

A reconstruction of the Vienna skull of *Hadropithecus stenognathus*

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Franz Sikora found the first specimen and type of the recently extinct *Hadropithecus stenognathus* in Madagascar in 1899 and sent it to Ludwig Lorenz von Liburnau of the Austrian Imperial Academy of Sciences. Later, he sent several more specimens including a subadult skull that was described by Lorenz von Liburnau in 1902. In 2003, some of us excavated at the locality and found more specimens belonging to this species, including much of a subadult skeleton. Two frontal fragments were found, and these, together with most of the postcranial bones, belong to the skull. CT scans of the skull and other jaw fragments were made in Vienna and those of the frontal fragments at Penn State University. The two fragments have been reunited with the skull *in silico*, and broken parts from one side of the skull have been replaced virtually by mirror-imaged complete parts from the other side. The parts of the jaw of another individual of a slightly younger dental age have also been reconstructed virtually from CT scans with mirror imaging and by using the maxillary teeth and temporomandibular joints as a guide to finish the reconstruction. Apart from forming a virtual skull for biomechanical and systematic analysis, we were also able to make a virtual endocast. Missing anterior pieces were reconstructed by using part of an endocast of the related *Archaeolemur majori*. The volume is 115 ml. *Hadropithecus* and *Archaeolemur* seem to have had relatively large brains compared with the other large-bodied subfossil lemurs.

computed tomography | Madagascar

The Austrian professional fossil collector (and trader), Franz Sikora, collected fossils from Andrahomana cave in south-eastern Madagascar at the end of the 19th Century. For a review of the site and the collections from it, see Burney *et al.* (1). Sikora sent some specimens to paleontologist Ludwig Lorenz von Liburnau at the Imperial Austrian Academy of Sciences in Vienna (Kaiserliche Akademie der Wissenschaften, Vienna), and among them was a mandible that Lorenz thought belonged to an anthropoid primate. He named it *Hadropithecus stenognathus* (2). In a subsequent publication, he figured a cranium found by Sikora and included sketches of superior and inferior views of it (3). Based on the photographs and without seeing the specimen itself, he named it *Pithecodon sikorae*. This skull was, in fact, a younger individual of the same species to which the jaw belonged, as Lorenz von Liburnau quickly realized when he received the specimen from Sikora. He published on it and several other upper and lower jaw fragments and limb bones in 1902 (4). Charles Lambertson of the Académie Malgache in Antananarivo collected the only other known *Hadropithecus* skull from Tsirave in southwest Madagascar in 1931. He described it and at the same time refigured Lorenz von Liburnau's (4) Plate 1 that illustrated the first cranial remains (5). The latter skull is from an older individual with extremely worn teeth. Tattersall (6) gives a full account of all this material together with much cranial material of the better known *Archaeolemur* species. Sikora's fossils from Madagascar were transferred in 1900 from

the Imperial Austrian Academy of Sciences first to the zoological department of the Natural History Museum of Vienna and later, in 1934, to the geological-paleontological department.

Much of a subadult skeleton belonging to this species was found during new excavations at Andrahomana in 2003 (7). Two frontal fragments were found, and these, together with most of the postcranial bones, belong to the skull. The right side only of the type mandible (NHMW1934 IV 1/1) was figured by von Liburnau, and it has since been lost. Only the left side with three molars (NHMW1934 IV 1/2) remains of the type. *Hadropithecus* is one of the most poorly known extinct Madagascan lemurs, but with the new fossils rejoined with the originals after more than a century, we have an opportunity to advance our knowledge of it. We decided to reconstruct the Vienna cranium (NHMW 1934 IV 1) as accurately as we could using medical CT scans together with scans of a partial right mandible (NHMW1934 IV 2/1a) and its left counterpart (NHMW1934 IV 2/1b).

Results

The finished reconstruction does not include missing parts of the anterior dentition and the premaxilla. In the future, these could be reconstructed from the Tsirave skull. An isolated upper canine found in 2003 that probably belonged to the Vienna skull was destroyed for ancient DNA analysis, but no DNA was found. It was inadvertently destroyed before a security cast could be made. A second upper molar was destroyed for enamel structure analysis (8), and a safety mold of this was scanned for use in the reconstruction to replace its damaged antimer.

The reconstruction shows a very short face hafted onto a globular braincase (Figs. 1 and 2). In superior view, with its temporal crest, and curved zygomatic arches with strong post-orbital constriction framing a large temporal fossa, the skull has a resemblance to *Australopithecus* (or *Paranthropus*) *boisei* skulls. This resemblance does not show in the details of the dentition however, because *A. boisei* has flattish, thick-enamelled cheek teeth that increase in area distally, whereas *H. stenognathus* has enlarged middle parts of the tooth row with cuspidate teeth that wear quickly to form complex, unguiform enamel ridges. Furthermore, *Hadropithecus* lacks the thick enamel with heavy decussation throughout that is characteristic of *Australopithecus boisei* (and, incidentally, *Archaeolemur*) (8, 9). Clearly both *Australopithecus* and *Hadropithecus* needed large masticatory muscles with a reduced emphasis on the anterior dentition, but

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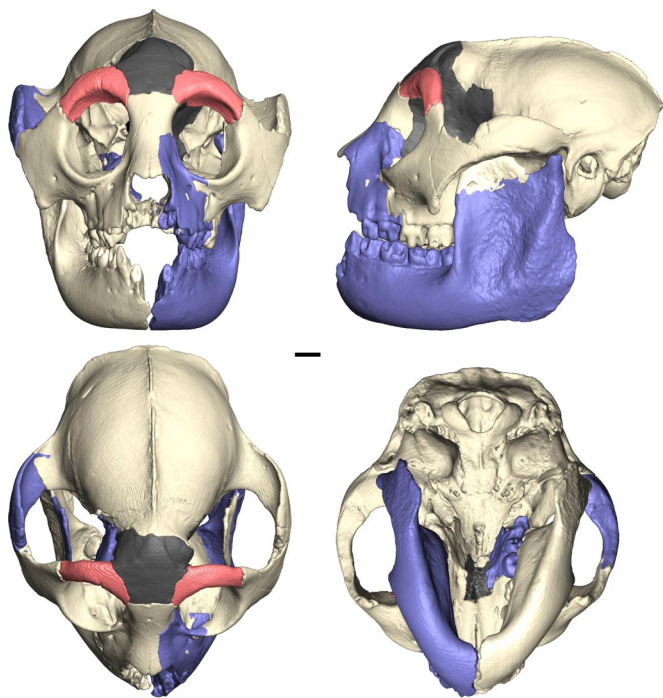


Fig. 1. Frontal, superior, inferior, and left lateral views of the reconstruction of the skull of *Hadropithecus*. The white portions are original fossils described by Lorenz von Liburnau, red colored areas are frontal fragments found in 2003, blue regions are mirror imaged from opposite side of this skull, and the gray section was reconstructed with wax from a 3D stereolithography print. (Scale bar: 10 mm.)

they must have eaten foods with substantially different material properties.

The skull shows maxillary, sphenoid, and extensive frontal paranasal sinuses. These latter, like those of some New World



Fig. 2. Three-quarters view of skull reconstruction with all reconstructed sections uniformly colored. (Scale bar: 10 mm.)

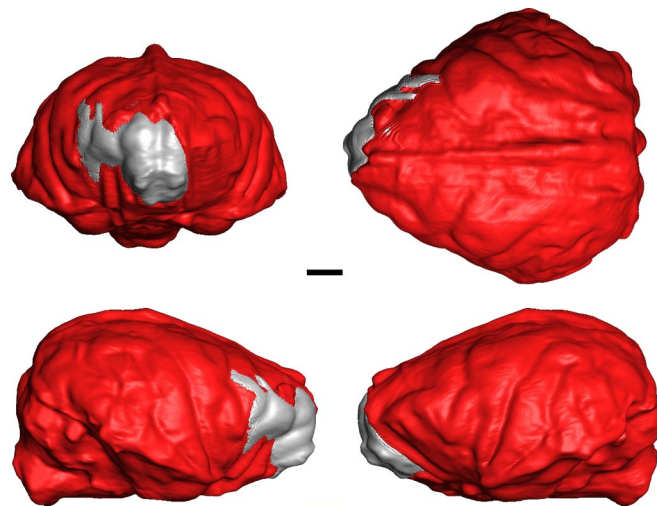


Fig. 3. Frontal, lateral, and superior views of the endocranial reconstruction of *Hadropithecus* with gray portion from *Archaeolemur* (AMNH 30007). (Scale bar: 10 mm.)

monkeys (10, 11), have developed convergently with those of some anthropoid apes.

The endocranium is relatively large compared with other strepsirhines. The volume of the endocranial cavity, with the most frontal part based on *Archaeolemur edwardsi* is 115.0 ml (Fig. 3). A displacement volume of the Tsirave skull made by W.L.J. is 106 ml. Conventional least-squares regression analysis shows that when the recently extinct lemurs are included in the sample, the two archaeolemurids have just above average cranial capacities relative to body mass for strepsirhines, and they are small for anthropoids (but see ref. 12). Compared to the other large-bodied subfossil strepsirhines, *Archaeolemur* appears to be significantly encephalized. *Daubentonia madagascariensis* and *Archaeolemur* species are the only extant or extinct strepsirhines with a cranial capacity that is as large as a haplorhine of the same body mass (Fig. 4).

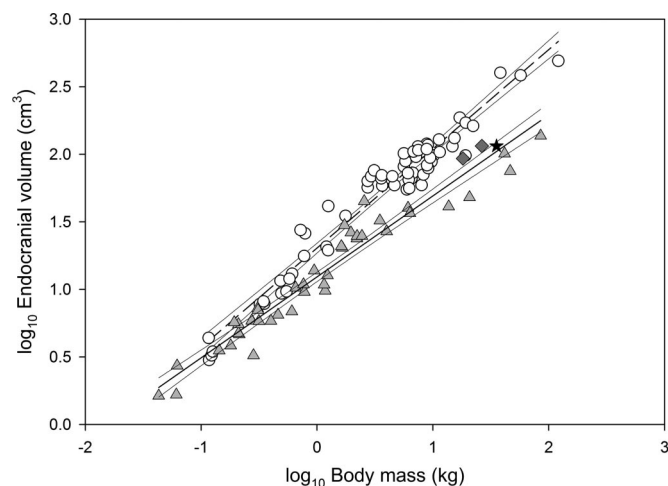


Fig. 4. Log-log plot of endocranial volume against body mass for extant primates. Least-squares linear regressions were calculated for haplorhines, open circles ($\log_{10}\text{ECV} = 0.737 \times \log_{10}\text{BM} + 1.305$; $r^2 = 0.953$) and strepsirhines, triangles ($\log_{10}\text{ECV} = 0.594 \times \log_{10}\text{BM} + 1.090$; $r^2 = 0.948$). *Hadropithecus* is indicated by the black star; *Archaeolemur* species are represented by gray diamonds; thin lines represent 95% confidence intervals. In view of these extremely high correlation coefficients, model II regressions would differ very little from the least-squares lines.

This reconstruction, together with correctly associated limb bones (7, 13) means that we have a reasonable idea of the proportions (skull, brain, teeth, thorax, and limbs) of a single individual of this peculiar strepsirhine primate. Full or partial skeletons of single individuals can, in some respects, be more important than the same number of parts from several individuals, because comparisons with whole skeletons of living taxa can be made more easily.

The locomotor adaptations of this species have been the subject of much speculation, but reconstruction of the true locomotion has been hampered by misattributions of limb bones to *Hadropithecus* and an overreliance on analogies to living cercopithecoids (14). This species was a mostly terrestrial quadruped that could undoubtedly climb but that shows no signs of suspensory or leaping adaptations (7, 13, 15). The size of the semicircular canals can be used to corroborate the locomotor reconstructions of extinct primates, and in the case of *Hadropithecus*, they show that it was less agile than living Old World monkeys (16).

One interesting comparison is with the closely related *Archaeolemur*. The species of this genus have very enlarged anterior teeth, rather than reduced ones as in *Hadropithecus*. They also have a unique shearing mechanism comprising three upper and lower premolars and have clearly bilophodont molars that resemble those of Old World Monkeys. These closely related genera appear to have very different feeding adaptations. The other comparison, suggested by Jolly (17) and generally endorsed by Tattersall (6), is with *Theropithecus gelada*. Jolly used limb proportions from Lamberton (5) that were wrongly attributed, and so that part of his argument can be discounted, but he pointed out that both species had relatively small, vertical incisors and enlarged thick-enameled cheek teeth that wear flat and make complex ridges of infolded enamel. *T. gelada* are mostly graminivorous, with grass blades, seeds, flowers, and rhizomes eaten, although they do eat other fall-back plants (18). Rafferty *et al.* (19) tentatively concluded, based on conventional microwear analysis of only two teeth, that *Hadropithecus* was decidedly not like the modern gelada baboon but probably did feed on hard objects. Godfrey *et al.* (20), using another microwear method with a sample of nine teeth, also concluded that it differed significantly from *Theropithecus* and that they were hard object feeders. J. R. Scott, *et al.* (unpublished work), using scale sensitive fractal analysis of five specimens of *Hadropithecus* tooth replicas, also supported a hard-object feeding regime. It is worth noting that $\delta^{13}\text{C}$ values from five *Hadropithecus* specimens (from four different sites in southern and western Madagascar) give a clear indication of a reliance on C4/CAM plants (8, 9), so that grass could have been part of the diet of this species. Exceptionally high $\delta^{15}\text{N}$ values (9) may suggest a preference for CAM over C4 plants, however. Codron *et al.* (21, 22) have shown that succulent plants (many of which are CAM) in South Africa can be $\delta^{15}\text{N}$ -enriched, and Loudon *et al.* (23) report heavy $\delta^{15}\text{N}$ as well as $\delta^{13}\text{C}$ values for *Lemur catta* at Tsimanampesotse, where CAM plant consumption is much greater than at Beza Mahafaly. Further research on the stable isotopes of succulent CAM plants and grasses in southern Madagascar will undoubtedly help to clarify likely dominant components of the diet of *Hadropithecus*.

The degree to which heavy microwear pitting reflects high exogenous grit as opposed to the consumption of hard foods *per se* will also require further exploration (9); the dental microstructure of *Hadropithecus* is better suited to resist tough foods than to resist hard foods (see ref. 24).

Methods

The original material in the Vienna Museum of Natural History was scanned using a Philips CT scanner in helical mode. Scan parameters for the cranium (NHMW 1934 IV 1) were: matrix of the dataset $x/y/z = 512/512/221$, voxel size = $0.29297/0.29297/0.4$ mm, 140 kV, 53 mA, ear kernel. Scan parameters for the mandibular fragments (NHMW1934 IV 2/1a,b) were: matrix of the dataset $x/y/z = 512/512/194$, voxel size = $0.21094/0.21094/0.4$ mm, 120 kV, 108 mA, inner ear kernel. The two orbital processes of the frontal bones were scanned on the HD350 medical CT scanner (Universal Systems) at the Center for Quantitative Imaging at Pennsylvania State University. They were then repositioned *in silico* without any scaling according to anatomical clues (25) into the Vienna cranium by using the imaging program *Amira* 3.1.1 (Visage Imaging). The following parts were reconstructed based on mirror imaging: right zygomatic arch; left facial portion with premolars; right second molar; right mandible, left coronoid process. The virtual reconstruction of the cranium was then produced as a real 3D model by using a Z-Corp 3-D printer (Z Corporation) in the Department of Engineering at Pennsylvania State University. The missing parts of the frontal bone over the frontal sinus, the ethmoid and sphenoid bones forming the medial wall of the orbit and temporal fossa, and small portions of the palate and zygomatic arch were conventionally reconstructed by using modeling wax and following the contours of the surrounding intact bones. The 3D model with wax reconstruction was CT scanned by using the HD350 CT at Pennsylvania State University, and the wax portion was extracted and repositioned into the Vienna cranium, again without scaling. The coronoid process of the right mandible that is figured in Lorenz von Liburnau's Plate 1 (NHMW1934 IV 2/1a) (4) has been missing for some time, perhaps even before the transfer from the Academy to the Museum or from the zoological to the geological-paleontological collection of the Museum, but it is still present on the much more fragmentary left side (NHMW1934 IV 2/1b). The coronoid from the left side was extracted, mirror imaged, and repositioned onto the right side mandible *in silico* in *Amira* 3.1.1 to create a composite right hemimandible. This entire reconstructed hemimandible was then mirror imaged to create a corresponding left-side mandible. Each of these mandibular pieces was articulated with the cranium by using the temporomandibular joints and upper teeth as a guide to proper occlusion. The missing anterior teeth and some apparent slight bilateral distortion of the cranium prevent perfect symmetry in the mandibular reconstruction. The endocranial surface of the cranium was selected using *Amira* 3.1.1 to produce a virtual endocast. The very anterior part of the braincase is missing, and so we used laser scan data of the anterior endocast of *Archaeolemur edwardsi* (AMNH 30007), which is of nearly identical size and shape to that of the Vienna skull. The volume of the endocast was calculated from the 3D reconstruction in *Amira* 3.1.1 by using the SurfaceArea measuring tool. Conventional least-squares regression analysis was performed by using body mass and endocranial volume data for a sample of modern primates from Kirk (26).

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1. Burney DA, *et al.* (2008) New findings at Andrahomana Cave, Southeastern Madagascar. *J Cave Karst Stud*, in press.
2. Lorenz von Liburnau LR (1899) A fossil anthropoid from Madagascar (translated from German). *Anz Kais Akad Wiss Wien* 36: 255–257.
3. Lorenz von Liburnau LR (1901) More extinct primates from Madagascar (translated from German). *Denkschr kais Akad Wiss Wien* 70:1–15.
4. Lorenz von Liburnau LR (1902) On *Hadropithecus stenognathus* (translated from German). *Denkschr kais Akad Wiss Wien* 72:243–254.
5. Lamberton C (1938) Contribution to the knowledge of the subfossil fauna of Madagascar. Note III. *Hadropithecus* (translated from French). *Bull Acad Malgache* 27:75–139.
6. Tattersall I (1973) Cranial anatomy of the Archaeolemurinae (Lemuroidea, Primates). *Anthropol Papers Am Mus Nat Hist* 52:1–110.
7. Godfrey *et al.* (2006) New discoveries of skeletal elements of *Hadropithecus stenognathus* from Andrahomana Cave, southeastern Madagascar. *J Hum Evol* 51:395–410.
8. Godfrey LR, *et al.* (2005) New insights into old lemurs: The trophic adaptations of the Archaeolemuridae. *Int J Primatol* 26:825–854.
9. Godfrey LR, Crowley BE, Muldoon KM, King SJ, Burney DA (2008) The *Hadropithecus* conundrum. *Am J Phys Anthropol Suppl* 46:105.
10. Hershkovitz P (1977) *Living New World Monkeys (Platyrrhini) with an Introduction to Primates* (University of Chicago Press, Chicago).

11. Rossie JB (2006) Ontogeny and homology of the paranasal sinuses in Platyrrhini (Mammalia: Primates). *J Morphol* 267:1–40.
12. Godfrey LR, et al. (2008) in *Elwyn Simons: A Search for Origins*, eds Fleagle JG and Gilbert CC (Springer, New York), pp 361–395.
13. Godfrey LR, Jungers WL, Wunderlich RE, Richmond BG (1997) Reappraisal of the postcranium of *Hadropithecus* (Primates, Indroidea). *Am J Phys Anthropol* 103:529–556.
14. Godfrey LR, Jungers WL (2002) in *The Primate Fossil Record*, ed Hartwig W (Cambridge Univ Press, New York), pp 97–122.
15. Lemelin P, et al. (2008) New hand bones of *Hadropithecus stenognathus*: Implications for the paleobiology of the Archaeolemuridae. *J Hum Evol* 54:405–413.
16. Walker A, Ryan TM, Silcox MT, Simons E, Spoor F (2008) The semicircular canal system and locomotion: the case of extinct lemuroids and lorisooids. *Evol Anth* 17:135–145.
17. Jolly CJ (1970) *Hadropithecus*: A lemuroid small-object feeder. *Man* 5:620–626.
18. Iwamoto T, Dunbar RIM (1983) Thermoregulation, habitat quality and the behavioral ecology of gelada baboons. *J Anim Ecol* 52:357–366.
19. Rafferty KL, Teaford MF, Jungers WL (2002) Molar microwear of subfossil lemurs: Improving the resolution of dietary inferences. *J Hum Evol* 43:645–657.
20. Godfrey LR, et al. (2004) Dental use wear in extinct lemurs: Evidence of diet and niche differentiation. *J Hum Evol* 47:145–169.
21. Codron D, Lee-Thorp JA, Sponheimer M, de Ruiter D, Codron J (2006) Inter- and intrahabitat dietary variability of chacma baboons (*Papio ursinus*) in South African savannas based on fecal delta C-13, delta N-15, and %N. *Am J Phys Anthropol* 129:204–214.
22. Codron J, et al. (2005) Taxonomic, anatomical, and spatio-temporal variations in the stable carbon and nitrogen isotopic compositions of plants from an African savanna. *J Arch Sci* 32:1757–1772.
23. Loudon JE, Whitelaw DC, Sponheimer M, Sauter ML, Cuzzo FP (2008) Lemurs eating isotopes: A stable isotope analysis of ring-tailed lemurs (*Lemur catta*) and their menu at the Beza Mahafaly Special Reserve. *Am J Phys Anthropol Suppl* 46:142.
24. Lucas P, Constantino P, Wood B, Lawn B (2008) Dental enamel as a dietary indicator in mammals. *BioEssays* 30:374–385.
25. Weber GW, Bookstein FL (2008) *Virtual Anthropology* (Springer, Vienna).
26. Kirk EC (2006) Visual influences on primate encephalization. *J Hum Evol* 51:76–90.