

# Appendix

## NOTES ON THE RECONSTRUCTIONS OF FOSSIL VERTEBRATES FROM LOTHAGAM

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**Figure 1.4.** Paw of *Lokotunjailurus emageritus*. The remarkable preservation of the manus in the Lothagam machairodont leaves no doubt as to the relative proportions of the claws. The huge dewclaw was absolutely larger than that of a modern lion of greater body size, whereas the claws of digits II to V were actually smaller than the corresponding elements in a modern leopard, which is, of course, much smaller than *Lokotunjailurus*.

To show more clearly the size differences between the claws of different digits, I have drawn the claws protracted, although during normal locomotion on the ground they would be retracted, as in modern felids. The shape and size of the claw sheaths are broadly determined by those of the ungual, or distal, phalanges. The position of the foot pads is determined by the skeletal elements of the manus: the phalangeal pads in digits II to IV are placed under the articulation between phalanges 2 and 3 of each digit, while the main pad is placed under the articulations between the metacarpals and the proximal phalanges. The carpal pad is slightly distal to the pisiform. The morphology of the main pad is constant among modern felids, and fossil footprints attributable to early felids from European sites of Early Miocene age suggest that this morphology was already well established by that time.

**Figure 4.14a.** Brevirrostrine crocodiles. These reconstructed heads are based on well-preserved skull material from Lothagam, complemented when necessary by material from other sites. In the case of *Rimasuchus lloydi*, cranial material from Koobi Fora was used to reconstruct parts of the skull that were less well preserved in the Lothagam specimens. The external features (scales, skin texture) in Lothagam *Crocodylus niloticus* and *C. cataphractus* can be safely reconstructed because there are extant representatives of both species. For the reconstruction of *Rimasuchus*, external features were modeled from extant *C. niloticus*.

**Figure 4.14b.** Longirostrine crocodiles. Skull morphology in *Euthecodon* is mostly based on Lothagam cranial material, but skulls from Koobi Fora have also been used for this reconstruction. *Eogavialis* is based on the holotype skull from Lothagam, and part of the posterior skull had to be restored. External features in *Euthecodon* are based on modern Crocodylidae, while those of *Eogavialis* follow those of *Gavialis*, the only surviving gavialid genus.

**Figure 5.1.** *Kubwaxerus pattersoni*. This restoration is based primarily on the holotype partial skeleton from Lothagam. Additional material from Lothagam, including hindlimb bones, helps provide a complete image of the animal's body proportions. External features such as coat pattern, ears, and vibrissae are based on living members of the tribe Protoxerini (African giant and sun squirrels), to which *Kubwaxerus* is closely related. *Kubwaxerus* is shown walking on the ground to reflect terrestrial adaptations of its postcranial skeleton that suggest that this animal, although largely arboreal, would have spent a significant amount of time foraging on the ground, perhaps searching for fallen nuts in the forest floor.

**Figure 6.1.** *Parapapio lothagamensis*. Although the cranial material from Lothagam provides a fairly clear picture of the head and face of this cercopithecoid, the available postcranials are fragmentary and mostly unassociated, which makes it difficult to reconstruct body proportions. Consequently, the relative proportions in this restoration are based on modern species of papionines, mostly of the genus *Macaca*. Video footage of various species of wild macaques and my own observations of captive specimens show that, like baboons (and unlike vervet monkeys), their forefeet are digitigrade while moving on the ground, although the angle of the metacarpals with the horizontal appears to be

lower than in baboons. *Parapapio* is thus shown with digitigrade hands as well.

**Figure 6.15.** Hominoidea indet. The patches of light that pass through the foliage and glint off the animal's teeth emphasize that the Lothagam hominoid is known mostly from its dentition. Consequently, this restoration is basically a hypothetical re-creation of how a hominoid close to the hominid–great ape dichotomy might look. What can be seen of the face is a combination of primitive facial features: prognathous muzzle, flattened nose, and prominent brow ridges. Although the eyes of modern chimpanzees may occasionally show a white or very light area surrounding the iris, I have deliberately avoided giving the Lothagam hominoid such a humanizing feature.

**Figure 7.1.** *Ekorus ekakeran*. The holotype skeleton from Lothagam is remarkably complete and allows very precise restoration of body proportions. Compared to the modern honey badger (*Mellivora capensis*), which is the largest extant terrestrial mustelid from Africa, the differences are many and striking in addition to *E. ekakeran*'s much larger size. Most relevant for the restoration of the fossil animal are differences in the morphology of the appendicular skeleton, including the shape of the scapula, the elbow articulation, the shape of the radius, the orientation and shape of the ilium, the morphology of the proximal femur, and the morphology and relative size of the phalanges. In all these features, *Ekorus* differs from *Mellivora* and the other badgers that are robust carnivores with an ambulatory locomotion and developed fossorial abilities. *Ekorus* more closely resembles cursorial and subcursorial carnivores like the cats and the hyenas. As a result, the articulated skeleton of *Ekorus* is restored to be more upright and gracile than that of any badger, even more than that of the wolverine *Gulo*.

In line with the relatively gracile build of *Ekorus*, I have shown the animal in a dynamic, trotting gait. Even the robust extant honey badger moves along with a steady trot during its nightly forages, as shown by video footage of wild specimens. It remains to be determined if *Ekorus* was digitigrade. The morphology of the feet suggests that, even if *Ekorus* was digitigrade, the metapodials would normally be at a low angle to the ground, so I have shown the “landing” hind foot (the left one) almost horizontal.

The muscle insertion areas in the forelimbs of *Ekorus* indicate that many of the muscles involved in fossorial activities (the teres major, along with the extensors and rotators of the forearm) were much less developed than in badgers, although in general the animal would have been more muscular than any dog or hyena, as well as more muscular than most cats.

For the coat pattern, I have used for reference the living species of terrestrial, predatory mustelids.

**Figure 7.20.** *Ictitherium ebu*. The holotype skeleton is complete enough to permit a confident restoration of body proportions. The elongation of the limb bones is striking, greater even than in the gracile living hyaenids—the striped hyena (*Hyaena hyaena*) and the aardwolf (*Proteles cristatus*). As in living hyaenids, the neck was very elongated, although it was not nearly as heavily muscled as in the larger extant species. A single lumbar vertebra indicates that, also as in living hyaenids, the back was considerably shortened. The hindlimbs were as long relative to the forelimbs as in the extant aardwolf, which implies that the back would be less sloping than in the extant spotted, brown, and striped hyenas. These proportions suggest that, as living hyaenids, *Ictitherium ebu* would normally use lateral sequence gaits for slow and medium-speed locomotion. The trot would normally not be employed because each forelimb would tend to get in the way of the advancing hindlimb of the same side in this diagonal-sequence gait. Accordingly, I have restored *Ictitherium* employing the pace, a gait often used by modern hyaenids.

The coat pattern in this restoration is based on that of modern hyaenids, especially *Hyaena* and *Proteles*, which probably retain a pattern that is primitive for the whole family. Some features incorporated in this restoration—such as the presence of stripes, especially in the legs, and the presence of long, erectile hairs in the upper neck and along the back—are present in all recent hyaenids except *Crocota* (which does have a much less developed mane). Other features—such as a dark muzzle, a rather unpatterned face, and large ears lacking a bursa—are common to all living hyaenids, and it seems thus reasonable to infer their presence in *Ictitherium*.

In contrast to this reconstruction of *Ictitherium ebu*, the skeletal restoration of *Ictitherium viverrinum* from Pikermi figured by Gaudry in the 1860s, and later reproduced in several textbooks, shows an animal with a primitive, civet-like vertebral column, with moderately long neck and long lumbar. In fact, no vertebral elements were available to Gaudry, who based his reconstruction solely on cranial and appendicular material; although his guess was a very reasonable one given the information available at the time, it now seems likely that the vertebral proportions of *I. viverrinum* were more hyena-like and less civet-like than shown in that restoration, which has been the “official” image of *Ictitherium* for generations of paleontologists.

**Figure 7.22.** *Lokotunjailurus emageritus*. As was the case with *Ekorus ekakeran* and *Ictitherium ebu*, the holotype skeleton of the Lothagam machairodont is re-

markedly complete and permits an accurate reconstruction of body proportions. *Lokotunjailurus* was a rather cursorial felid, with gracile limb bones, more elongated metapodials, and a relatively smaller head than in a modern lion. In contrast to those of later machairodonts such as *Homotherium*, the lumbar vertebrae were not particularly shortened. All these features contribute to make this an especially gracile, elegant cat. The enormous dewclaw would probably be a visible feature of the living animal in spite of being partly covered with flesh and fur (figure 1.4). The upper canines, although long and flattened, would have scarcely protruded beyond the upper lip in the living animal, at least when it had a relaxed face, as shown in this restoration.

The reconstructed coat pattern is based on that of several species of modern felids, which is probably similar to the primitive pattern for the whole family Felidae. Of course, attributing a primitive pattern to an extinct species is just a conservative, probabilistic choice, and *Lokotunjailurus* might well have developed a more derived design.

**Figure 8.1.** *Stegotrabelodon orbus*. Very little is known at present of the postcranial skeleton of *Stegotrabelodon*, so the body proportions shown in this restoration are mostly conjectural and broadly intermediate between the long-bodied, short-limbed gomphotheres and the taller living elephants. The space between the two rami of the mandible was probably occupied by a well-developed tongue, and it is very likely that the oral cavity was delimited by a well-developed lower lip.

**Figure 8.11.** *Deinotherium bozasi*. As in the case of *Stegotrabelodon*, the postcranial skeleton of *Deinotherium bozasi* is very poorly known, so for this restoration the body proportions of the better known European species *Deinotherium giganteum* were used for reference. The anatomy of the more primitive deinotherine genus *Prodeinotherium* from Africa and Europe was also studied, but it is important to remember that this was a smaller and more primitive animal, so we should be cautious when transferring some of its features to the more evolved *D. bozasi*.

The presence of a developed lower lip is suggested by the morphology of the mandible and, as in the case of *Deinotherium*, it would have helped to close the mouth and keep the food within the oral cavity during mastication. In modern elephants the lower lip appears as a continuation of the pointed shape of the toothless mandibular symphysis.

Differences in the nasal region of the skull indicate that the trunk of deinotheres was not structurally identical to that of modern elephants, and it seems likely that the muscular control of trunk movements was con-

siderably less sophisticated. In this restoration the trunk is shown as relatively shorter than in modern elephants, but still long enough to have allowed the animal to drink from shallow water holes while standing in the typical elephantine posture indicated by the graviportal anatomy of deinother forelimbs.

**Figure 8.12.** *Leptorycteropus guilielmi*. The holotype skeleton of this species is rather fragmentary, but enough is preserved to show that the animal was not only much smaller but also considerably more lightly built than the modern armadillo. The back had the arched shape typical of the extant species, but the limbs were relatively longer and less muscular. The length of the tooththrow indicates that the muzzle would have been relatively shorter. The gait shown in this restoration is the same observed in modern armadillos, a single-foot walk in diagonal sequence, but the more gracile proportions of the animal provide for a more dynamic picture.

**Figure 9.1.** *Brachypotherium lewisi*. The head of *B. lewisi* as shown in this illustration is based on the skull restoration offered by Hooijer and Patterson (1972), which was in turn based on two skulls, each of them crushed in different and somehow complementary ways. The resulting restoration showed a skull that differs from typical European brachypotheres in having a straighter and less concave, dorsal profile.

As the postcranial skeleton of *B. lewisi* is poorly known, body proportions in this restoration are mostly based on European brachypotheres, especially *Brachypotherium* (*Diaceratherium*) *aurelianense*, which is probably close to the ancestry of *B. lewisi*. The more complete remains of an earlier brachypotherine, *B. heinzeli*, from Rusinga Island, indicate that Early Miocene African brachypotheres had already developed the short-limbed anatomy characteristic of their European relatives.

**Figure 9.6.** *Eurygnathohippus turkanense*. The larger Lothagam hipparionine was a robustly built animal, as indicated by the preserved limb bones. Parts of the anatomy not preserved in the Lothagam species were restored following the well-known, and more primitive, European taxon *Hippotherium primum*.

The presence of at least some degree of striping, especially in the legs and shoulders, is possibly primitive for the Equidae and is thus incorporated in this restoration.

**Figure 9.8.** *Eurygnathohippus feibeli*. The preserved limb bones of this hipparionine (including a complete tibia and metacarpal besides more fragmentary material) show that it was not only smaller but much more gracile than *E. turkanense*.

**Figure 10.1.** *Hexaprotodon harvardi*. The limb proportions of this species can be confidently restored based on the large collection of limb bones from Lothagam, which includes many complete but isolated bones and a complete associated hind limb. These show that this animal, although unmistakably hippo-like, would have been considerably more gracile than an extant hippopotamus. Another clear difference would be the outline of the head in side view, where the orbits would not be nearly as protuberant as in the extant species.

**Figure 10.28.** *Hexaprotodon harvardi* (right) and *H. lothagamensis*. These two hippo species from Lothagam are drawn here to scale, in frontal view and with heads lowered, because it is the dorsal aspect of the head that most clearly shows the differences between them. The remains of *H. lothagamensis* are unfortunately much more fragmentary, and the anterior part of the skull is not known, but its shape can be restored with some confidence based on the preserved anterior part of the mandible. The anterior mandible of *H. lothagamensis* is comparatively very narrow, so it follows that the maxilla would have been correspondingly narrow. Besides, the lower canines are not flaring, and since the upper canines would have occluded directly with the lower ones, the position of the latter is also an indication of the maximum width of the muzzle. The resulting picture shows *H. lothagamensis* as not only distinctly smaller, but also much less hippo-like than *H. harvardi*, looking even more primitive than the extant pigmy hippo.

There are also some postcranial remains from Lothagam that, although not directly associated with cranial remains of *H. lothagamensis*, are of the right size to have belonged to this species, and so they too have been used as a reference for this reconstruction.

**Figure 10.42.** *Nyanzachoerus syrticus tulotus*, male (left) and female. The beautiful and well-preserved cranial remains from Lothagam allow an accurate reconstruction of the head of these enormous pigs. All the knobs and protuberances of the head are based on the osteological evidence, and although a little extra thickness has been added to reflect the presence of soft tissue, this has been a conservative estimate and it is possible that at least some of these protuberances would have been even more spectacular in the living animal.

The body proportions in this restoration are based on sets of associated limb bones from Lothagam and Sahabi that by their large size are likely to represent *N. syrticus*. Both samples point to a huge animal, larger than the extant giant forest hog (*Hylochoerus*), and with proportionally longer metapodials, suggesting a slightly more cursorial adaptation.

**Figure 10.47.** *Nyanzachoerus pattersoni*. Lothagam fossils assigned to this species are rather fragmentary, so this restoration is based on material from the Kenyan sites of Kanapoi and the Baringo Basin. Beautiful cranial material from these sites clearly shows the differences with *N. syrticus*, especially the enormously developed zygomatic protuberances, the more moderate ornamentations in the muzzle, and the somewhat larger tusks, all of which would be readily appreciable in the living animal. Postcranial elements from Kanapoi suggest a body plan similar to that of the earlier species.

**Figure 10.49.** *Cainochoerus* sp. Most parts of the body of this tiny suid are represented in the Lothagam sample, but unfortunately most of the elements are fragmentary. The sample of *Cainochoerus africanus* from the South African site of Langebaanweg includes many postcranial elements as well and, combining both sources, it is possible to get a reasonable picture of the cainochoeres as living animals. The Lothagam specimens were even smaller than the South African ones, so that the reconstructed height at shoulder is only 26 cm! The shape of the limb bone articulations shows that the locomotion was more cursorial than in typical pigs. This, coupled with the gracile build of the skeleton, would surely have made the living animal look remarkably similar to a modern peccary even if there was no direct relationship.

**Figure 11.1.** *Paleotragus* sp. This restoration is based mainly on the remarkable sample of *Paleotragus germani* from the Algerian site of Oued el Hammam, which includes ossicones, dental series, many complete long bones, and several vertebral elements. The resulting picture is that of a large giraffid with a reconstructed shoulder height a little over 2 meters, with considerably elongated neck and limbs that give the animal an appearance intermediate between an okapi and a giraffe. Tooth row length is absolutely longer than in modern giraffes, indicating a rather elongate head. Skull morphology is otherwise poorly known in this species, so it was restored following the better represented *Paleotragus microdon* and the closely related genus *Samotherium*, both from China.

**Figure 11.5.** Lothagam Bovidae. Complete bovid skulls are very rare, and most of these head restorations are based on frontlets or calvariae. This meant that skull shape had to be restored in each case from related forms, either fossil or extant.

The tragelaphine *Tragelaphus kyaloae* is based on a pair of horn cores from West Turkana, and the skull morphology follows that of closely related extant species like the sitatunga (*T. spekei*). The pattern of face markings is rather constant among modern tragelaphines,

including white spots on the sides and a V-shaped marking in front of the eyes, so a similar pattern is inferred for the fossil species. The texture of the horn sheaths is also borrowed from modern tragelaphines.

The two species of *Tragoportax* are restored on the basis of frontlets from Lothagam, with skull morphology following that of the better known European species of the genus, such as *T. gaudryi* from the Turolian of Spain. The pattern of face markings follows that of the extant boselaphine *Boselaphus tragocamelus*, the Indian nilgai, which, it may be noted, is similar to that of the tragelaphines except for the absence of the V-shaped frontal marking.

The horn shape of the two species of *Kobus* is based on calvariae from Lothagam, while skull morphology follows that of modern species like *Kobus kob*. The restoration of the other reduncine, *Menelekia leakeyi*, is based on horn cores from Lothagam and Koobi Fora. The convex dorsal profile of the nasals is borrowed from a closely related species, *Menelekia lyrocera*, whose skull is well known from other localities in the northern Turkana Basin. All three reduncine species are reconstructed with annulated horn sheaths, and this condition is observed in all extant members of this tribe.

The small impala, *Aepyceros premelampus*, is restored based on the holotype of the species, a beautifully preserved frontlet with horn cores. Skull morphology, horn sheath texture, and face markings are based on the extant impala (*Aepyceros melampus*).

**Figure 13.1.** Nawata Formation habitat. This restoration attempts to show the likely transition of habitats from river and riverine woodland on the left side of the scene, to edaphic grassland and more open woodland on the right. On the right side background, beyond the grassland, another thicket of woodland corresponds to a distant meander of the river or to an oxbow lake or abandoned meander. The environments are broadly similar to those found today around large African rivers like the Luangwa in Zambia and the Chobe in Botswana. The scene is set in the dry season, when ungulates like the impalas (*Aepyceros premelampus*) and large hipparions (*Eurygnathohippus turkanense*) shown here are attracted to the permanent water of the river, and thus they become more prone to predation by the large, carnivorous crocodile *Rimasuchus lloydi*. In contrast, adult *Stegotetralodon orbis* would have little to fear

from crocodiles and would wade and drink at leisure. Suids such as *Nyanzachoerus syrticus* (right, mid-distance) would frequent the transitional habitats, and the boselaphine bovids of the species *Tragoportax cyrenaicus* (right, background) would alternately graze in the floodplains and browse in the woodlands, depending on the season. Papionine monkeys of the genus *Parapapio* (center, mid-distance) would probably forage both on the ground and in the trees, seeking protection from terrestrial predators in the high branches.

**Figure 13.14.** Apak Member habitat. This scene is set in a nearly dry riverbed, where the larger mammals would gather to drink from the shrinking water holes. Bovids like *Tragelaphus kyalae* (right, foreground) and the impalas *Aepyceros premelampus* (mid-distance), would normally dwell in the gallery forest and thus be among the frequent visitors to these water holes. Water-dependent proboscideans would be attracted to the sand river; we see here the deinotheres, *Deinotherium bozasi* (left, mid-distance), and the long-tusked gomphotheres of the genus *Anancus* (right, mid-distance).

**Figure 13.15.** Kaiyumung Member habitat. Shown in the foreground is the transition zone between dry woodlands and floodplain grasslands, while in the background denser vegetation indicates the vicinity of the river. A troop of large baboons of the species *Theropithecus brumpti* appears in the foreground, while two giant pigs of the species *Notochoerus eulius* approach from the right. In life, notochoeres would be readily distinguished from members of the earlier genus *Nyanzachoerus* by their huge tusks and less prominent facial protuberances, but, like the nyanzachoeres, notochoeres were huge pigs that stood more than 1 meter at the shoulder. A white rhino of the extinct species *Ceratotherium praecox* grazes in the left mid-distance.

## References Cited

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