

Reconstruction of an extraordinary extinct primate from Madagascar

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The minicontinent of Madagascar has been separated by 350 miles of ocean from its neighbor Africa for at least the past 120 million years, i.e., since long before the beginning of the Age of Mammals (1). As a result, the island's flora and fauna show extremely elevated levels of endemism overall (2), and its native mammals show a curious combination of low diversity at the ordinal level with extraordinarily high diversity at lower taxonomic levels (3). Today, for example, Madagascar harbors an astonishing 30% of all primate families and some 21% of all primate genera (3), all of them represented nowhere else. Yet, high as these figures are, they would have been substantially higher a mere 2,000 years ago, before the arrival of Madagascar's first human inhabitants and the probably not coincidental extinction of a substantial proportion of the island's primate (lemur) fauna. In this issue of PNAS, Ryan *et al.* (4) report how new fossil discoveries and the use of computer-aided visualization techniques have significantly advanced our knowledge of cranial construction and body proportions in *Hadropithecus*, one of the most unusual of the recently extinct lemur genera.

The extinct lemurs are well documented from "subfossil" remains collected at numerous sites ranging from ≈ 500 to $\approx 26,000$ years old (5). And to describe *Hadropithecus* as unusual among them is to say that it is unusual indeed. The surviving lemurs of Madagascar all lie well toward the lower end of the mammal body-size distribution, with body weights ranging from ≈ 50 g to 6.0 kg (3). All, with one very partial exception, are also strictly arboreal. In contrast, every one of the eight subfossil genera was substantially larger in size, with estimated body weights ranging from ≈ 10 kg to ≈ 200 kg (6). Moreover, the extinct forms were as diverse adaptively as they were in size. Thus the "sloth lemurs" *Babakotia* and *Palaeopropithecus* were among the most specialized arboreal suspensory forms ever to evolve among the mammals (7); the extremely odd *Megaladapis* was an arboreal vertical clinging form (8) with positional behaviors that have been compared with those of the koala (9); and, in stark contrast, *Hadropithe-*

cus and its close relative *Archaeolemur* have been reported as pronograde terrestrial quadrupeds (10, 11) (Fig. 1). These two last genera, and the extremely short-faced and deep-skulled *Hadropithecus* in particular, were also exceptional in showing extended dental development schedules that presumably reflected prolonged overall developmental periods (12); and compared with other members of the Malagasy lemur fauna (living and extinct), they were also highly encephalized (4, 9).

The first subfossil remains of *Hadropithecus* were recovered at around the turn of the 20th century from the Andrahomana cave, near the southern tip of Madagascar. These specimens were sent at various times to Ludwig Lorenz von Liburnau at the Imperial Austrian Academy of Sciences. In 1899, on the basis of its highly distinctive dentition, Lorenz assigned an (adult) lower jaw to the new genus and species *Hadropithecus stenognathus*, and, as the name he chose implies, concluded that it had ape affinities (13). Later finds, which included an incomplete subadult skull and some postcranial parts, demonstrated to Lorenz that his new form was in fact an "advanced" lemur that grouped with the previously described *Archaeolemur* (14). In 1931, an adult skull of *H. stenognathus* was discovered at the site of Tsiravé in southwestern Madagascar (15); but the species remained among the most poorly understood of the extinct lemurs, its known remains conspicuously lacking a full associated skeleton.

In 2003, more than a century after the initial find, a group that included some of the authors of the current PNAS contribution returned to Andrahomana. There they found numerous bones of an immature postcranial skeleton that, astonishingly, turned out to belong to the same individual as the initial subadult skull and a handful of postcranial pieces that Lorenz had reported with it (4, 11, 14).

Clinching evidence that the two sets of remains come from the same individual is provided by two frontal fragments from the 2003 excavation that perfectly match the missing areas of the original cranium described a hundred years earlier. It is this positive association between the two sets of remains (and the resulting quasi-



Fig. 1. Reconstruction by the artist Stephen Nash of a *Hadropithecus* individual as it may have appeared in life. Pelage coloration and distribution are, of course, conjectural.

complete skeleton) that Ryan and co-authors (4) report in this issue. They demonstrate the match through the "virtual" refitting of the new frontal parts to the 1902 cranium via medical CT imaging. The fit is exact. Similar on-screen manipulations also permitted mirror-imaging of complete skull components on one side to broken areas on the other, and the addition of the lower jaw similarly reconstructed. The result is a detailed three-dimensional image of the Vienna *Hadropithecus* skull, lacking only the anteriormost extremities of the lower and upper jaws. Beyond the considerable intrinsic interest inherent in the almost complete image of one of only two crania known of a primate species that boasts a truly unique and altogether remarkable morphology, the new reconstruction is notable in uniting pieces residing in entirely different institutions separated by an ocean. The original skull components were CT scanned in Vienna, where they form part of the collections of the Natural History Museum, whereas the two new frontal fragments were scanned at Pennsylvania State University, where the resulting digital images were electronically united.

The positive association of the cranium with a more or less complete postcranial skeleton of *Hadropithecus*

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stenognathus provided an opportunity to reevaluate the bodily proportions and adaptations of this highly apomorphic primate species. The relatively high encephalization of this individual relative to members of other lemur species was confirmed, as was the status of *Hadropithecus* as a terrestrial quadruped, albeit one that could climb fairly readily. However, the size of the semicircular canals of the inner ear,

visible in the CT scan, suggests a relative lack of agility. The unique dental morphology of this form has been seen as evidence of seed eating, but stable carbon isotope analyses cited here suggest that grasses may have been consumed. And this is only the beginning: The existence of a substantially complete skeleton of a single individual of *Hadropithecus* will provide a firm platform for future understanding of one

of the most unusual and interesting primates ever to have evolved.

The research reported in this issue of PNAS was accomplished by a joint American–Malagasy–Austrian team that provides a model for future international collaborations in the area of primate evolution, and it further points the way toward the refinement of knowledge in the field by the application of new technologies.

1. Coffin MF, Rabinowitz P (1987) Reconstruction of Madagascar and Africa: Evidence from the Davie Fracture Zone and the Western Somali Basin. *J Geophys Res* 92:9385–9406.
2. Goodman SM, Benstead JP, eds (2003) *The Natural History of Madagascar* (Chicago Univ Press, Chicago).
3. Mittermeier RA, et al. (2006) *Lemurs of Madagascar* (Conservation International, Washington, DC), Second Ed.
4. Ryan TM, et al. (2008). A reconstruction of the Vienna skull of *Hadropithecus stenognathus*. *Proc Natl Acad Sci USA* 105:10699–10702.
5. Burney DA, et al. (2004) A chronology for late prehistoric Madagascar. *J Hum Evol* 47:25–63.
6. Godfrey LR, Jungers WL (2003) Subfossil lemurs. *The Natural History of Madagascar*, eds Goodman SM, Benstead JP (Univ of Chicago Press, Chicago), pp 1247–1252.
7. Jungers WL, et al. (1997) Phalangeal curvature and positional behavior in extinct sloth lemurs (Primates, Palaeopropithecidae). *Proc Natl Acad Sci USA* 94:11998–12001.
8. Wunderlich RE, et al. (1996) New pedal remains of *Megaladapis* and their functional significance. *Am J Phys Anthropol* 100:115–139.
9. Walker AC (1974) Locomotor adaptations in past and present prosimian primates. *Primate Locomotion*, ed Jenkins FA (Yale Univ Press, New Haven), pp 349–382.
10. Godfrey LR, et al (2005) New insights into old lemurs: The trophic adaptations of the Archaeolemuridae. *Int J Primatol* 26:825–854.
11. Godfrey LR, et al. (2006) New discoveries of skeletal elements of *Hadropithecus stenognathus* from Andrahomana Cave, southeastern Madagascar. *J Hum Evol* 51:395–410.
12. Schwartz GT, et al. (2002) Dental microstructure and life history in subfossil Malagasy lemurs. *Proc Natl Acad Sci USA* 99:6124–6129.
13. Lorenz von Liburnau L (1899) Einen fossilen Anthropoiden von Madagascar. *Anz Kais Akad Wiss Wien* 36:255–257.
14. Lorenz von Liburnau L (1902) Über die *Hadropithecus stenognathus*. *Lz Denkschr Kais Akad Wiss Wien* 72:243–254.
15. Lambertson C (1938) Contribution à la connaissance de la faune subfossile de Madagascar. Note III. Les Hadropithecus. *Bull Acad Malg* 27:75–139.