.

Age and Occurrence Late Quaternary, southern and western Madagascar; possibly central and northern Madagascar.

Diagnosis Skull length averages 128 mm; similar in morphology to but smaller in size than *A. edwardsi*; differs from latter in having less development of sagittal and nuchal crests; shallower (less steep) facial profile; as in *A. edwardsi*, lower incisors long, slender, and obliquely implanted; their tips wear flat; central upper incisors enormous and spatulate; upper canine is very broad and low crowned; p2 caniniform and robust; molars buccolingually expanded (broader than they are long), the first two with classic bilophodonty; third molars reduced but may exhibit incipient bilophodonty.

Description Body mass estimated at ~18 kg; intermembral index 92. Like its congener, *Archaeolemur majori* has short metapodials and phalanges, and relatively straight proximal phalanges. The pelvic girdle is broad, the scapula is relatively short (along the spine) but broad, with a particularly well-developed infrapinnous fossa, and both fore- and hindlimbs are relatively short.

ARCHAEOLEMUR EDWARDSI (Filhol, 1895)

Partial Synonymy *Nesopropithecus roberti* Forsyth-Major, 1896; *Bradylemur robustus* G. Grandidier, 1899; *Archaeolemur platyrrhinus*, Standing, 1908.

Age and Occurrence Late Quaternary, central Madagascar; possibly western, northern, and southeastern Madagascar.

Diagnosis Skull length averages 147 mm; differs from its congener in having relatively greater postorbital constriction;

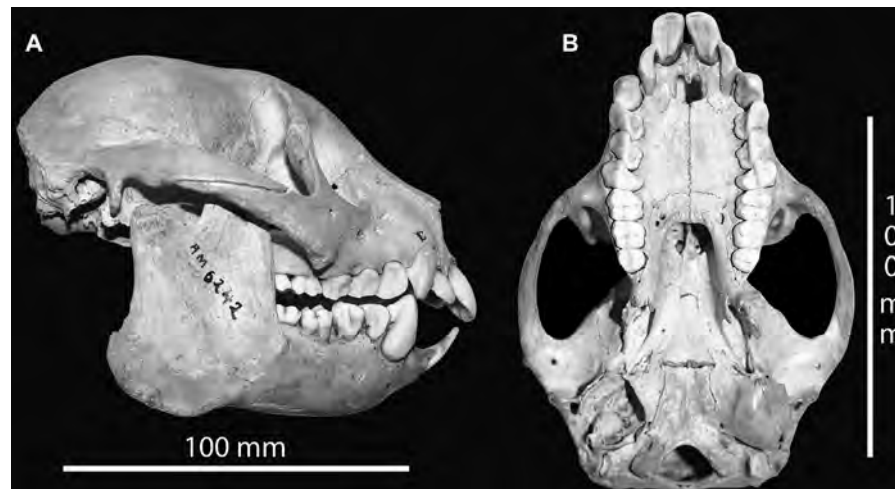


FIGURE 21.3 Archaeolemuridae: A) Lateral view of skull of *Archaeolemur majori* (from Tsirave, collection of the Université d’Antananarivo); B) Ventral view of same skull of *A. majori*.

larger teeth (particularly the molars); relatively broader upper third molars; steeper facial profile; and greater development of sagittal and nuchal crests.

Description This is the larger of the two species of this genus, at ~26.5 kg (Jungers et al., 2008). There are few differences between *A. edwardsi* and *A. majori* other than body size. They are similar in morphology and in proportions; thus, for example, the intermembral index of *A. edwardsi* is 92, just as in *A. majori*. There are minor differences in robusticity, with the larger species tending also to be more robust. The hand of *Archaeolemur* sports a free os centrale, large pisiform, reduced pollex, and hamate with reduced hamulus. On the foot, the calcaneus, cuboid and fifth metatarsal have large tuberosities, and the hallux is reduced. There are enormous apical tufts on the distal phalanges of all digits. Unlike other extinct and extant lemurs, there is no evidence of a grooming claw.

Remarks on Genus *Archaeolemur* Recent research on dental microstructure has demonstrated that crown formation time was more prolonged in *Archaeolemur* than in *Megaladapis* or *Palaeopropithecus*, but not as prolonged as in *Hadropithecus* (Godfrey et al., 2005). Burney et al. (1997) and Vasey and Burney (unpubl.) found evidence for mollusk and small vertebrate consumption, in addition to herbivory, in fecal pellets that apparently belonged to *Archaeolemur*. The molars of *Archaeolemur* show high prism decussation and relatively thick enamel (Godfrey et al., 2005); this is normally indicative of hard-object feeding.

Genus *HADROPITHECUS* Lorenz von Liburnau, 1899

HADROPITHECUS STENOGNATHUS

Lorenz von Liburnau, 1899

Figure 21.4A

Partial Synonymy *Pithecodon sikorae* Lorenz von Liburnau, 1899.

Age and Occurrence Late Quaternary, southern, western, and central Madagascar.

Diagnosis See Lorenz von Liburnau (1902); Tattersall (1973). Skull length ~141 mm; face short, facial profile steep, mandible deep and very robust; zygomatic arch and postorbital bar well

developed and robust; neurocranium relatively broad; as in *Archaeolemur*, premolar series modified into a continuous shearing blade; unlike *Archaeolemur*, anterior premolars, upper canine, and all incisors diminutive; all upper premolars have protocone developed to some extent; P4 is broader than M1 and completely molariform; lower incisors orthally implanted.

Description Body mass estimated at approximately 35 kg (Jungers et al., 2008). The limb bones of *Hadropithecus* recall those of *Archaeolemur* in many respects but differ in proportions; for example, the humerofemoral index (~103) is considerably higher and the brachial index (ca. 84) considerably lower (Godfrey et al., 2006a). The femur is considerably more robust and its shaft more anteroposteriorly compressed. *Hadropithecus* exhibits a number of traits (especially of the cheiridea) that may reflect greater terrestriality (e.g., virtually no hamulus or hook on the hamate, a more mediolateral orientation of the articular facet of the hamate for the triquetrum; Godfrey et al., 2006a; Lemelin et al., 2008), but the limb bone anatomy (including the greater anteroposterior compression of the femoral shaft, and greater asymmetry of the femoral condyles) suggests that this species was not cursorial. This inference has now gained support from study of the semicircular canals (Walker et al., 2008).

Remarks on genus *Hadropithecus* Recent discoveries have confirmed that Lamberton's (1938) hindlimb attributions for *Hadropithecus* are incorrect; the actual hindlimb bones of *Hadropithecus* are described by Godfrey et al. (1997b, 2006a). Stable carbon isotope values indicate a diet unlike that of any other lemur, high in C4 and/or CAM plant products (Burney et al., 2004). Recent research on dental microstructure has demonstrated a unique dental developmental pattern, wherein crown formation was prolonged (approaching the developmental timing of chimpanzees), suggesting late molar eruption and prolonged infancy (Godfrey et al., 2005, 2006a, 2006b, 2006c).

Family MEGALADAPIDAE Forsyth-Major, 1894

The family Megaladapidae, or "koala lemurs," includes only one genus, *Megaladapis* with two subgenera, *Megaladapis* and

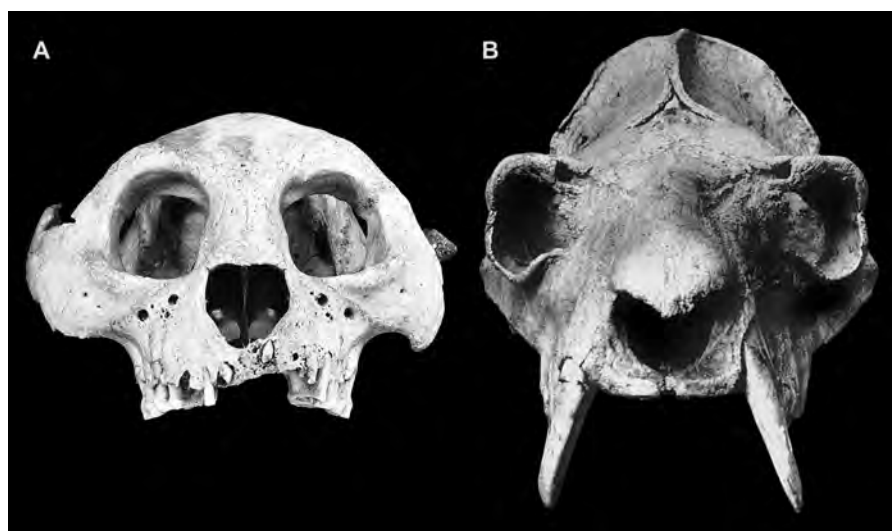


FIGURE 21.4 Frontal views of skulls of *Hadropithecus stenognathus* (A; from Tsirave, collection of the Académie Malgache) and *Megaladapis edwardsi* (B; southern Madagascar, collection of the Université d'Antananarivo). Not to scale.

Peloriadapis (Vuillaume-Randriamanantena *et al.*, 1992). The adult dental formula (0.1.3.3/2.1.3.3) is identical to that of *Lepilemur*. There is a typical strepsirrhine tooth comb comprising six teeth, and no permanent upper incisors. The angled mandibular symphysis fuses completely in adults. A diastema of variable length is present between the upper canine and the first premolar, and between the caniniform lower premolar and p3. Molar size increases from M1 to M3, and molars exhibit mesiodistally long shearing crests or “ectolophs.” There is a posterior extension of the mandibular condyle’s articular surface (and reciprocal expansion of the postglenoid process), another apparent homoplasy with *Lepilemur*. The skull is narrow, elongate, and bears both sagittal and nuchal crests. A small neurocranium is hafted onto the long and massive facial skeleton via a very large frontal sinus. There is strong postorbital constriction, a large temporal fossa, robust zygomatic arches, and a broad interorbital region. The nuchal plane is vertical and the occipital condyles face posteriorly; the paroccipital processes are long. The orbits are relatively small, laterally divergent and encircled by bony tori. The facial axis is retroflexed (i.e., marked airohynchy). The autapomorphic nasals are long, projecting beyond prosthion, and flexed downward above the nasal aperture. The olfactory tracts are very long, and the optic foramina are relatively small. The auditory bulla is not inflated, the tympanic ring is fused laterally, and the tubular external auditory meatus is petrosal in origin (MacPhee, 1987). The mandible sports an expanded gonial region and a robust corpus.

The limbs are relatively short and very robust, and the upper limb is longer than the lower one (Jungers *et al.*, 2002). Humero-femoral and intermembral indices are greater than 100. Slow, deliberate locomotion, inferred from postcranial morphology and proportions, has now been confirmed in a study of the semicircular canal system (Walker *et al.*, 2008). Both hands and feet are relatively enormous, with divergent and robust pollex and hallux. Moderately curved proximal phalanges (Jungers *et al.*, 1997). Spinous processes of thoracolumbar vertebrae are blunt and very reduced (but not to the extent seen in *Palaeopropithecus*). Transverse processes arise from the vertebral arch in the thoracolumbar region. The ilium is long, with the gluteal surface facing posteriorly; it broadens cranially and terminates with hooklike anterior superior spines. The sacrum is long and rectangular, and the sacral hiatus is narrow (the tail was no doubt quite short). The olecranon fossa of the humerus is shallow, the olecranon process of the ulna is prominent and retroflexed, and the ulnar styloid process is large and projecting. The femoral head is large and globular, and the knee exhibits an unusual “bow-legged” angle between femur and tibia. The femur is flattened in the anteroposterior plane. The fibula is robust and curved. The pisiform is dorsopalmarly expanded; the scaphoid tubercle and the hamate hamulus are similar in length to modern pronograde lemurs (Hamrick *et al.* 2000).

Genus *MEGALADAPIS* Forsyth-Major, 1894
MEGALADAPIS (PELORIADAPIS) EDWARDSI
 (G. Grandidier, 1899)
Figure 21.4B

Partial Synonymy Peloriadapis edwardsi G. Grandidier, 1899; *Megaladapis insignis* Forsyth-Major 1900b; *Megaladapis brachycephalus* Lorenz von Liburnau 1900; *Megaladapis dubius* Lorenz von Liburnau 1900; *Palaeolemur destructus* Lorenz von Liburnau 1900; *Megaladapis destructus* Lorenz von Liburnau 1901.

Age and Occurrence Late Quaternary, southern and southwestern Madagascar.

Diagnosis Largest of the koala lemurs. Lacks upper incisors, variable diastemata, M3 largest cheek tooth, airohynch facial skeleton. Long projecting upper canines, prominent caniniform lower P3. Functional tooth comb present; mandibular symphysis fused. Bulla is flat and external auditory tube is “tubular.” Higher intermembral and humero-femoral indices in comparison to congeners.

Description Very large body size (approximately 85 kg; Jungers *et al.*, 2008). Cranial length averages 296 mm. Absolutely short diastemata. Extremely large molars (e.g., mesiodistal length of M¹ is 18.8 mm on average). Intermembral index ca. 120. Very robust long bones. Relatively straight humeral and radial diaphysis. Extremely varus knee joint. Dominance of medial condyle of proximal tibia and very lateral projection of tibial tuberosity. Relatively small tubercle on fifth metatarsal. Flattened surface of talar trochlea and malleolar facets. Low crural index. Reduced spinous processes, small sacral hiatus. Iliac blades long, broadening superiorly with hooklike anterior superior spines; rugose iliac crest for origin of abdominal musculature.

MEGALADAPIS (MEGALADAPIS) MADAGASCARIENSIS
 Forsyth-Major, 1894

Partial Synonymy Megaladapis filholi G. Grandidier, 1899.

Age and Occurrence Late Quaternary, southern and southwestern Madagascar.

Diagnosis Smallest of the koala lemurs, especially in the postcranium. Close phenetic affinities with *M. grandidieri* (Vuillaume-Randriamanantena *et al.*, 1992). Limb bones very robust; humerus broadens distally with large brachioradialis flange. Prominent tuberosity on fifth metatarsal. Large calcaneus with medially projecting tuberosity. Long, robust, and divergent hallux. Talar trochlea less flattened, more grooved.

Description Smallest of the three species of *Megaladapis*, at approximately 46.5 kg (Jungers *et al.*, 2008). Skull length averages 245 mm. Mean length of M¹ is 14.0 mm. Longer diastemata. Intermembral index ca. 114. Humeral head exhibits greater longitudinal curvature. Olecranon fossa is deeper. Broad distal humerus with projecting medial epicondyle and broad brachialis flange. Radial diaphysis quite curved. Relatively large lesser trochanter. Prominent lateral tubercle of fifth metatarsal. Axial skeleton and bony girdles are still poorly known.

MEGALADAPIS (MEGALADAPIS) GRANDIDIERI
 Standing, 1903
Figure 21.5

Partial Synonymy Megalindris gallienii Standing, 1908.

Age and Occurrence Late Quaternary, central Madagascar.

Diagnosis “Medium-sized” koala lemur. Teeth are small relative to the postcranium. Strong phenetic affinities with *M. madagascariensis*. Relatively long diastemata. Some limb bones (e.g., tibia and fibula) overlap in length and robusticity with *M. edwardsi*. Shortest mass-adjusted femora and least curved proximal phalanges of the koala lemurs.

Description Body mass estimated at ~74 kg (Jungers *et al.*, 2008). Skull length estimated at 289 mm; M1 length is 15.4 mm. Absolutely and relatively large diastemata. Shearing crests more prominent on molars (Jungers *et al.*, 2002). Larger body size but morphologically similar to *M. madagascariensis*. Intermembral index ca. 115. Postcrania recall those

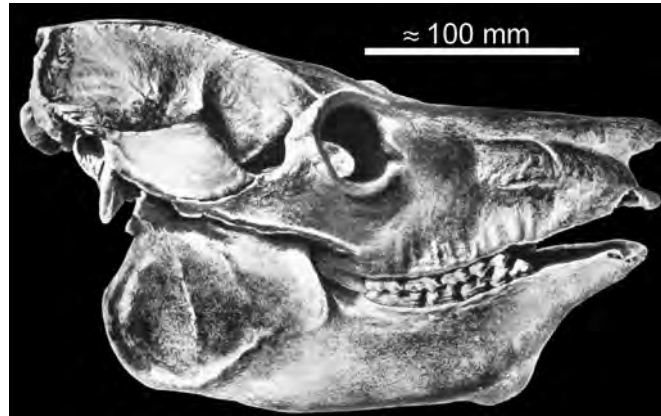


FIGURE 21.5 Lateral view of skull of *Megaladapis grandidieri* from Ampasambazimba, reproduced from Lamberton, 1934c: Plate II.

of *M. madagascariensis*, but are larger overall. One large tibia and apparently associated fibula formerly misidentified as belonging to *Archaeoindris* (Vuillaume-Randriamanantena et al., 1992).

Remarks on the Genus Megaladapis *Megaladapis* sp. cf. *grandidieri/madagascariensis* (provisional) from the extreme north and northwest of Madagascar is intermediate in size between *M. madagascariensis* and *M. grandidieri*, and very similar anatomically to both. The variant of *Megaladapis* from Anjoihibe has particularly small teeth. Schwartz et al. (2005) demonstrate rapid dental development in *Megaladapis* despite its enormous size, although not as rapid as in *Palaeopropithecus*.

Family LEMURIDAE Gray, 1821

This family is comprised mainly of extant forms as well as the extinct genus *Pachylemur*, which resembles *Varecia* in numerous characteristics but is much larger in body size (Walker, 1974; Seligsohn and Szalay, 1974). The adult dental formula is as in other lemurids (2.1.3.3/2.1.3.3); there is a typical lemurid tooth comb, and the mandibular symphysis remains unfused throughout life. The orbits are relatively small. Separate genus status for *Pachylemur* is supported by differences in the postcranial skeletons and inferred positional behavior of *Pachylemur* vs. other lemurids. Whereas the appendicular skeleton closely resembles that of other lemurids in some morphological details, the limbs are shorter and more robust relative to the vertebral column, and the proportions are different. The two species in the genus *Pachylemur* (*Pachylemur insignis* and *P. jullyi*) are sometimes considered regional variants of the same species.

Genus *PACHYLEMUR* Lamberton, 1948
PACHYLEMUR INSIGNIS (Filhol, 1895)
 Figures 21.6A and 21.6B

Partial Synonymy *Lemur intermedius* Filhol, 1895; *Varecia insignis* Walker, 1974.

Age and Occurrence Late Quaternary, southern and southwestern Madagascar, perhaps northwest.

Diagnosis Skull length averages 117 mm; as in *Varecia*, distinguished from *Lemur* and *Eulemur* by suite of dental traits (elongate talonid basins, protocone fold on the first upper molar, anterior expansion of the lingual cingulum of first and second upper molars); differs from *Varecia* in having

orbits more frontally oriented; broader skull; more massive jaws; larger teeth; differs from *P. jullyi* in having: smaller palate, smaller teeth; mandibular cheek teeth are more buccolingually compressed; superior temporal lines generally do not meet at midline; talonid basins of the lower molars skewed into a rhombus that opens distolingually; buccal cusps positioned mesial to adjacent lingual cusps (Vasey et al., 2005).

Description Adult dental formula (2.1.3.3/2.1.3.3), dental morphology similar in most respects to *Varecia*, but about three to four times larger in body size, and far more robust. This is the smaller of the two species of *Pachylemur* at ~11.5 kg (Jungers et al., 2008). Intermembral index ca. 97. Intermembral index higher than in *Varecia* (the fore- and hindlimbs more equal in length), but mass-adjusted limb lengths are shorter. Greater tubercle and greater trochanter project just proximal to humeral and femoral heads, respectively. Short lumbar vertebral bodies; lumbar spinous processes are somewhat reduced and exhibit less anticlinaly.

PACHYLEMUR JULLYI (G. Grandidier, 1899)

Partial Synonymy *Paleochirogalus jullyi* Grandidier, 1899; *Lemur jullyi* Standing, 1904; *L. maxiensis* Standing, 1904; *L. majori* Standing 1908.

Age and Occurrence Late Quaternary, central Madagascar, possibly north.

Diagnosis Similar to congener but larger in skull and tooth size; average skull length ~125 mm; mandibular molars wider, talonid basins squarer with adjacent cusps transversely aligned (Vasey et al., 2005).

Description Larger of the two species of *Pachylemur* at ~13 kg (Jungers et al., 2008); intermembral index ~94. Sagittal and nuchal crests generally occur. Humerofemoral, intermembral, brachial and crural indices are all slightly higher than in *P. insignis*.

Remarks on the Genus Pachylemur DNA confirms a close relationship of *Pachylemur* to *Varecia* (Crovella et al., 1994); dental anatomical data also support such a relationship (Seligsohn and Szalay 1974; Tattersall, 1982). The dominant element in the diet of *Pachylemur*, as in *Varecia*, was probably fruit. It was likely the most important large-seed disperser of the extinct lemurs (Godfrey et al., 2008). Its *Varecia*-like teeth show a rather high incidence of caries and uneven dental wear (Vasey et al., 2005). Seligsohn and Szalay (1974) argue, on basis of molar morphology, that in comparison to *Eulemur*,

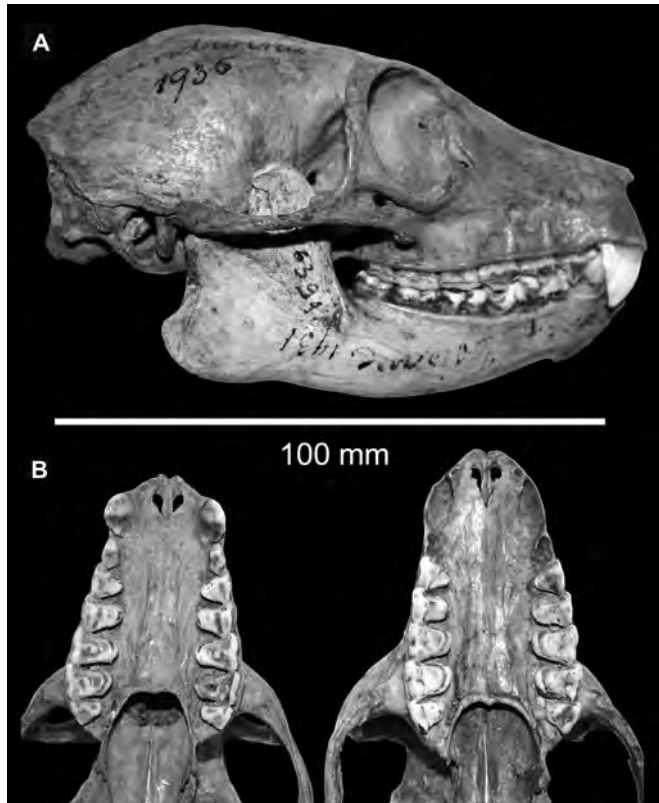


FIGURE 21.6. A) lateral view of a composite skull of *Pachylemur insignis* (cranium from Tsiandroina, mandible from Tsirave, both in southern Madagascar, collection of the Université d'Antananarivo); B) occlusal view of maxillary dentition of *P. insignis* (left, southern Madagascar) and *P. jullyi* (right, central Madagascar), both in the collections of the Université d'Antananarivo. A and B are not to scale; scale bar applies only to A.

Pachylemur would have consumed fewer leaves and more stems and hard fruits. They cite evidence for hard fruit consumption in *Varecia*. *Pachylemur* from the north is not known from a whole skull; materials are insufficient to designate species affinities with any confidence.

Family DAUBENTONIIDAE Gray, 1863

This family comprises a single genus (*Daubentonia*) with two species, the still-extant *D. madagascariensis* and the giant extinct aye-aye, *D. robusta*. Incisors are hypertrophied and curved, chisel-like, with enamel on the anterior surface only. Both upper and lower incisors are laterally compressed and open rooted; the mesial enamel and distal dentine create a sharp cutting edge through differential wear. Whereas the incisors are known for both extinct and extant species, no skull belonging to the extinct form has been found. Existing skeletal remains demonstrate broad similarities. In the extant form (and likely the extinct), a long diastema separates the anterior teeth from the reduced cheek teeth. The cheek teeth are flattened and exhibit indistinct, rounded cusps; there is a single peglike upper premolar. Adult dental formula is 1.0.1.3/1.0.0.3.

Genus *DAUBENTONIA* E. Geoffroy Saint-Hilaire, 1795
DAUBENTONIA ROBUSTA (Lamberton, 1934b)

Partial Synonymy Chiromys Illiger, 1811, *Cheiromys* G. Cuvier 1817, *Chiromys robustus* Lamberton, 1934b

Age and Occurrence Late Quaternary, southwestern Madagascar.

Diagnosis Postcranial skeleton very similar in morphology to that of extant congener but much more robust (Lamberton, 1934b; Simons, 1994); differing in limb proportions (e.g., humerofemoral index higher); limbs short in comparison to body mass; intermembral index ~85. As in congener, femoral head relatively small, ilia narrow and rodlike; incisors hypertrophied, and manual digit III with thin, filiform phalanges and elongated metacarpal; forelimb short and robust in comparison to the hindlimb

Description Body mass estimated at ~14 kg (Jungers et al., 2008), roughly 5 times that of living congener. Of the skull, only the incisors are known (Grandidier, 1929; MacPhee and Raholimavo, 1988). The postcrania exhibit a number of distinctive features (Simons, 1994); for example, the brachialis flange is enormous and winglike, accommodating a massive brachioradialis (Soligo, 2005).

Remarks on the Genus Daubentonia *Daubentonia* possesses a suite of appendicular and especially manual adaptations that facilitate the manual extraction (through bored holes) of nuts, insects, insect larvae, and other foodstuffs. The metacarpophalangeal joint of the third digit of extant aye-ayes allows an extraordinary range of movement; the aye-aye can insert this digit at odd angles into the longitudinal channels created by wood-boring insects (Erickson, 1994, 1995). Aye-ayes exhibit postcranial as well as craniodental convergences to *Dactylopsila* (the striped possum),

which forages in a similar manner (Cartmill, 1974; Godfrey et al., 1995). Invertebrates most likely complemented a primary diet of nuts and other plant products. The giant extinct aye-aye and still extant aye-aye appear to have been allopatric, with the former restricted to the drier habitats of the southwest.

General Discussion: The Extinction of the Subfossil Lemurs

The extinct lemurs of Madagascar formed a key portion of a megafauna that was unique in many ways. In the first place, this is the only primate-dominated assemblage among the world's extinct late Quaternary megafaunas. Additionally, the extinction losses here were more severe than on any of the continents and most other large islands. Madagascar lost all of its endemic animals above 10 kg, including not merely the big strepsirrhine primates but also birds, reptiles, and the other large mammals. It is also one of the most recent of the prehistoric megafaunal crashes, so the evidence is relatively fresh.

As we have documented here and elsewhere (Godfrey et al., 1997a, 2006b; Godfrey and Jungers, 2002; Jungers et al., 2002; see also Tattersall, 1982), the adaptive diversity represented by the combination of extant and extinct lemurs is extraordinary. Primate body masses on Madagascar once ranged from roughly 30 g to over 150 kg, and not long ago there were “monkey lemurs,” “sloth lemurs,” “koala lemurs,” and giant aye-ayes to round out the amazing roster of Malagasy primates. Along with elephant birds, giant tortoises and hippos, all lemurs ~10 kg and larger are missing now from the still impressive array of endemic vertebrates. What and/or who killed the giant lemurs and other megafauna of Madagascar?

Various theories have been offered to account for this last of the great megafaunal extinctions (reviewed in Burney et al., 2004; Burney, 2005). Several hypotheses are dramatically uncausal and imply rapid extirpation of the subfossil lemurs and other large-bodied terrestrial vertebrates at the hands of colonizing Indonesians: “great fires” (e.g., Humbert, 1927), “blitzkrieg hunting” (e.g., Martin, 1984), and “hypervirulent diseases” (MacPhee and Marx, 1997). Although the fingerprints of humans are surely present at this Holocene crime scene, a recently compiled ^{14}C chronology for late prehistoric Madagascar is incompatible with the extreme versions of these extinction scenarios (Burney et al., 2004). The anthropogenic “smoking gun” smoldered for a very long time, much too long, in fact, to validate the predictions of any model of overnight eradication of the subfossil lemurs and other megafauna.

The accumulated evidence, backed by 278 age determinations (primarily ^{14}C dating) documents late Pleistocene climatic events as well as the apparently human-caused transformation of the environment in the late Holocene (reviewed in Burney et al., 2004). Multiple lines of evidence (including modified bones of extinct species and the appearance in sediment cores of exotic pollen of introduced *Cannabis*) point to the earliest human presence at ca. 2300 ^{14}C yr BP (350 cal yr BC). A decline in megafauna, inferred from a drastic decrease in spores of the coprophilous fungus *Sporormiella* spp. (a proxy for megafaunal biomass) in sediments at 1720 \pm 40 ^{14}C yr BP (230–410 cal yr AD), is followed by large increases in charcoal particles in sediment cores (Burney et al., 2003). This pattern begins in the

southwest part of the island and spreads to other coasts and the interior over the next millennium. The record of human occupation is initially sparse but shows large human populations throughout the island by the beginning of the second millennium AD.

Dating of the extinct large lemurs, as well as pygmy hippos, elephant birds, and giant tortoises, demonstrates that most if not all the extinct taxa were still present on the island when humans arrived. Many overlapped chronologically with humans for a millennium or more. Among the extinct lemurs, *Hadropithecus stenognathus*, *Pachylemur insignis*, *Mesopropithecus pithecoides*, and *Daubentonia robusta* were still present near the end of the First Millennium AD. *Palaeopropithecus ingens*, *Megaladapis edwardsi*, and *Archaeolemur* sp. (cf. *edwardsi*) may have survived until the middle of the second millennium AD. The accumulated evidence suggests that humans may have collapsed these ecosystems through a combination of impacts, including overhunting (e.g. MacPhee and Burney, 1991; Perez et al. 2005); landscape modification (e.g., Burney, 1993; Burney et al., 2003) and perhaps other interacting factors, such as invasive species and climatic desiccation (Dewar, 1984; Burney, 1999).

The extinction explanation we favor in lieu of single-cause, very rapid scenarios is thus the “synergy” hypothesis (Burney, 1999). Extinctions are still regarded primarily as the handiwork of humans, but hunting, burning, and habitat transformation and degradation interact in a very slow and mosaic fashion, and the various human impacts may well have differed in significance from region to region across the island. Background climatic change (e.g., desiccation in the southwest) and the introduction of domesticated species (e.g., livestock proliferation in the northwest) are regarded as probable contributing factors in the extinction process but cannot serve as stand-alone explanations. For example, in the southwest it seems likely that the open-country, nonprimate grazers and browsers (e.g., tortoises, elephant bird, and hippos) were reduced drastically in density by intense human predation within a few centuries of colonization. As plant biomass increased as a consequence, fires of human origin increased in frequency and ferocity, and this promoted major ecological restructuring, including the loss of wooded savannas and the preferred (arboreal) habitats of subfossil lemurs. Slowly reproducing, large-bodied lemurs, probably already at low population densities, were unable to “bounce back,” and extinction proceeded slowly but inexorably. Few places, if any, in Madagascar were untouched by humans as they expanded into other areas at different times, but the result, the “deadly syncopation” (MacPhee and Marx, 1997), was invariably the same. Regrettably, the lethal synergies we have proposed are still in place in Madagascar, and the extinction window remains all too open.

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