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ARTICLES

The Extinct Sloth Lemurs of Madagascar

LAURIE R. GODFREY AND WILLIAM L. JUNGERS

Paleontological expeditions to Madagascar over the past two decades have yielded large quantities of bones of extinct lemurs. These include abundant postcranial and cranial remains of new species belonging to a group of giant extinct lemurs that we have called sloth lemurs due to their remarkable postcranial convergence with arboreal sloths. New fossils have come from a variety of locations in Madagascar, including caves in the Northwest (Anjohibe) and the Ankarana Massif, located in the extreme north, as well as pits in the karstic plains near Toliara in southwestern Madagascar. The most spectacular of these is the extremely deep pit (>100 m) called Ankilitelo, the "place of the three kily trees." These new materials provide insights into the adaptive diversity and evolution of sloth lemurs. New carpal and pedal bones, as well as vertebrae and other portions of the axial skeletons, allow better reconstruction of the positional behavior of these animals. New analytical tools have begun to unlock the secrets of life-history adaptations of the Palaeopropithecidae, making explicit exactly what they had in common with their relatives, the Indriidae. Paleoecological research has elucidated the contexts in which they lived and the likely causes of their disappearance.

The sloth lemurs, or Palaeopropithecidae, comprise four of the eight recognized genera of extinct lemurs and more than a third of the extinct species (Table 1; Figs. 1 and 2). Four genera are currently recognized as belonging in this family: *Palaeopropithecus* (the type genus), the truly gigantic *Archaeoindris,* the much smaller-bodied *Mesopropithecus,* and the mid-sized, recently discovered *Babakotia.* This family exhibits the greatest range in body size of all families of Malagasy lemurs (from under 10 kg to over 200 kg) and the most extreme modification of the hind limb and axial skeleton. The elongation of the forelimb and reduction of the hind limb are all the more remarkable because their closest relatives, the Indriidae, have some of the longest hindlimbs and shortest forelimbs in the Order Primates. A sister taxon relationship of the Palaeopropithecidae to the Indriidae is supported by molecular data[1] and a host of dental morphological and developmental specializations.

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Both have been working on the evolution, ecomorphology, and extinction of primates in Madagascar for the last three decades. Both have collaborated on paleontological expeditions in Madagascar with Elwyn L. Simons at Duke University and David Burney at Fordham University.

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Western scientists first learned of the existence of giant mammals on the island of Madagascar in the mid-seventeenth century through the writings of French colonial governor Etienne de Flacourt. In addition to providing his own descriptions of the biota of Madagascar, Flacourt[2] recorded putative Malagasy eyewitness accounts of huge and dangerous beasts roaming the Great Red Island. In some rural regions of Madagascar, even today, as during the past hundred years, stories of hornless "water cows" and other large creatures can be heard.[3,4] Indeed, Alfred Grandidier,[5–7] the Western scientist credited with discovering Ambolisatra, the first subfossil site, needed only to follow the led of a village headman to a marsh in southwestern Madagascar in which, he was assured, the bones of the "Song'aomby" (literally, the "cow that isn't a cow," or pygmy hippopotamus) could be found (Box 1). Among the bones that Grandidier retrieved from that marsh in 1868 was the distal humerus of a sloth lemur, *Palaeopropithecus*—perhaps the first specimen of a giant extinct lemur to be examined by a Western scientist. It was not described until decades later,[8] and its association with sloth lemur skulls remained obscure for decades more. But no longer could there be any doubt that fabulous megabeasts once thrived in Madagascar.

The nomen *Palaeopropithecus ingens* was allocated to a mandible found at another subfossil site in southwestern Madagascar just before the turn of the twentieth century.[9] The mandible was chimp-sized but had sifaka-like teeth. Similar mandibles and associated skulls were recovered from a marsh site, Ampasambazimba, in the interior of the island, and *Palaeopropithecus maximus* was named.[10] Postcranial bones were assigned to *Palaeopropithecus,* almost always incorrectly.

Other whole or partial crania with sifaka-like teeth were recovered at Ampasambazimba in the early 1900s. They ranged dramatically in size: Some (*Mesopropithecus pithecoides*)[10] were barely larger than the crania of diademed sifakas, while others (*Archaeoindris fontoynontii*)[11] rivaled the size of gorilla crania. The gorilla-sized *Archaeoindris* was established on the basis of a mandible and two fragmentary maxillae. A femur belonging to *Archaeoindris* was attributed to an-

TABLE 1. Taxonomy of the Sloth Lemurs

Family Palaeopropithecidae (Tattersall, 1973)		
	Genus *Palaeopropithecus* (G. Grandidier, 1899)	
		Palaeopropithecus ingens (G. Grandidier, 1899)
		Palaeopropithecus maximus (Standing, 1903)
		(*Palaeopropithecus* sp. nov.)
	Genus *Archaeoindris* (Standing, 1909)	
		Archaeoindris fontoynontii (Standing, 1909)
	Genus *Babakotia* (Godfrey and coworkers, 1990)	
		Babakotia radofilai (Godfrey and coworkers, 1990)
	Genus *Mesopropithecus* (Standing, 1905)	
		Mesopropithecus pithecoides (Standing, 1905)
		Mesopropithecus globiceps (Lamberton, 1936)
		Mesopropithecus dolichobrachion (Simons and coworkers, 1995)

other lemur species, *Lemuridotherium.*[12] The only known cranium and possibly associated mandible of *Archaeoindris* were discovered much later at Ampasambazimba.[13]

In the 1930s, Charles Lamberton launched a series of paleontological expeditions (mainly in the Southwest) that were to add to the list of recognized species of extinct lemurs. In 1936 he described, at first under another genus name, additional crania belonging to *Mesopropithecus.*[14,15] In 1938, Decary[16] recovered specimens belonging to a new species of *Palaeopropithecus* at Anjohibe, but the uniqueness of these specimens was not recognized at the time. In 1965, Mahé[17] found additional specimens of the same species at Amparihingidro in the Northwest. Yet more species of sloth lemurs were discovered in the late twentieth century. Beginning in the early 1980s, Elwyn Simons[18–20] launched a series of expeditions to central, northwestern, northern, and southwestern Madagascar. Among the more spectacular discoveries of Simons and his team were those of a nearly complete skeleton of the new species of *Palaeopropithecus* from the northwest[21,22]; a new genus and species of giant lemur, *Babakotia radofilai,* from the north and northwest[23]; and a new species of *Mesopropithecus (M. dolichobrachion)* from the extreme north.[24]

BEHAVIORAL RECONSTRUCTION OF THE SLOTH LEMURS

Early reconstructions of the life ways of *Palaeopropithecus* and other giant lemurs were confounded by postcranial misattributions as well as fanciful interpretations of both cranial and postcranial features. On the basis of its cranium, paleontologist Herbert F. Standing[25] reconstructed *Palaeopropithecus* as an aquatic creature, swimming at the water's surface with its eyes, ears, and nostrils barely above water. Such behavior, Standing believed, could explain not merely the elevation of the nasals and the upward orientation of the axes of the orbits, but also the alignment of the nasal aperture, orbits, and external auditory meatus in a plane perpendicular to that of the occipital condyles, the "elongation" and "flattening" of the skull, the narrowing of the postorbital region, the flattening of the bullae, and the placement of the lacrimal fossa inside the orbital rim (Fig. 3).

Standing[25] believed that the postcra-

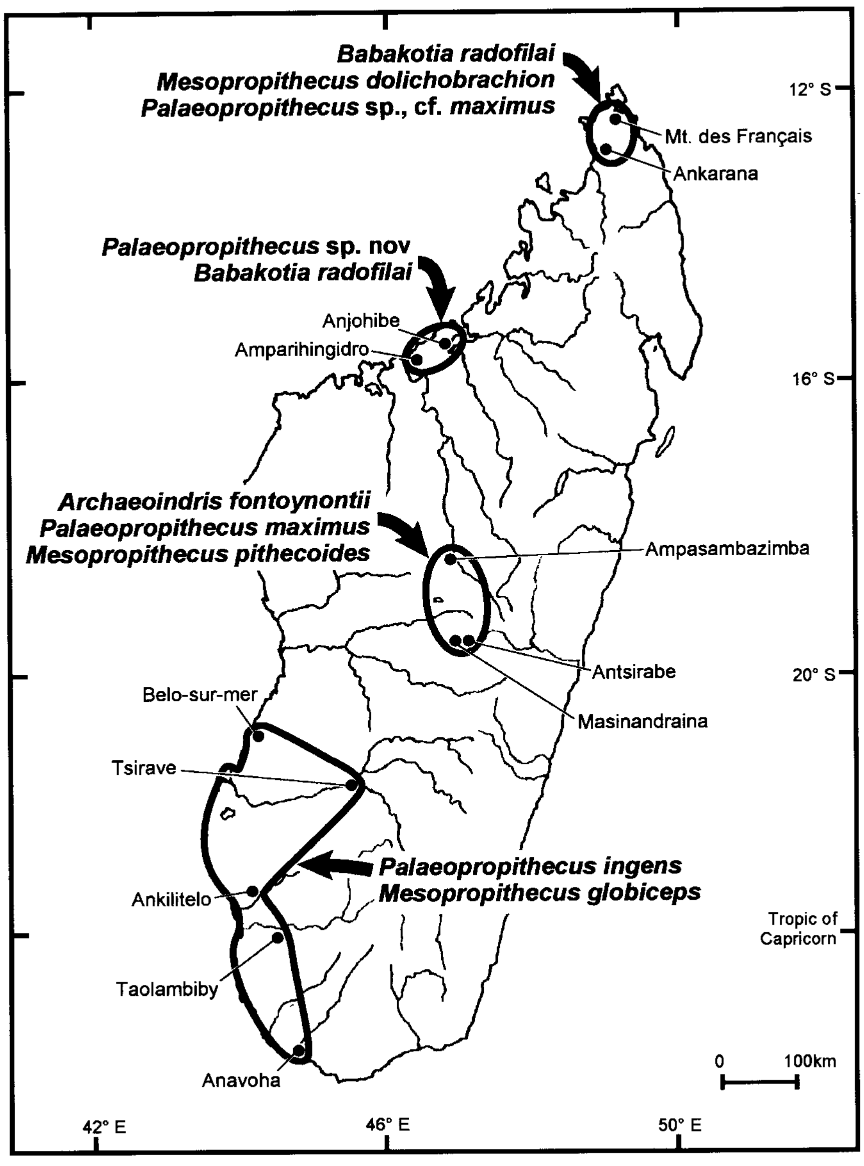

Figure 1. Map of Madagascar, showing the known geographic distributions of sloth lemur species, and highlighting selected subfossil sites.

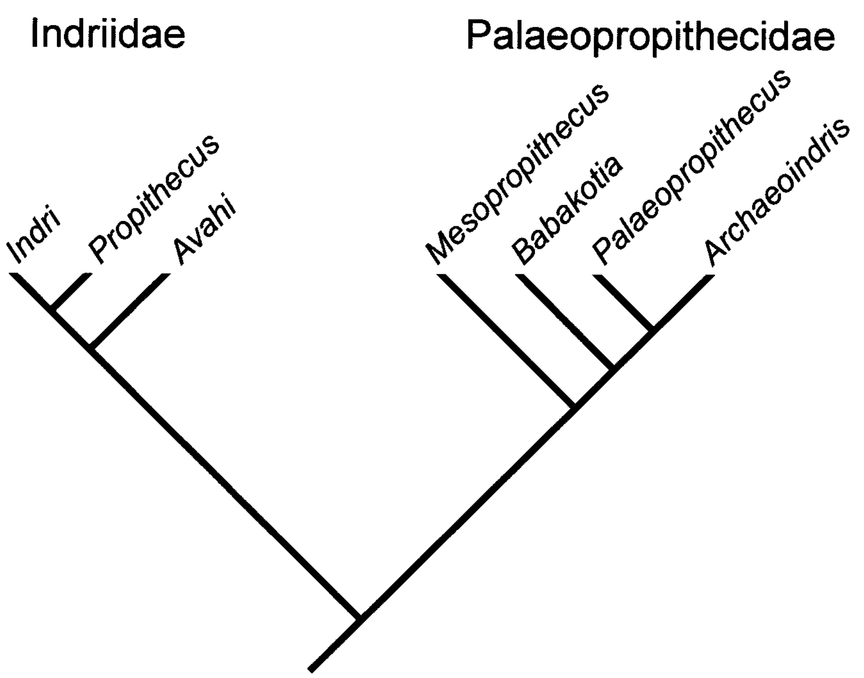

Figure 2. Working cladogram for the Indriidae and the Palaeopropithecidae. The Palaeopropithecidae share a host of postcranial characteristics that bear testimony to their slow climbing and suspensory habits (see text). They can also be distinguished craniodentally from the Indriidae, their closest relatives, by the increased lateral flare and greater robusticity of the zygoma, stronger postorbital constriction, more robust postorbital bar, more convergent and often confluent temporal lines, with the frequent development of sagittal and nuchal crests, even in the smallest taxa. The orbits are relatively smaller than in the Indriidae, but, as in all lemurs and lorises, there is no postorbital closure. *Palaeopropithecus* and *Archaeoindris* share a suite of peculiar, derived traits craniodental specializations (described in the caption to Figure 3).

In addition to providing his own descriptions of the biota of Madagascar, Flacourt recorded putative Malagasy eyewitness accounts of huge and dangerous beasts roaming the Great Red Island. In some rural regions of Madagascar, even today, as during the past hundred years, stories of hornless "water cows" and other large creatures can be heard.

nia of *Palaeopropithecus* provided independent evidence of swimming adaptations. Unfortunately, the postcranial bones that he brought to bear on his argument did not even belong to *Palaeopropithecus*.[26] Actual postcranial bones of *Palaeopropithecus* had been ascribed to other taxa, including the long-snouted *Megaladapis* and a presumed gigantic tree sloth that Alfred Grandidier's son, Guillaume, called *Bradytherium*.[27] In turn, a femur of *Hadropithecus* and forelimb bones of *Megaladapis* were attributed to *Palaeopropithecus*. The *Hadropithecus* femur exhibited a torsion that Standing[25] believed might facilitate swimming, while the short, massive *Megaladapis* humerus seemed an ideal paddle, with its prominent deltoid crest and limited capacity for elbow extension.[11]

Italian paleontologist Guiseppe Sera embraced Standing's aquatic theory of giant sloth lemur locomotion and carried it further. Beginning in 1935 with a confused assemblage that included a humerus and radius of *Megaladapis*, a fibula of *Megaladapis* misidentified as a clavicle, and the astrago-navicular of a crocodile, Sera[28] reconstructed *Palaeopropithecus* as an arboreal-aquatic acrobat with a locomotor repertoire combining climbing, diving, and swimming. In 1938 he broadened his aquatic theory to encompass other extinct lemurs.[29] *Megaladapis*, for example, became a dorsoventrally flattened skate- or ray-like swimmer, its underwater concealment while feeding on aquatic mollusks and crustaceans facilitated by the varus orientation of its knee and rotation of the iliac blade into the frontal plane!

Whereas *Mesopropithecus* and *Archaeoindris* were spared such grotesque misrepresentation, neither entirely escaped attributional errors. Carleton[30] mistook postcrania of *Propithecus diadema* at Ampasambazimba for those of *Mesopropithecus pithecoides* and somehow took these to imply monkey likenesses. References to *Archaeoindris* as being similar to *Megaladapis* in its locomotor behavior were also based, at least in part, on attributional errors.[31] Interpretations of the locomotion of *Archaeoindris* were hampered as well by a dearth of specimens. Only six postcrania belonging to *Archaeoindris* have ever been found: a damaged humerus, the "*Lemuridotherium*" femur, and four shafts of the long bones of an immature individual. Postcrania of *Mesopropithecus* are better represented in the fossil record, but until recently some critical elements, including the radius, ulna, vertebrae, hand and foot bones, and the pelvis, were unknown.

The paleontologist who did the most to correct early problems of attribution and interpretation was Charles Lamberton. Others had begun to tackle the problems of synonymy and association,[12,30,32] but it was up to Lamberton[33,34] to dispose once and for all of Guillaume Grandidier's fossil sloth theory and Sera's theory of aquatic lemur locomotion. In 1957,

Box 1. Early Descriptions, Early Discoveries

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The first of the extinct lemurs to be described by a Western scientist was the "tretretretre." In the seventeenth century, French naturalist and explorer Étienne de Flacourt[2] described this creature as living in southeast Madagascar. According to Flacourt's translation of Malagasy accounts, this was a large, frightening, and solitary beast with a short and curly coat, rounded ear pinnae, flat face, long digits, and a short tail. While a number of authors have suggested that this might describe a *Megaladapis,* such an inference is strongly contradicted by the extreme elongation of the facial skeleton of all species belonging to that genus. A better match is provided by the sloth lemur, *Palaeopropithecus.* Sloth lemurs, like living indriids, had faces that were considerably shorter than those of *Megaladapis.* Also, we know from skeletal remains that *Palaeopropithecus* had long, curved digits and a vestigial tail (see Box 2). Rounded ear pinnae characterize all of the indriids and might well have characterized their close relatives.

Proof of the prior existence of giant lemurs and other megafauna in Madagascar came in the form of "subfossil" remains (so-called because they are too fresh to be fossilized), first reported in the scientific literature of the Western world in the mid-1800s. *Palaeopropithecus* was quite possibly also the first of the extinct lemurs to be unearthed by a Western scientist. That scientist was Alfred Grandidier, French geographer, ethnologist, and father of naturalist Guillaume Grandidier, who later contributed volumes to the literature on the extinct megafauna of Madagascar. Alfred was fascinated by Malagasy accounts of fantastic beasts, especially the "Song'aomby," or the "cow that isn't a cow," which some had interpreted as a ferocious, man-eating donkey.[3,4] When, in 1868, a Malagasy village chief showed him a marsh where the bones of the Song'aomby could be found, Grandidier understood that the Song'aomby was actually an extinct hippopotamus. Grandidier's own fascinating account of the events of that day was published more than 100 years later in his "Souvenirs de voyages d'Alfred Grandidier."[7] This is a translation from the original French (p. 13):

"I had stopped to cook my lunch at Ambohisatrana [that is, the place where satrana, or dwarf palm tree plants grow, later called Ambolisatra, the satrana plantation] where I was visited by the chief of the region, with whom I discussed, as was usual for my conversations with the native people, the local industry and animals (particularly the Song'aomby, a cow-like animal). Because I asked for information regarding the Song'aomby (previously known to me only through a very poor description that Flacourt had provided under the name Mangarsahoc), the chief of the region indicated the location of a nearby marsh, and informed me that I could find this animal's bones there. On that advice, I hurried to the location—barefooted and barelegged, with pants cut at the knees, as I am prone to do. I entered the marsh, and lowering myself, tapped the bottom where I sensed a large object, and lifted it. After washing it, I found to my surprise and joy that it was a femur—the thighbone of a bird. The bird must have been enormous, like the famous Roc of 1001 Nights. Enthusiastically, I returned to the water and, with some of my men, dug into the mud that carpeted the floor of the marsh. I retrieved more bones of the colossal bird, *Aepyornis,* known previously only from its 8-liter eggs and a few indeterminable pieces sent by Mr. Abadi and described in 1850 by Isidore Geoffroy Saint-Hilaire. Alongside these bird bones were numerous other bones belonging to an unknown species of hippopotamus that I named *Hippopotamus Lemerlei* in honor of our odd-job man at Tuléar, as well as bones of other new and interesting animals."

Among the "bones of other new and interesting animals" that Alfred Grandidier had found was a distal humerus of a sloth lemur, *Palaeopropithecus.* That humerus was not formally described until 1895, when it was named *Thaumastolemur grandidieri.*[8] Shortly thereafter, it was incorrectly synonymized with *Megaladapis madagascariensis.*[69] It wasn't until nine decades later that *Thaumastolemur's* taxonomic priority over *Palaeopropithecus* was recognized[70] and then quickly suppressed by the International Commission for Zoological Nomenclature, for lack of use.[71] "*Thaumastolemur*" is now judged to be an invalid generic name for *Palaeopropithecus* (1993; Opinion 1737, Bulletin of Zoological Nomenclature 50(2):190–191).

Lamberton[35] published a devastating rebuttal to Sera,[28,29,36] correcting his numerous misattributions point by point and tactfully marveling at his unbridled imagination. Lamberton[37] also corrected Carleton's[30] postcranial attributions for *Mesopropithecus.* He failed to correct early attributional errors for *Archaeoindris,* however. Associations between postcrania and crania of *Archaeoindris* were not really established until 1988[31] (but see also Walker[38] and Jungers[39]).

By the mid-twentieth century, most of the major attributional problems that had plagued early interpretations had been cleared. Carleton and Lamberton had both forcefully demonstrated that *Palaeopropithecus* was suspensory. What remained to be debated, was the relative strength of alternative models of suspensory locomotion for *Palaeopropithecus,* largely on the basis of the evidence of new elements of the

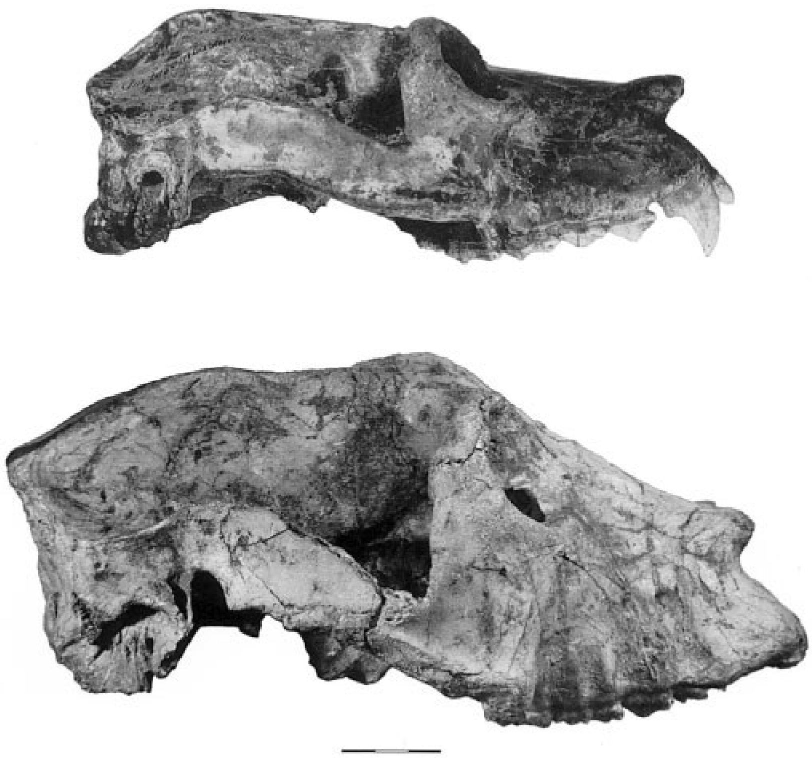


Figure 3. Lateral view of skulls of *Palaeopropithecus maximus* (top) and *Archaeoindris fontoynontii* (bottom), both from Ampasambazimba. *Archaeoindris* shares with *Palaeopropithecus* derived features of the auditory and nasal regions of the skull (e.g., the auditory bullae are deflated; the superior portion of the premaxillae and part of the nasals contribute to a pair of protuberances over the nasal aperture) as well as the dentitions and postcrania. The teeth are very similar in morphology and proportions (e.g., stubby incisors comprise a modified toothcomb; a diastema seperates the anterior and posterior lower premolars; the third maxillary and mandibular molars are reduced in size, and the first and second molars are long and buccolingually compressed). The mandibular symphsyis is long and fused early. These taxa form a distinct clade within the Palaeopropithecidae. However, their facial profiles are different, and, in many features, *Archaeoindris* is less derived. For example, the orbits of *Archaeoindris* lack the distinctly thickened rimming that characterizes those of *Palaeopropithecus*, and they are less dorsally directed. The nasal protuberances are less developed. The cheek teeth are less wrinkled and slightly higher-crowned.

carpals and tarsals of previously known species, as well as the anatomy of the new species of sloth lemurs. Carleton[30] had favored a sloth model, Lamberton[34] an orang model. Subfossil discoveries in the late 1900s tipped the balance in favor of the sloth model, convincing us that *Mesopropithecus* was a member of the family Palaeopropithecidae (and not an indriid, as previously thought).[24,40] The spectrum of postcranial variation within the Palaeopropithecidae, including *Mesopropithecus* and the newly discovered *Babakotia*, is much like that observed in lorises and sloths. *Mesopropithecus* is the most quadrupedal and loris-like, while *Palaeopropithecus* is the most sloth-like, with hooklike hands and feet entirely unsuited for weight bearing in terrestrial locomotion (Table 2). Numerous postcranial adaptations suggest a commitment to slow, vertical climbing and suspensory modes of locomotion in the sloth lemurs (Box 2).[19,24,26,41–45] Limited scansoriality has been postulated for the gorilla-sized *Archaeoindris*,[26,31,46] which has been likened to a ground sloth.[39] However, its very high femoral neck-shaft angle and other highly derived postcranial features, which are shared only with *Palaeopropithecus*, suggest more committed arboreality.

The nearest relatives to the Palaeopropithecidae, the living Indriidae, are "vertical clingers and leapers" with elongated hands and feet, special adaptations for what has been called "thigh-powered" leaping,[47–51] and intermembral indices much lower than those of the Palaeopropithecidae. They typically feed in vertical sitting or hanging positions. They sometimes use their hindlimbs (or hindlimbs and forelimbs) to support their weight in suspension. Occasionally, they use forelimb suspension in traveling.[38,52] Thus, these animals exhibit the odd behavioral combination of being both specialized leapers and adept climbers and hangers.[86] It is likely that the common ancestor of the Indriidae and Palaeopropithecidae was less specialized for leaping than are modern indriids, and sometimes used suspension in feeding and traveling. After their split, the palaeopropithecid lineage would have sacrificed leaping entirely, while the indriid lineage emphasized leaping.

The dentitions of the indriids and palaeopropithecids are strikingly similar.[26,53] All indriids and palaeopropithecids have a derived dental formula (2.1.2.3/2.0.2.3), with no mandibular canine, only two pairs of premolars, and high molar shearing quotients. M^1 and M^2 have four main cusps plus strong parastyles and weak metastyles. M^3 is reduced. The lower molars have accentuated trigonid and talonid basins; there are five cusps on

Standing believed that the postcrania of *Palaeopropithecus* provided independent evidence of swimming adaptations. Unfortunately, the postcranial bones that he brought to bear on his argument did not even belong to *Palaeopropithecus*.

TABLE 2. Characteristics of the Palaeopropithecidae

Taxon	Body Mass (kg)[46]	Diet[54,55]	Salient Characteristics; Inferred Positional Behavior[46]
Mesopropithecus (3 species)	9–11 kg	Leaves, fruit, and seeds	Curved proximal phalanges; hindfoot somewhat reduced; intermembral indices ca. 97–113. Quadrupedal, loris-like slow climber; some fore- and hindlimb suspension
Babakotia (1 species)	15–18 kg	Leaves, fruit, and seeds; some hard objects	Curved proximal phalanges; hindfoot more reduced than in *Mesopropithecus;* intermembral index ca. 118.5. Slow climber, apparently more suspensory than *Mesopropithecus* but less than *Palaeopropithecus*
Archaeoindris (1 species)	190–210 kg	Leaves, fruit, and seeds	Humerus longer than femur; a high femoral neck-shaft angle and other features of the postcrania suggest scansoriality
Palaeopropithecus (3 species)	25–55 kg	Leaves, fruit, and seeds	Long, hook-like hands and feet, very curved proximal phalanges, and very reduced hallux and hindfoot; intermembral indices ca. 138–144. Highly suspensory and convergent with *Bradypus* in many aspects of its skeletal anatomy

M_1 (protoconid, paraconid, metaconid, entoconid, and hypoconid) and there may be a hypoconulid on M_3. The lower premolars are bilaterally compressed. There is a long and oblique mandibular symphysis and deep genial fossa. The mandibular corpus is deep, especially in the region of the gonial angle, but relatively thin, and the mandibular condyle is compressed and rounded in coronal view. Palaeopropithecids and indriids also have a robust zygomatic with distinct cranial convexity in sagittal view. Their common ancestor would have possessed a conventional toothcomb (with procumbent, elongated teeth) but with only four elements. The toothcomb is present in *Mesopropithecus* and *Babakotia,* but lost in *Palaeopropithecus* and *Archaeoindris.*[46] Analysis of molar microwear[54,55] suggests a mixed diet similar to the diets of extant indriids.

It is also noteworthy that all palaeopropithecid species for which immature individuals are known can be shown to have had unusually accelerated dental development, apparently for early processing of fibrous foods (Box 3).[56,57] Crown initiation and mineralization is accelerated both relative to cranial growth and on an absolute scale. Some of the anatomical correlates of this developmental pattern include a diminution of the deciduous teeth and an unusual pattern of permanent premolar loss (apparently P^2 in maxilla and P_3 in mandible). These characteristics may link all palaeopropithecids and indriids.

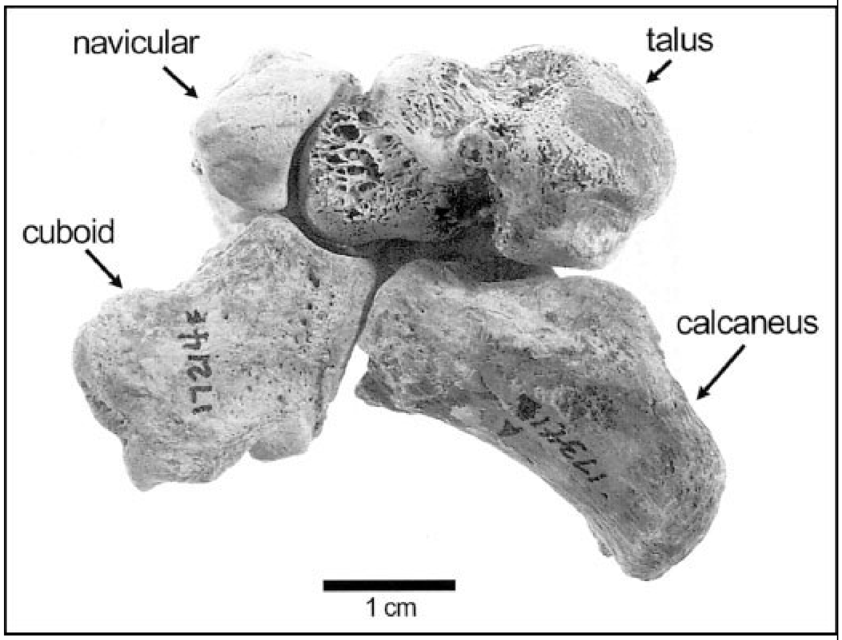
Recent studies have begun to probe possible life-history correlates of this developmental pattern. Living indriids grow slowly and tend to delay first reproduction; their weanlings also tend to be relatively small in body.[58–60] Yet they all exhibit accelerated dental development, attaining ecological adulthood long in advance of sexual maturation and the cessation of somatic growth. As compared to sympatric lemurids, sifakas also tend to experience relatively low adult mortality under moderate resource crunches.[59,60] We have suggested that this pattern may reflect an ability to survive on low-quality (that is, highly fibrous) staple or fallback foods and a life-history “strategy” of low maternal input and slow returns in an unpredictable and periodically stressful environment.[60] Evidence is accumulating that palaeopropithecids followed similar developmental trajectories.[56,57]

THE DISAPPEARANCE OF THE SLOTH LEMURS

Madagascar was one of the last land masses to be colonized by people, and the impacts of that colonization on the giant lemurs and other megafauna were immediately felt (Boxes 4 and 5). Nevertheless, radiocarbon dates confirm that several of the giant lemurs, including *Palaeopropithecus, Archaeolemur,* and *Megaladapis,* survived into the past millennium, along with gigantic flightless birds, hippos, and other subfossil fauna.[20,61–66] A few may have succumbed only very recently. A specimen of *Palaeopropithecus ingens* from Ankilitelo in southwest Madagascar was recently radiocarbon-dated at 510 ± 80 BP.[20] Confidence limits on this date include the historical period.[4,66] The causes of the extinctions have been hotly debated (Box 5), but a major impact by humans can no longer be contested.

Gabriel Ferrand[67] was one of several European folklorists who, in the last nineteenth century, recorded Malagasy tales of fabulous hippo-like, elephant-bird-like, and lemur-like beasts. There was a ferocious, hornless, dim-sighted “not-cow-cow” that sprayed urine, and charged and

Box 2. Extreme Sport
W. L. Jungers and L. R. Godfrey



The tarsal bones of *Palaeopropithecus* are unique among primates in their shape and articulation. The calcaneus is short and quite small, and the head of the talus articulates with the navicular and the cuboid.

All of the sloth lemurs (*Mesopropithecus, Babakotia, Palaeopropithecus,* and *Archaeoindris*) exhibit postcranial convergences with true sloths to some degree.[46] However, the culmination of extreme suspensory adaptations in the palaeopropithecids can be seen in the skeleton of the family's namesake, *Palaeopropithecus*—probably the most antipronograde arborealist ever to evolve in the order Primates. All species of this genus are characterized by extreme forelimb dominance, with a humerofemoral index hovering around 150 (by comparison, siamang and orangutans top out in the 130 range). This remarkable proportionality is driven primarily by extreme reduction of the hind limb relative to estimated body mass.

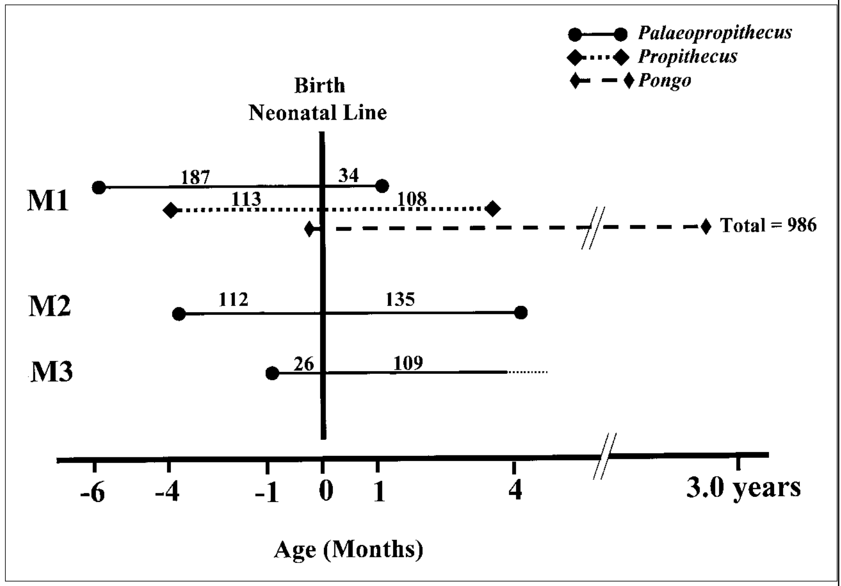
The hands and feet of *Palaeopropithecus* are long, hook-like appendages with pronounced phalangeal curvatures[44]; even the distal phalanges are "bent." The proximal phalanges have pronounced flexor ridges for deep osseofibrous tunnels through which the digital flexor tendons ran. The metacarpophalangeal joints have a "tongue-and-groove" geometry, unique among primates, that guides and limits movement of the rays to stereotypical flexion and extension. The hallux is very reduced in length; we suspect that the pollex was too. Although virtually every joint of the postcranium of *Palaeopropithecus* shows modifications for enhanced mobility or hanging, the wrist and ankle joints are especially derived in this respect. Further, the olecranon process of the ulna is very reduced, as in hominoids, and the globular femoral head sits atop a neck aligned almost vertically with the femoral shaft.

The carpus has an overall "flexed set" relative to the forearm, and the conical ulnar styloid process articulates exclusively with the triquetrum in a mortar-and-pestle arrangement.[45] The ankle of *Palaeopropithecus* is simply bizarre, and epitomizes mobility. Neither the tibia nor the fibula has a real malleolus, and both articulate with a semi-spherical talar trochlea in a mobile arrangement that recalls the hominoid shoulder joint. The calcaneus is extremely small, so reduced, in fact, that it was originally mistaken for a pisiform.[21] It served as little more than a bony guide for the tendons of the pedal digital flexors. The head of the talus is planar-flexed and projects distally far beyond the tiny calcaneus; it articulates uniquely among primates with both the navicular and cuboid. The total foot has an inverted set, so that it is difficult to imagine it functioning in pronograde weight support.

The vertebral column is equally specialized for suspensory postures and locomotion. One of the most remarkable features of the thoracolumbar vertebrae is the extreme reduction of the spinous processes to mere nubbins, another feature that harkens back to sloth-like anatomy. The transverse processes of the lumbar vertebrae have migrated dorsally onto the vertebral arches in hominoid fashion, and the laminae are quite broad. We speculate that the ligamentum flavum was especially well developed as a passive fibroelastic mechanism for resisting vertebral flexion in upside-down postures. The virtual lack of spinous processes continues down onto the sacrum. The sacral hiatus is small, as is the articular facet for the first caudal vertebra. We suspect that the tail was vestigial in *Palaeopropithecus.* Locomotion on the ground would have been ungainly, perhaps comical, and probably quite rare, except to creep across the ground from one feeding tree to the next when presented with gaps in the forest canopy.

mauled people. There was a jealous and powerful ogre-bird that could not fly. There was another ogre with the body of an animal but the face of a human that could be rendered helpless on smooth rock outcrops because it was unable to move on flat surfaces. It is tempting to think that this description might have been based on

Box 3. Big Bodies, Fast Teeth
G.T. Schwartz and L.R. Godfrey



Chronology of dental development in *Palaeopropithecus, Propithecus,* and *Pongo.* Indicated above the bars are the days devoted to crown formation before and after birth in each of these three taxa.

Large-bodied extant primates generally have slow dental crown formation. This tends to be correlated with prolonged dental eruption, delayed maturation, and a generally slow pace of life history. In anthropoid primates, M1 crowns initiate during the last third of the gestation period; in the case of the largest-bodied anthropoids with the slowest life histories, they initiate only just before birth.

It is possible to reconstruct the timing of molar crown formation in extinct species because of one unique property of teeth: They preserve within them an indelible record of their growth. Teeth grow incrementally, like trees or shells, and the cells that produce the two main tissue components of tooth crowns (ameloblasts in enamel and odontoblasts in dentine) do so in accordance with the body's circadian rhythm. As these cells secrete enamel and dentine, they leave in their wake a trail of incremental markings, of which there are two types: short-period, or daily lines (cross striations) and long-period lines (striae of Retzius). It is these incremental features that provide the "road map" for charting tooth-crown formation times, the timing of tooth initiation and completion, and the timing of birth and age at death. Ultimately, these features allow paleontologists to reconstruct the trajectory of dental development in extinct species.

Given a likely body mass of ca. 45 kg (comparable to that of orangutans),[46] *Palaeopropithecus ingens* might be expected to exhibit slow dental development. Recently, Schwartz and others[57] conducted a microstructural analysis of the molars of this giant sloth lemur. Histological thin sections of the molar series were prepared from a single juvenile *P. ingens* specimen from Ankazoabo Cave, in southwestern Madagascar. Both short- and long-period lines were visible throughout the entire enamel crown. These were used to reconstruct individual molar crown formation times, the time of initiation and completion of each molar crown, and the sequence of molar crown development. All of these data were then used to generate a timeline of molar development relative to the time of birth.

For a primate of its body and molar size, *Palaeopropithecus ingens* has remarkably short crown formation times: M1 = 221 days (0.61 years); M2 = 247 days (0.68 years); and M3 > 135 days (>0.37 years). The degree of sequential molar developmental overlap is great, with all three molars initiating before birth, as is evident from the presence in all three molars of a neonatal line. Taken together, these data point to a relatively short overall period devoted to molar crown development. Indeed, the process is completed several months after birth. This pattern differs not merely from that of large-bodied primates, but from that of other mammals of comparable body size. It can be achieved in an animal the size of *Palaeopropithecus* only through exceedingly high daily rates of enamel secretion.

Remarkably, the same pattern of accelerated dental development is evident in extant indriids, such as the sifaka. A nearly identical timeline for first molar formation has been confirmed for *Propithecus verreauxi.*[57] In this species, as in its much larger relative, M1 crown formation time is 0.61 years. The M1 crown initiates equally early (98 to 113 days prenatally).

Our study of dental development in giant lemurs is helping to elucidate the relationships among body mass, dental development and aspects of the life histories of primates. Clearly, a simple relationship between body size and the pace of dental development is not tenable.

Box 4. Butchered Sloth Lemurs

V.R. Perez, D.A. Burney, L.R. Godfrey, and M. Nowak-Kemp

Cut-mark analysis of specimens of *Palaeopropithecus ingens* belonging to the Oxford University Museum of Natural History has provided the first definitive evidence of the hunting and consumption of giant lemurs in Madagascar. Specimens from Taolambiby, a subfossil site in southwestern Madagascar, show classic signs of butchering, including sharp cuts near joints, spiral fractures, and percussion striae. These specimens were discovered by Hon. Paul Ayshford Methuen, who sailed to Madagascar in 1911 expressly to collect bones of the extinct lemurs for the Oxford Museum. Methuen spent a few years as a member of the staff at the Transvaal Museum before abandoning biology for life as an artist at his estate, Corsham Court, near Chippenham, England. Methuen's subfossil lemur collection remained in obscurity at the Oxford Museum until it was effectively rediscovered at the turn of the twenty-first century.

This left humerus of *Palaeopropithecus ingens* in the Methuen collection (OXUM 14342A) shows cut marks just above the medial epicondyle. The orientation and location of these cutmarks suggest that this animal was disarticulated and processed for consumption.

We have found definitive cut marks on six of the seventeen specimens of *Palaeopropithecus* long bones in the Methuen collection that we have examined. These six bones have a total of forty-three cuts, all of which show classic signs of having been produced by butchery. Some appear to have resulted from dismembering and skinning, whereas others appear to have resulted from filleting. The location and morphological characteristics of the marks provide clues to their origins.[72–75] Ninety-five percent of the marks on these sloth lemur bones are V-shaped; that is, the sides of the kerf walls meet at the base. This suggests the use of a sharp-edged implement that compressed the cortex to the sides as it was drawn across the surface of the bone,[76–78] as might be expected when cadavers are skinned and disarticulated.[72,74,79] Disarticulation and skinning marks tend to be located near the joints and to be comparatively deep, V-shaped, and aligned at acute angles to the long axis of the bone. Filleting marks, which result from the removal of muscle, run along the long axis of the shaft and are found at or near points of muscle origin or insertion. These are present on three bones: a right ulna and a left and right tibia.

The dating of these sloth lemur bones was largely unsuccessful. Most of the cut material from Taolambiby contained too little collagen for reliable ^{14}C dating. However, the exception was a right proximal radius of *Palaeopropithecus ingens* that had conspicuous butchery marks. Collagen extracted from this bone yielded an age of 2,325 $\pm$ 43 years BP. This is surprisingly early given that abundant evidence from introduced and ruderal pollen types, dates on human-modified hippo bones, and drastic increases in charcoal particles from sites all over Madagascar point to human arrival about two millennia ago, give or take a couple of centuries (summarized by Burney[66]). After calibration against the tree-ring record at 2σ, the *Palaeopropithecus* bone result is 417 to 257 BC. If this date is correct, this sloth lemur may have been killed and eaten by some of the first people to reach Taolambiby. Whoever they were, these folks were perhaps among the island's earliest human inhabitants.

Box 5. Extinction in Madagascar: The Anatomy of a Catastrophe

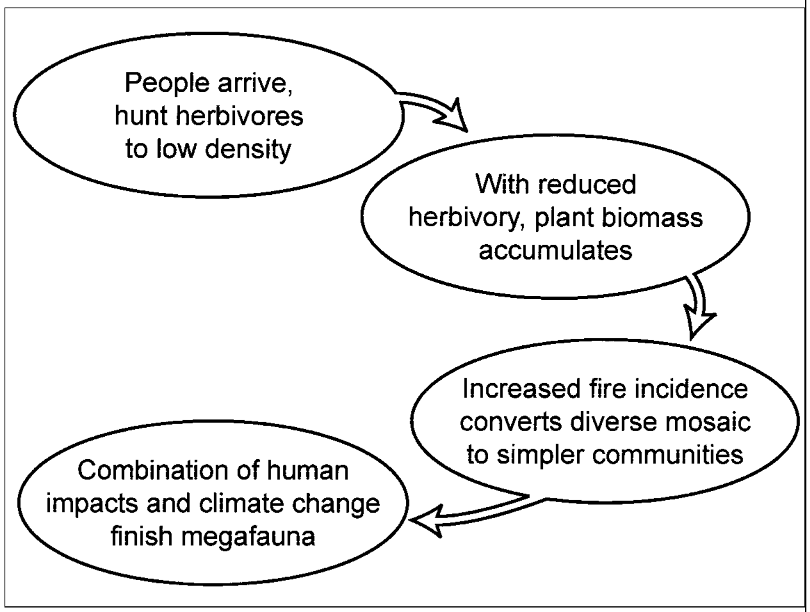
D.A. Burney

The last and most extreme of a long chain of extinction events took out diverse megafaunas of mammals, birds, and reptiles from Australia, the Americas, and the world's larger islands. Whereas most places lost three-quarters or four-fifths of their large mammal genera, Madagascar lost all of its native mammals over ca. 10 kg, including pygmy hippos and giant lemurs, as well as the huge elephant birds and giant tortoises. Despite a lot of scientific detective work, the cause or causes of these extinctions are still shrouded in mystery.

Early botanists working in Madagascar, such as Henri Humbert,[80] suggested that the early Malagasy precipitated these extinctions by introducing fire and transforming the animals' habitat. Mahé and Sourdat[61] cited evidence of desiccation in the dry southern region as a reason for megafaunal decline there. Many scientists have invoked climate changes of various sorts to try to explain late prehistoric extinctions elsewhere. Paul Martin[81] extended to Madagascar his "blitzkrieg" model for rapid extinction following overkill. Robert Dewar[62] wondered if the introduction of livestock to Madagascar might have had something to do with it, while MacPhee and Marx[82] suggested that an unknown "hypervirulent disease" could account for losses here and worldwide.

All these hypotheses were spawned in the absence of sufficient evidence to mount a definitive test. Recently, many pertinent facts have come to light that suggest that all of these explanations might be insufficiently complex. Recent data show that people arrived in Madagascar around two millennia ago or possibly a few centuries earlier (see Box 4). However, it took them over a millennium to colonize the more humid parts of the interior,[66] perhaps due to setbacks from tropical diseases that afflict humans in this region.

Evidence also has been found for climate changes that immediately predated human arrival,[84] hunting by humans[64] (see Box 4), and changes in fire regime (although fires also predate humans in some areas[83]). No evidence has been found to support disease theories, but it is not clear what that evidence would look like. No known disease is equally and rapidly lethal for primates, other mammals, birds, and reptiles.



A simple conceptual model for the author's synergy hypothesis, proposed to explain the extinctions in Madagascar. The empirical evidence suggests that human overexploitation of the megafauna may have set in motion a series of environmental changes that led to ecosystem collapse.

Whatever happened, the great number of new automated mass spectroscopy ^{14}C dates on collagen from a wide array of extinct creatures show that many of them survived until a few centuries ago. Some, such as *Hippopotamus* and perhaps even *Archaeolemur,* may have held out in remote pockets until the nineteenth century or even later.[3,4,66]

Perhaps extinction theorists would do well to borrow some ideas from system modelers, especially those in an area of mathematics known as complexity theory.[85] Humans arrived in Madagascar on the heels of the increasingly dry and uncertain climates documented for the Southern Hemisphere during the late Holocene. It is not hard to imagine that the array of impacts they exerted could have acted synergistically.[66] Perhaps unexpectedly strong interactions occurred that moved the ecosystems of Madagascar far from their normal equilibria into a phase transition from which there was no return.

For instance, what if the vegetation of Madagascar's wooded savannas, semiarid bushlands, and forests had been closely cropped for millions of years by the presumably abundant native grazers and browsers, and these communities were suddenly disrupted by overhunting? Long before extinction set in, fires would have increased in frequency and severity in this accumulating plant biomass, changing many areas to the depauperate steppe grasslands and spiny bushlands characteristic of so much of the island today. The opening of these habitats would have made it easier for hunters to find the survivors and, with the introduction of livestock and exotic carnivores such as dogs and cats, new impacts would emerge. Every human and natural challenge would have compounded the impact of each of the others, driving the ecosystems to new states that were less favorable to survival of the struggling megafauna. Such a combinatorial solution fits the data better than any previous hypothesis and equally well describes the present biodiversity crisis in Madagascar.

Palaeopropithecus; surely this giant sloth lemur would not have been able to negotiate smooth, flat surfaces. We probably will never know whether or not Etienne de Flacourt's[2] "tretretretre" or Gabriel Ferrand's[67,68] flat-faced ogre do indeed describe *Palaeopropithecus*. But there can be no question that in the two thousand years since they first colonized Madagascar, the human inhabitants of Madagascar bore witness to some of the most remarkable primates ever to have evolved: Madagascar's giant sloth lemurs.

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