= Mesopropithecus =

Mesopropithecus is an extinct genus of small to medium @-@ sized lemur , or strepsirrhine primate , from Madagascar that includes three species , M. dolichobrachion , M. globiceps , and M. pithecoides . Together with Palaeopropithecus , Archaeoindris , and Babakotia , it is part of the sloth lemur family (Palaeopropithecidae) . Once thought to be an indriid because its skull is similar to that of living sifakas , a recently discovered postcranial skeleton shows Mesopropithecus had longer forelimbs than hindlimbs ? a distinctive trait shared by sloth lemurs but not by indriids . However , as it had the shortest forelimbs of all sloth lemurs , it is thought that Mesopropithecus was more quadrupedal and did not use suspension as much as the other sloth lemurs .

All three species ate leaves , fruits , and seeds , but the proportions were different . M. pithecoides was primarily a leaf @-@ eater (folivores) , but also ate fruit and occasionally seeds . M. globiceps ate a mix of fruits and leaves , as well as a larger quantity of seeds than M. pithecoides . M. dolichobrachion also consumed a mixed diet of fruits and leaves , but analysis of its teeth suggests that it was more of a seed predator than the other two species .

Although rare , the three species were widely distributed across the island yet allopatric to each other , with M. dolichobrachion in the north , M. pithecoides in the south and west , and M. globiceps in the center of the island . M. dolichobrachion was the most distinct of the three species due to its longer arms . Mesopropithecus was one of the smallest of the extinct subfossil lemurs , but was still slightly larger than the largest living lemurs . Known only from subfossil remains , it died out after the arrival of humans on the island , probably due to hunting pressure and habitat destruction .

= = Classification and phylogeny = =

Mesopropithecus is a genus within the sloth lemur family (Palaeopropithecidae) , which includes three other genera : Palaeopropithecus , Archaeoindris , and Babakotia . This family in turn belongs to the infraorder Lemuriformes , which includes all the Malagasy lemurs .

Mesopropithecus was named in 1905 by Herbert F. Standing using four skulls found at Ampasambazimba . He noted that the animal had characteristics of both Palaeopropithecus and the living sifakas (Propithecus) . In 1936 , Charles Lamberton defined Neopropithecus globiceps (based on one skull from Tsirave) and N. platyfrons (based on two skulls from Anavoha) . He thought that Neopropithecus was a separate , intermediate genus between Mesopropithecus and Propithecus . In 1971 , paleoanthropologist Ian Tattersall merged N. platyfrons into N. globiceps and Neopropithecus into Mesopropithecus .

Until 1986 , Mesopropithecus was only known from cranial (skull) remains from central and southern Madagascar , and because these are similar to teeth and skulls of living indriids , particularly those of Verreaux 's sifaka (Propithecus verreauxi) , Mesopropithecus was often assigned to the family Indriidae . For example , in 1974 , Tattersall and Schwartz labeled Mesopropithecus as a sister group to sifakas . With the discovery of an associated skeleton of M. dolichobrachion near Ankarana in 1986 , it became clear that Mesopropithecus shared distinct traits with sloth lemurs . Unlike the indriids , but like the sloth lemurs , they had elongated forelimbs and other adaptations for arboreal suspension (hanging in trees) , linking them most closely to family Paleaeopropithecidae . A comparison of these morphological traits between the sloth lemurs and indriids suggest that Mesopropithecus was the first genus to diverge within the sloth lemur family .

= = = Species = = =

Three species are recognized within Mesopropithecus :

M. pithecoides , described in 1905 , was the first species to be formally named . Its specific name , pithecoides , derives from the Greek word pithekos , meaning " monkey " or " ape " , and the Greek suffix -oides , meaning " like " or " form " , and reflects Standing 's impression that the animal resembled monkeys in form . It was a small to medium @-@ sized lemur , weighing approximately 10 kg (22 lb) and having an intermembral index (ratio of limb proportions) of 99 . Its skull was

similar to that of M. globiceps , but had a broader snout and was more robust , particularly in its sagittal and nuchal crests (ridges on the skull for muscle attachments) and massive zygomatic arches (cheekbones) . Its skull length averaged 98 mm (3 @.@ 9 in) , ranging from 94 @.@ 0 to 103 @.@ 1 mm (3 @.@ 70 to 4 @.@ 06 in) . It was predominantly folivorous (leaf @-@ eating) , but also consumed some fruit and (rarely) seeds . It was moderately abundant on the high , central plateau of Madagascar . It shared its range with the larger sloth lemurs , Palaeopropithecus maximus and Archaeoindris fontoynontii . One sample of its subfossil remains has been radiocarbon dated , yielding a date of 570 ? 679 CE .

M. globiceps was discovered in 1936 and originally classified in its own genus , Neopropithecus . The name globiceps comes from its prominent forehead and derives from the Latin word globus , meaning " ball " , and the New Latin suffix -ceps , meaning " head " . Like M. pithecoides , it was a small to medium @-@ sized lemur , weighing approximately 11 kg (24 lb) and having an intermembral index of 97 . It had the most narrow snout and gracile skeleton of the Mesopropithecus species , similar to but smaller than M. pithecoides , making it more like the living sifakas . Its teeth were similar to but larger than those of living sifakas , except for its lower premolars , which were shorter , and the M3 (third upper molar) , which was moderately constricted by the cheek and tongue . Its skull length averaged 94 mm (3 @.@ 7 in) , ranging from 93 @.@ 4 to 94 @.@ 8 mm (3 @.@ 68 to 3 @.@ 73 in) . It was a mixed feeder , eating fruit , leaves , and a moderate amount of seeds , having a diet similar to that of the living indri (Indri indri) . Although its forelimbs were more like those of living indriids , its hindlimbs and axial skeleton (skull , spine , and ribs) were more specialized for suspension , as in Palaeopropithecus and Babakotia . It was found in the south and west of Madagascar . Three samples of its subfossil remains have been radiocarbon dated , yielding dates of 354 ? 60 BCE , 58 ? 247 CE , and 245 ? 429 CE .

M. dolichobrachion was discovered in 1986 and formally described in 1995 . It was found in the caves of Ankarana , northern Madagascar , around the same time that the first remains of Babakotia were unearthed . The species name dolichobrachion is Greek , coming from dolicho- (" long ") and brachion (" arm ") , and means " long @-@ armed " . It was a medium @-@ sized lemur , slightly larger than the other two members of its genus , weighing approximately 14 kg (31 lb) . It differed significantly from the other two in its limb proportions and its postcranial morphology . Most notably , it was the only species in the genus to have forelimbs that were longer than the hindlimbs , due to a substantially longer and more robust humerus (yielding an intermembral index of 113) , as well as more curved phalanges (finger and toe bones) . For these reasons , it is thought to have been more sloth @-@ like in its use of suspension . This was further supported by a study of a single lumbar vertebra . This vertebra was similar to that of Babakotia in having a moderately reduced , dorsally oriented spinous process and a transverse processes (plates of bone that protrude from the vertebrae) that points to the side (laterally) . The vertebra was intermediate in length when compared with other sloth lemurs , and its laminae (two plates of bone that connect to the spinous process) were not as broad as seen in Palaeopropithecus . In M. dolichobrachion , skull length averaged 102 mm (4 @.@ 0 in) , ranging from 97 @.@ 8 to 105 @.@ 5 mm (3 @.@ 85 to 4 @.@ 15 in) . The only notable difference from the two other species in its teeth was that the third upper molar had a relatively wider trigon and smaller talon (groups of cusps on the molar teeth) . It was a mixed feeder , eating leaves , fruits , and seeds . This species was more of a seed predator than the other two species , but was not as specialized as closely related Babakotia radofilai . M. dolichobrachion was rare and shared its range with two other sloth lemurs , Babakotia radofilai and Palaeopropithecus maximus . It was the most distinct member of its genus and was geographically restricted to the extreme north of the island .

= = Anatomy and physiology = =

The genus Mesopropithecus includes some of the smallest of the recently extinct subfossil lemurs , but all species were still noticeably larger than all living (extant) lemurs . They ranged in weight from 10 to 14 kg (22 to 31 lb) . They were also the least specialized of the sloth lemurs , more closely resembling living indriids in both skull and postcranial characteristics . Skull length ranged

from 93 @.@ 4 to 105 @.@ 5 mm (3 @.@ 68 to 4 @.@ 15 in) . The dentition and cranial proportions , however , more closely resembled those of the sifakas . The dental formula of Mesopropithecus was the same as in the other sloth lemur and indriids : either 2 @.@ 1 @.@ 2 @.@ 31 @.@ 1 @.@ 2 @.@ 3 or 2 @.@ 1 @.@ 2 @.@ 32 @.@ 0 @.@ 2 @.@ 3 × 2 = 30 . Mesopropithecus had a four @-@ toothed toothcomb , like all indriids and most other sloth lemurs . It is unclear whether one of the permanent teeth in the toothcomb is an incisor or canine , resulting in the two conflicting dental formulae . Like other sloth lemurs and indriids , Mesopropithecus had rapid tooth development .

Despite the similarities , there are several features that distinguish Mesopropithecus skulls from those of living indriids . The skull , including the zygomatic arch , is more robustly built . The temporal lines join together anteriorly into a sagittal crest and there is a distinct nuchal ridge that joins the rear of the zygomatic arch . The skull has a more rounded braincase , slightly smaller and more convergent orbits , more pronounced postorbital constriction (narrowing of the skull behind the eye sockets) , more robust postorbital bar (bone that encircles the eye socket) , a steeper facial angle , more robust and cranially convex zygomatic bone , and a broader , squared snout . The upper incisors and canines are larger . The more robust mandible (lower jaw) and mandibular symphysis (point where the two halves of the lower jaw meet) suggest a more folivorous diet , which requires extra grinding . The orbits are as large (in absolute size) as those in smaller living indriids , which suggests low visual acuity . Mesopropithecus and its closest sloth lemur relative , Babakotia , did share a few ancestral traits with indriids , unlike the largest sloth lemurs , Palaeopropithecus and Archaeoindris . These include the aforementioned four @-@ toothed toothcomb , an inflated auditory bulla (bony structure that encloses part of the middle and inner ear) , and an intrabullar ectotympanic ring (bony ring that holds the eardrum) .

While the skull of Mesopropithecus most closely resembles that of modern sifakas , the postcranial skeleton is quite different . Rather than having elongated hindlimbs for leaping , Mesopropithecus had elongated forelimbs , suggesting they predominantly used quadrupedal locomotion , slow climbing , with some forelimb and hindlimb suspension . In fact , they were the most quadrupedal of the sloth lemurs , having an intermembral index between 97 and 113 , compared to the lower value for indriids and higher values for the other sloth lemurs . (In arboreal primates , an intermembral index of 100 predicts quadrupedalism , higher values predict suspensory behavior , and lower values predict leaping behavior .) Wrist bones found in 1999 further demonstrate that Mesopropithecus was a vertical climber and the most loris @-@ like of the sloth lemurs . Analysis of a lumbar vertebra of M. dolichobrachion further supported this conclusion .

Our understanding of the morphology of Mesopropithecus has not always been so complete . Until recently , important pieces of the skeleton had not been discovered , including the radius , ulna , vertebrae , hand and foot bones , and the pelvis . In 1936 , Alice Carleton mistakenly associated postcranial remains of the diademed sifaka (Propithecus diadema) from Ampasambazimba with Mesopropithecus pithecoides and came to the false conclusion that its morphology was like that of a monkey . This mistaken attribution was corrected in 1948 by Charles Lamberton .

= = Distribution and ecology = =

Mesopropithecus species appear to have been generally rare within their wide range . Collectively , the three species have been found in the north , south , west , and center of Madagascar , although they appear to have been geographically separated (allopatric) from each other . Subfossil discoveries indicate that they lived in the same region (sympatric) with other sloth lemurs in the north and center of Madagascar . The subfossil remains of M. globiceps have been found at seven subfossil sites on Madagascar : Anavoha , Ankazoabo @-@ Grotte , Belo sur Mer , Manombo @-@ Toliara , Taolambiby , Tsiandroina , Tsirave . The subfossil remains of both M. pithecoides and M. dolichobrachion have only been found at one site each , Ampasambazimba and Ankarana respectively .

M. pithecoides from the central plateau was a specialized leaf @-@ eater (folivore) , but the other two species had a more mixed diet , eating fruits and seeds in addition to leaves . The level of seed

predation varies between the three species , with tooth wear indicating that M. dolichobrachion exhibited the greatest level of seed predation within the genus .

= = Extinction = =

Because Mesopropithecus died out relatively recently and is only known from subfossil remains , it is considered to be a modern form of Malagasy lemur . It may have been among the last subfossil lemurs to go extinct , possibly surviving until 500 years ago , although radiocarbon dating places the most recent remains at 570 ? 679 CE for a M. pithecoides from Ampasambazimba . The arrival of humans roughly 2 @,@ 000 years ago is thought to have sparked the decline of Mesopropithecus through hunting , habitat destruction , or both .