

Fossils explained 51

Sloths

Today, sloths are a poorly known group of herbivorous mammals represented by only two genera and six species which are restricted to the tropical forests of South and Central America (Fig. 1). Their fossil record is long, ranging from the Eocene to the present, and reveals a previously far more diverse, widespread group. Some 90 or more genera of sloths are known from the fossil record of South, Central and North America as well as the Caribbean and Antarctica, making them a large and important group of fossil mammals. While sloths were once divided into two distinct groups (ground sloths and tree sloths), abundant evidence now shows that tree sloths are not a natural group. Furthermore, certain sloths traditionally regarded as 'ground sloths' were quite probably capable of climbing. A number of assumptions that one might make about fossil sloths – such as that they were all terrestrial, or physically big – have been challenged by recent discoveries.

Sloth stereotypes

The stereotypical fossil sloth is *Megatherium americanum* from Pleistocene South America, a species first described by George Cuvier in 1812 for a skeleton collected in Argentina. *M. americanum* was huge (Fig. 2), reaching 6 m in length and weighing more than 4 tonnes (it was exceeded in size only by its close relative *Eremotherium*), but by no means was giant size true of all fossil sloths. The majority of forms seem to have been similar in size to a large bear (approximately 2.5 m long and 800 kg) and many were smaller. Some were less than 1 m long and *Neocnus toupiti* from Pleistocene Haiti was even smaller than any of the extant tree sloths.

Almost as important in the history of vertebrate palaeontology as *Megatherium* is the North American sloth *Megalonyx*, conventionally stated to have been named by Thomas Jefferson in 1799. Alas, this historical nugget is not correct (the genus was actually named by Richard Harlan in 1825) but it is true that Jefferson imagined *Megalonyx* to be a giant lion-like cat, and to have still survived in the North American wilderness.

Relatives and origins

Sloths are part of the placental mammal group Xenarthra (also containing armadillos and anteaters), a group identified by the presence of unique accessory articulations on their vertebrae called xenarthrales. Within Xenarthra, sloths seem to be more closely related to anteaters than to armadillos. Exactly how xenarthrans are related to other placental mammals is controversial. Radical rearrangements of the placental mammal family tree have recently been suggested by molecular studies and, according to these, xenarthrans might either be most closely related to Afrotheria (that includes elephant shrews, armadillos, seacows and elephants), or Boreoeutheria (that includes primates, rodents, carnivores and ungulates).

Exactly which taxonomic name should be used for

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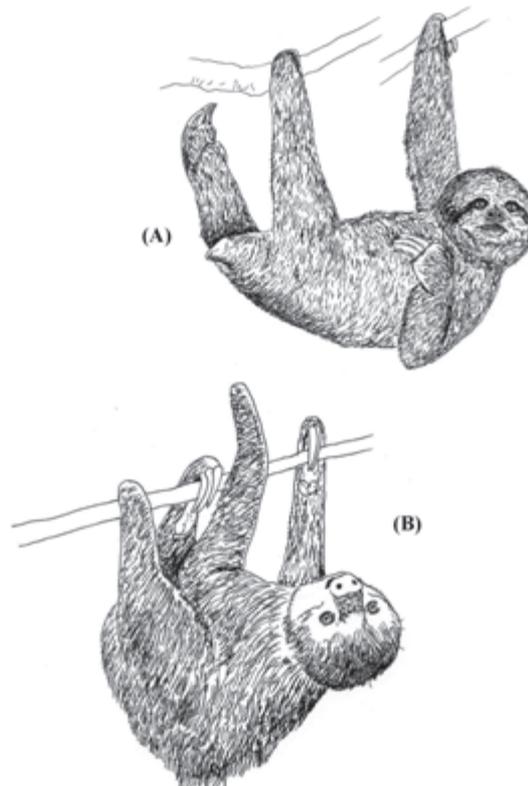


Fig. 1. Representatives of the two living sloth genera. **a.** *Bradypus*. **b.** *Choloepus*. Both inhabit South and Central America and achieve a total length of 40–80 cm. Despite their strong overall similarity, the two belong to radically disparate branches of the sloth family tree (see Fig. 9).

Fig. 2. Skeleton of the huge Pleistocene megatheriid *Megatherium americanum* (total length c. 6 m). Note the bulge on the lower jaw that housed the long tooth roots. Photograph used with permission, courtesy of the Natural History Museum, London.



sloths is mildly controversial, with most workers using *Tardigrada* Brisson, 1762 for the group. However, the name *tardigrade* is more usually applied to the invertebrates also known as water bears. Partly as a consequence of this problem, some workers have argued that *Phyllophaga* Owen, 1842 should be used instead.

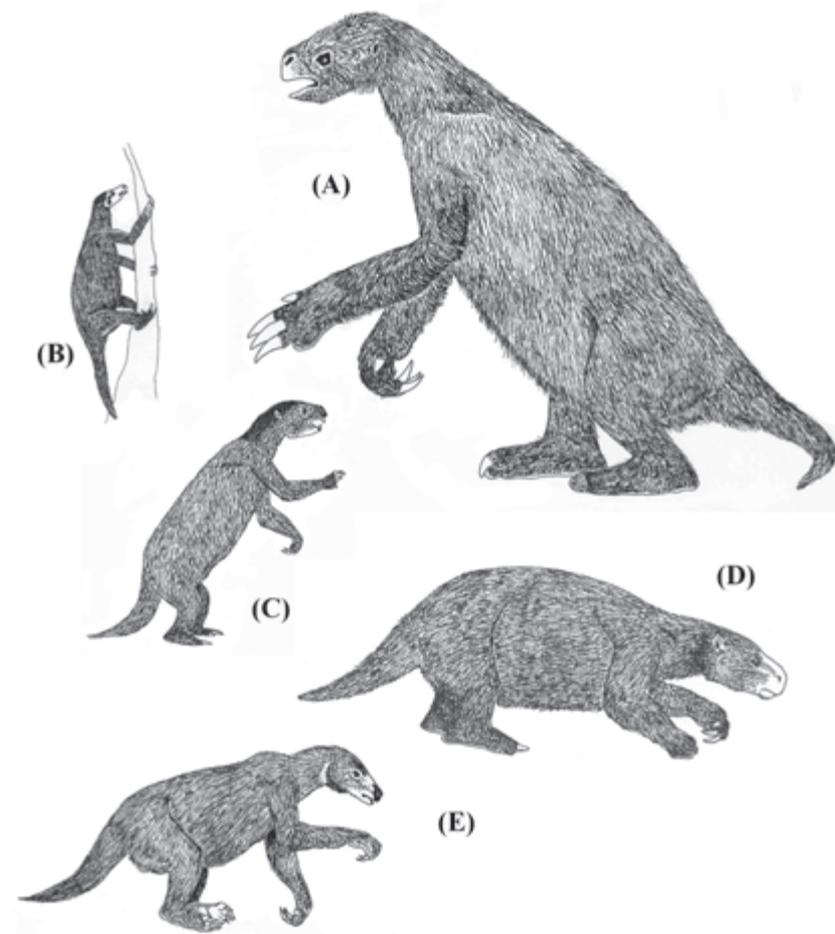
Sloths have conventionally been regarded as exclusively American. However, the recent discovery of an Eocene sloth from Seymour Island, Antarctica, reveals a wider distribution of the group and raises the possibility that xenarthrans did not originate in South America as has long been thought. As early as the Oligocene, sloths had colonized the Greater Antilles as far east as Puerto Rico, apparently via a short-lived land-span (known as the Greater Antilles–Aves Rise, or ‘GAARlandia’) connected to north-western South America. Although it is often stated that sloths only migrated to North America once the Panamanian Isthmus had formed about 2.5 million years before present, the oldest North American sloths (the mylodontid *Thinobadistes* and the megalonychid *Pliometanastes*) are actually from the Late Miocene, and thus predate the land bridge by several million years. Presumably these sloths swam to North America! By the end of the Pleistocene there were sloths as far north as Alaska.

Sloths in the Holocene

Ground sloths were contemporaries of humans for thousands of years, and archaeological evidence indicates that sloths like *Megalonyx* were hunted by Palaeoindian people. The discovery in 1888 of pieces of *Mylodon* hide inside an apparently walled-in Argentinian cave called variously Cueva Eberhardt, Cueva de Milodon or Cueva Ultima Esperanza, has led to the proposal that these sloths had been kept captive by people, and perhaps farmed. However, the supposed wall turned out to be part of the collapsed cave roof, and radiocarbon dating showed that humans and sloths did not use the cave at the same time. Ground sloths on the American mainland do

Fig. 3. Life restorations of a diversity of fossil sloths. **a.**

Eremotherium, a Pleistocene megatheriid from both South and North America. **b.** *Hapalops*, a Miocene megatherioid from South America. **c.** *Megalocnus*, a megalonychid from Pleistocene Cuba and Hispaniola. **d.** *Mylodon*, a Pleistocene mylodontid from South America. **e.** *Nothrotheriops*, a Pleistocene nothrotheriid from North America. Only drawn approximately to scale.



not seem to have survived to more recently than about 8600 years before present but it appears that two sloths from Haiti, *Synocnus comes* and *Parocnus serus*, survived to as recently as 500 years before present. Their remains have been discovered in association with pottery and the bones of domestic pigs.

A minority view among zoologists today is that one ground sloth species may survive, the enigmatic mapinguari of the Amazon. While the mapinguari's coarse reddish fur, armour-studded skin and massive hand claws make it sound something like a sloth, attributed to it are a number of fantastic features that cast doubt on its reality. These include the presence of a mouth-like organ on its belly that secretes a noxious gas and a frightening voice that sounds like a jet engine.

Sloth morphology

A typical fossil sloth can be imagined as a rather bear-shaped, shaggy-furred mammal with particularly powerful forelimbs, a barrel-shaped ribcage, a stout tail, prominent curved hand and foot claws and a markedly broad, robust pelvis (Fig. 7).

Sloth skulls are diverse in form and range from the deep and broad, snub-faced morphology seen in *Bradypus* and derived megalonychids, to the elongate almost horse-like skulls of megatheriids and others (Fig. 4). Some megalonychids had a domed cranium resulting from marked enlargement of the sinuses within the frontal bones. The sloth palate is rough and covered in pits and grooves and there are distinctive deep laminae that descend ventrally from the pterygoid bones. The tip of the sloth mandible is usually spout-shaped and there is a foramen, representing an external opening of the mandibular canal, on the side of the lower jaw. In sloths with particularly long-rooted teeth there is a distinct bulge on the ventral margin of the lower jaw (Fig. 2).

Sloths have peculiar teeth. They do not possess deciduous teeth, having instead a single set of open-rooted teeth that grow continuously throughout life. As such, the lack of a replacement dentition has made it difficult to compare sloth teeth with those of other mammals. Incisors are absent, and it is not really possible to distinguish between the similar premolars and molars. The living tree sloth *Choloepus*, as well as some mylodontids, megalonychids and nothrotheriids, possess canine-like teeth which are distinctly separated from the other teeth. In the Pleistocene megalonychid *Megalocnus* (Fig. 3c) from Cuba, and in certain other genera, the two most anterior upper jaw teeth are more like incisors than canines.

Sloth teeth lack enamel and are composed instead

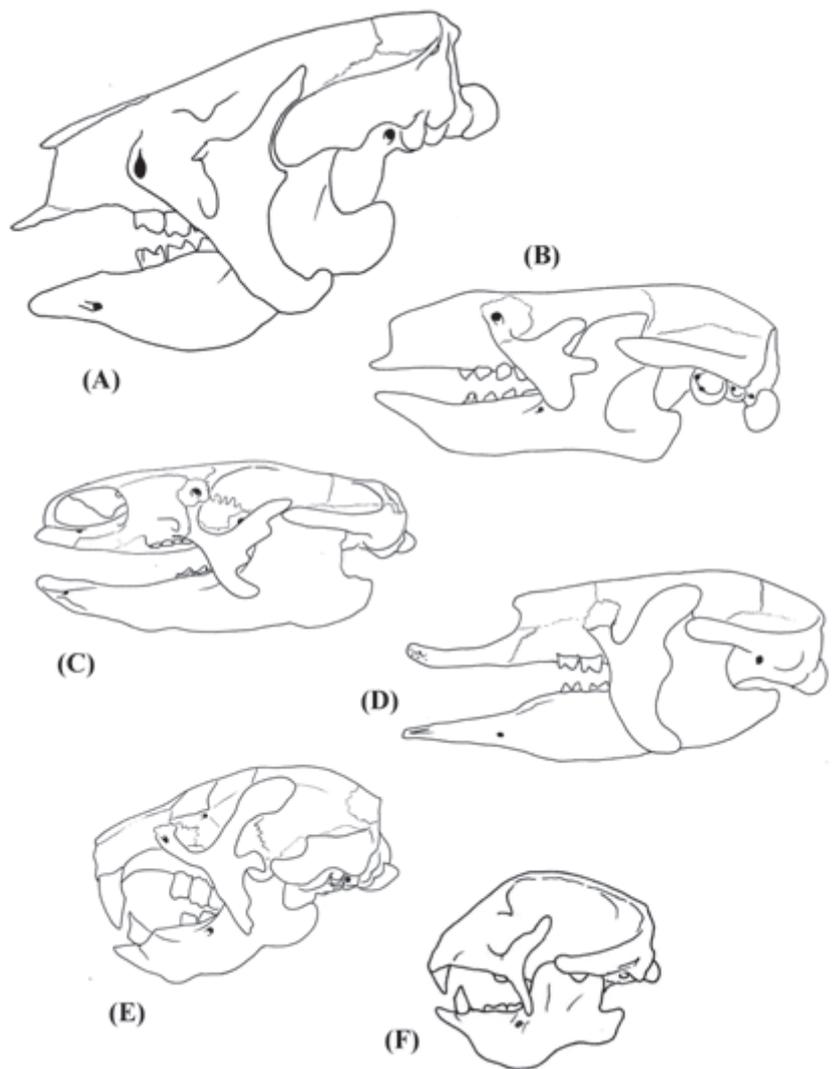


Fig. 4. Skulls from various representative sloths. **a.** *Eremotherium*, a Pleistocene megatheriid known from both South and North America. **b.** *Nematherium*, a mylodontid from Early Miocene South America. **c.** *Scelidotherium*, a scelidotheriine mylodontid from the Pliocene and Pleistocene of South America. **d.** *Thalassocnus*, a nothrotheriid from the Miocene and Pliocene of the Pacific coast of South America. **e.** *Acratocnus odontrionus*, a choloepodine megalonychid from the Pleistocene of Puerto Rico. **f.** *Acratocnus simorhynchus*, an even shorter-snout choloepodine, from the Pleistocene of Hispaniola. Not to scale, redrawn from various sources.

of two different kinds of dentine plus an outer layer of cementum, the softer dentine forming the innermost region of the tooth. The teeth in a sloth's upper jaw do not occlude with those in its lower jaw in the standard 'one to one' mammalian way. Instead, each upper jaw tooth occludes with two lower jaw teeth. Furthermore, when sloth teeth erupt they are devoid of the cusps and basins normally seen in mammalian teeth and are simple and cylindrical in form. Some fossil sloths had squarish or sub-rectangular teeth and, in these forms, transverse ridges and adjacent valleys are particularly prominent.



Fig. 5. Arm of the mylodontid *Glossotherium* from Pleistocene South America. This genus shares with several other mylodontids wide and relatively straight claws, and robust forelimb bones that possess massive muscle attachment sites and high strength values. These features suggest proficient digging abilities.

The forelimbs of most sloths are about subequal in length to the hindlimbs, the most prominent exceptions being the long-armed tree sloths of the genus *Bradypus*. Mylodontids had a particularly prominent process on the ulna. Recent studies have shown that the length of this process, the olecranon, relative to the rest of the ulna is a good indicator of digging ability in mammals as it provides the attachment area for the triceps, the main muscle used in digging. Forelimb bone strength in mylodontids was also high and shows that the forelimbs were resistant to impact with the ground. Furthermore, the wide, straight and relatively flat claws of these sloths resemble those of living mammals that dig (Fig. 5). Accordingly, mylodontids seem to have been proficient diggers that unearthed roots and tubers and they may even have constructed burrows.

Sloths are amazingly diverse and unusual in hand morphology (Fig. 6). Among megatheriids, primitive species of *Eremotherium* had five digits (albeit it with a short thumb and a fifth digit with only one phalanx) while later *E. laurillardi* was tridactyl, possessing only digits III–V (Fig. 6c).

The sloth pelvis is massive and broad (Fig. 7) and unusual in that the ischia are connected to the vertebral column (in most tetrapods only the ilia are connected), a feature that sloths share with all other xenarthrans with the sole exception of *Cyclopes*, the pygmy anteater. The femur in fossil sloths varies from robust to very robust, with the femora of giant megatheriids being almost rectangular (Fig. 7). The tibia in most fossil sloths is proportionally short and is also massively constructed. As is true of the hand, some sloth groups reduced the number of toes with only three present in some megatheriids (Fig. 8).

Mummified sloth skin preserved in the arid caves of Chile, Argentina, Arizona and Nevada provides excellent information on ground sloth skin and fur. Small bony ossicles were embedded in the skin of the mylodontids *Myllodon*, *Glossotherium* and *Paramylodon*, and probably also in *Eremotherium*, but are definitely not present in the mummified skin of *Nothrotheriops*. The fur itself was either yellowish or reddish brown.

Locomotion and posture

The configuration of the ground sloth foot and ankle indicates that most of these animals were plantigrade (that is, they placed the entire surface of the foot on the ground). However, it was argued as early as the 1840s that at least some ground sloths walked with a pedolateral foot posture: that is, with most of the weight supported by the outer margins of the feet. This bizarre configuration meant that the dorsal

surface of the foot faced laterally (Fig. 8).

The centre of gravity in the ground sloth body and the strength of their hindlimb bones, pelvis and vertebrae indicate that at least some forms could walk bipedally and fossil trackways confirm this. Most sloths have hands and hand claws that appear well suited for the manipulation of foliage and the robust tail seen in most fossil sloths suggests that they may have sat in a tripod posture when foraging and eating. The tripod abilities of ground sloths have proved inspirational to palaeontologists working on other fossil tetrapod groups.

Living tree sloths are good swimmers so it seems reasonable to assume that ground sloths were too. However, a few fossil sloths reveal morphological features which indicate that they were habitual, rather than occasional, swimmers and amphibious habits have been suggested for both scelidotheriine mylodontids and nothrotheriids. As discussed below, one group of nothrotheriid seems to have been truly semi-aquatic.

The diversity of fossil sloths

Recent work indicates that the living three-toed sloths (*Bradypus*) are most closely related to all other sloths, a group named Eutardigrada (Fig. 9). Three-toed sloths are superficially similar to two-toed sloths (*Choloepus*), a remarkable case of convergent evolution. An interesting consequence of this discovery is that *Bradypus* has a ghost lineage extending back to the Eocene at least. In the classification used here, Eutardigrada consists of four family-level groups, the mylodontids, megatheriids, nothrotheriids and megalonychids. A fifth family-level group, Orophodontidae, has been named for sloths that are probably part of Mylodontidae.

Mylodontids, best known for the Pleistocene South American genus *Myllodon*, appear to be the most primitive eutardigrades and seem mostly to have been medium-sized ground-dwelling sloths, some of which were accomplished diggers. They include the scelidotheriines, a Pliocene–Pleistocene group characterized by broad molar teeth, the Miocene–Pleistocene lestodontines, and *Paramylodon*, well known thanks to the well-preserved remains discovered in the Californian Rancho la Brea tar pits.

Nothrotheriids include the amphibious sloths of the genus *Thalassocnus* and the Shasta ground sloth *Nothrotheriops* (Fig. 3e). *Nothrotheriops* became extinct about 11 000 years ago and is well represented by hundreds of bones discovered in the south-western USA. The abundant dung produced by this sloth has been discovered and analyzed. Nothrotheriids have long been a controversial group to classify, but it now appears that Nothrotheriidae

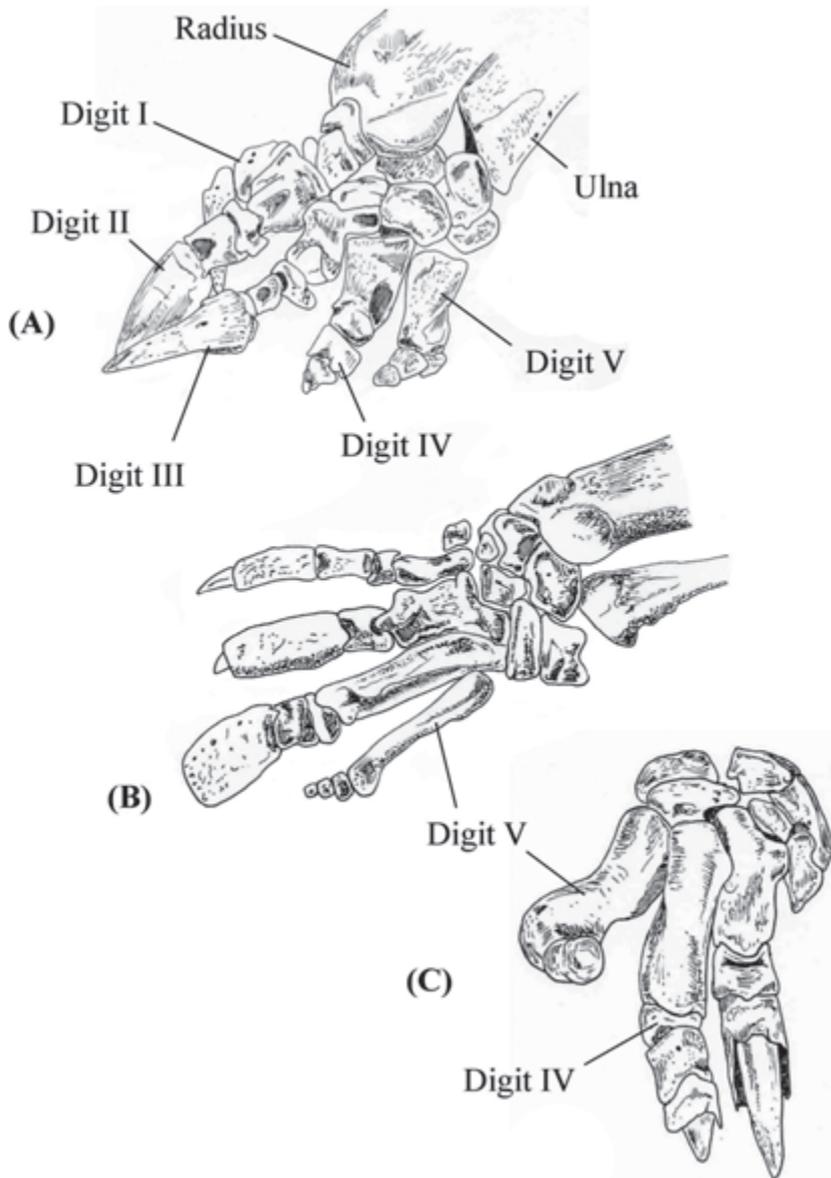


Fig. 6. Several sloth hands, chosen to depict the diversity in sloth digital formula. **a.** Pleistocene mylodontid *Glossotherium robustum*, in which the hand is pentadactyl. **b.** Pleistocene megatheriid *Megatherium americanum*, in which the thumb is absent. **c.** Pleistocene megatheriid *Eremotherium laurillardii*, in which digits I and II have been lost. Not to scale, redrawn from various sources.

was most closely related to Megatheriidae (Fig. 9).

One of the most surprising discoveries made in sloth palaeontology concerns a nothrotheriid lineage from the Pacific coast of South America. These sloths, all belonging to the genus *Thalassocnus*, are tremendously abundant within the Miocene and Pliocene marine sediments of the Pisco Formation and are associated with a fossil fauna of fish, whales, penguins and other sea creatures. The terrestrial environment adjacent to the former shoreline of the region appears to have been a barren desert, and thus these sloths were apparently coastal animals that ate marine vegetation. *Thalassocnus natans*, the first species to be described, exhibited snout bone features suggesting the presence of a prehensile lip like that seen in living seacows and hind limb and tail bone features recalling those seen in swimming rodents

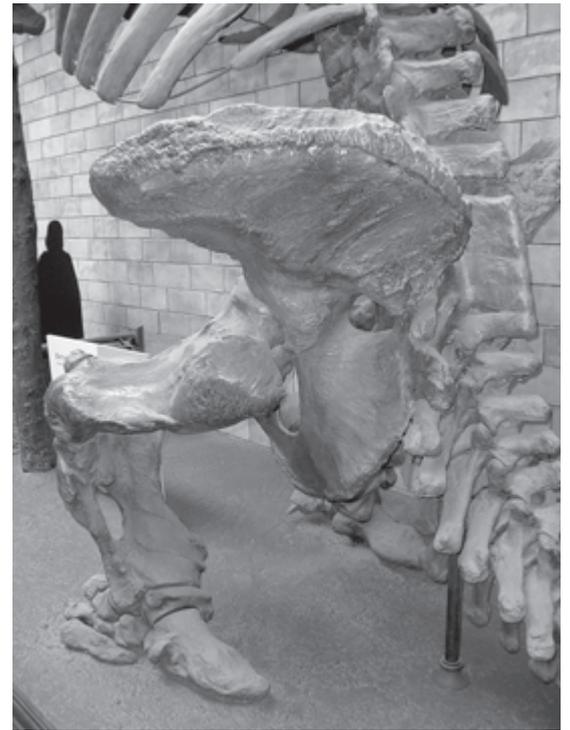


Fig. 7. The broad, flaring pelvis and proportionally short, robust left hindlimb of the giant megatheriid *Megatherium americanum*. As is typical for xenarthrans, the ischium in *Megatherium* has a bony connection with the tail vertebrae. The human silhouette at the left gives a sense of scale. Photograph used with permission, courtesy of the Natural History Museum, London.

and other amphibious mammals. Perhaps it rested on the land and, two or three times during the day, swam out to feed on kelp or sea grass. One member of this group, *T. carolomartini*, carried these trends to an extreme by having a markedly elongate snout, a broad spatulate tip to its lower jaw, and postcranial bones that resembled those of a sea-lion more than those of a sloth. It may therefore have spent much more time swimming at sea than *T. natans*. Incredible as it may seem then, from the late Miocene into the early Pliocene, the beaches and shorelines of Peru were home to hundreds of amphibious sloths.

Megatheriids include the most famous fossil sloth, *Megatherium*, as well as its giant relative *Eremotherium* (Fig. 3b). *Megatherium* first appeared in the early Pliocene of Bolivia and there is some indication that different *Megatherium* species inhabited different palaeo-environments, with some known only from high altitude regions and others from temperate lowland environments.

Finally, megalonychids include the arboreal two-toed sloths (*Choloepus*), and hence are still around today. Most of the group's key features are related to their canine-like teeth. Basal megalonychids like *Megalonyx* were large, terrestrial sloths (body length



Fig. 8. Right foot of the giant megatheriid *Eremotherium*. Though this is how the foot looks in lateral view: the lateral surface of the foot is the anatomical dorsal surface. Only digits III-V were present in this sloth, and of these only digit III possessed a claw (this was curved toward the midline, and its tip is thus not visible in lateral view).

c. 3 m) but the most derived members of the group appear to have become increasingly suited for arboreal life, a trend that culminated in *Choloepus*. Many of these derived megalonychids were endemic forms unique to the Greater Antillean islands and include the smallest (*Neocnus*) and youngest (*Synocnus* and *Parocnus*) of fossil sloths. While cladistic studies show that megalonychids are the youngest major sloth clade, the oldest reported member of this group is from the Middle Eocene of Seymour Island, Antarctica. If this Eocene sloth really is a megalonychid, then all of the major divergences within sloth phylogeny must have occurred at or prior to this time.

Fossil sloth biology, behaviour and lifestyle

Little direct data is available on fossil sloth behaviour and lifestyle. However, because the living sloths

phylogenetically bracket the fossil ones, we can make some reasonable inferences about fossil sloth behaviour based on what we know about the living species. Living sloths are long-lived for their size (*Choloepus* weighs 4–8.5 kg, yet individuals have lived in captivity for more than 30 years), use their hand claws in self-defence, give birth to a single baby that clings to the mother, and do not appear to be particularly sociable. Sloths have been described as having ‘an extreme tenacity to life’ and are reportedly capable of surviving injuries that would kill most other mammals. Conceivably, the same behavioural traits were true of fossil sloths.

Reconstructing other aspects of fossil sloth palaeobiology is problematical however because the similarities seen in living sloths may be convergent responses to a similar leaf-eating lifestyle, rather than attributes common to all sloths. Living sloths are notoriously slow-moving and sluggish and possessed of an extremely slow metabolism, their metabolic rates being only 40–45 per cent of those expected for a mammal of their body size. All living sloths share large, multi-compartmented stomachs that house symbiotic cellulose-digesting bacteria. Digestion is slow, with food remaining in the stomach for more than a month in some cases.

Both two-toed and three-toed sloths have specialized hairs that encourage the growth of blue-green algae. In *Choloepus*, the algae grow in longitudinal grooves in the hairs, while in *Bradypus* there are transverse cracks that become progressively wider with age. During the wetter parts of the year, the algae bloom and the sloths turn green. Moths eat the algae and birds eat the moths. Again, it remains unclear whether this is a convergent feature unique to living tree sloths, or whether extinct sloths also grew algae on their fur. Extinct sloths for which hair is known lack either the longitudinal grooves or transverse cracks seen in living forms, but the remains of powdery green algae have been discovered on the hairs of some extinct sloths, so this relationship may have been widespread after all.

Because some mylodontids exhibit the forelimb features indicative of good digging abilities, it has been proposed that sloths like *Glossotherium* and *Scelidotherium* were the creators of the giant burrows preserved in the Pleistocene sediments of Argentina. These burrows are more than a metre tall, almost 2 m wide, and in some cases more than 20 m long. The sides and roofs of these burrows are scored with

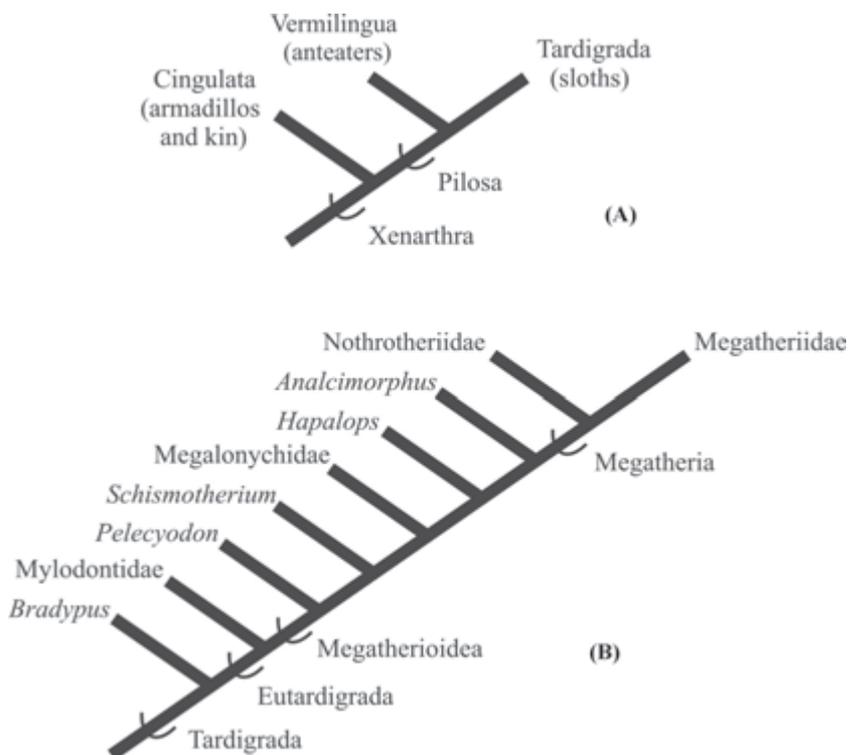


Fig. 9. Cladograms representing the affinities of, and between, sloths. **a.** The major divergences within Xenarthra, the placental mammal clade that includes sloths and their relatives. **b.** The phylogeny of sloths, simplified to show only the major divergences. Based on Gaudin (2004).

parallel claw marks. While the idea of large animals creating or dwelling in giant burrows may seem outlandish, living bears create cave-like dens and it has recently been discovered that pygmy hippos also dig giant burrows. The preservation of sloth bones and dung in caves suggests that some species sought refuge in these shelters, or perhaps entered the caves to mine for salt. The latter behaviour is widespread in living mammals, being most famously practised by the elephants living near Kenya's Mount Elgon.

Some ground sloth species appear to exhibit pronounced sexual dimorphism: in *Eremotherium laurillardii* presumed males are about 50 per cent bigger than presumed females.

Sloth diet

Ground sloths have conventionally been regarded as strict herbivores that used their powerful forelimbs and large curved claws to manipulate foliage, and evidence from sloth morphology and fossil dung supports this view. It remains possible, however, that some species were omnivorous, occasionally consuming carrion and small animals.

One of the most bizarre suggestions made about any fossil sloth is the proposal that *Megatherium* was an active carnivore, adept at stabbing and dispatching large herbivores. This hypothesis rests entirely on the discovery that the forelimb anatomy of *Megatherium* would have allowed it to perform both rapid, powerful forelimb strikes and the carrying of heavy loads. This idea seems extraordinarily unlikely however as all the morphological details of this giant, slow moving animal are clearly in agreement with the more conventional concept of it as a herbivore. If *Megatherium* and other sloths were capable of deploying rapid forelimb strikes, it seems logical that they did so to defend themselves from the large and formidable carnivorans they were contemporaneous with: giant lions, dire wolves, sabre-toothed cats, short-faced bears and so on.

Good evidence for the true diets of fossil sloths comes from their fossil dung. Some sloth dung, despite being 11 000 or so years old, looks and smells fresh and will even burn. DNA extracted from dung samples matches that recovered from bones, so in some cases dung can be referred with confidence to a sloth species, and this has been done with dung belonging to *Nothrotheriops shastensis*. DNA analysis of the plant fragments within the *N. shastensis* dung show that this animal fed on an impressive diversity of plant species ranging from pines, grapes and roses to mints, grasses and lilies, though with different species being favoured according to their availability at the time.



Fig. 10. Skull of the mylodontid *Glossotherium* from Pleistocene South America. This sloth exhibits a particularly deep, broad snout and a broad tip to the lower jaw. Photograph used with permission, courtesy of the Natural History Museum, London.

Suggestions for further reading

- Bargo, M.S., Vizcaíno, S.F., Archuby, F.M. & Blanco, R.E. 2000. Limb bone proportions, strength and digging in some Lujanian (Late Pleistocene-Early Holocene) mylodontid ground sloths (Mammalia, Xenarthra). *Journal of Vertebrate Paleontology*, v.20, pp.601–610.
- Cartelle, C. & De Iuliis, G. 1995. *Eremotherium laurillardii*: the Panamerican late Pleistocene megatheriid sloth. *Journal of Vertebrate Paleontology*, v.15, pp.830–841.
- Fariña, R.A. & Blanco, R.E. 1996. *Megatherium*, the stabber. *Proceedings of the Royal Society of London B*, v.263, pp.1725–1729.
- Gaudin, T.J. 2004. Phylogenetic relationships among sloths (Mammalia, Xenarthra, Tardigrada): the craniodental evidence. *Zoological Journal of the Linnean Society*, v.140, pp.255–305.
- Hofreiter, M., Betancourt, J.L., Sbriller, A.P., Markgraf, V. & McDonald, H.G. 2003. Phylogeny, diet, and habitat of an extinct ground sloth from Cuchillo Curá, Neuquén Province, southwest Argentina. *Quaternary Research*, v.59, pp.364–378.
- Muizon, C. de, McDonald, H.G., Salas, R. & Urbina, M. 2004. The youngest species of the aquatic sloth *Thalassocnus* and a reassessment of the relationships of the nothrothere sloths (Mammalia: Xenarthra). *Journal of Vertebrate Paleontology*, v.24, pp.387–397.