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GEOLOGY AND PALAEOBIOLOGY OF THE CENTRAL AND SOUTHERN NAMIB

VOLUME 2: PALAEONTOLOGY OF THE ORANGE RIVER VALLEY, NAMIBIA

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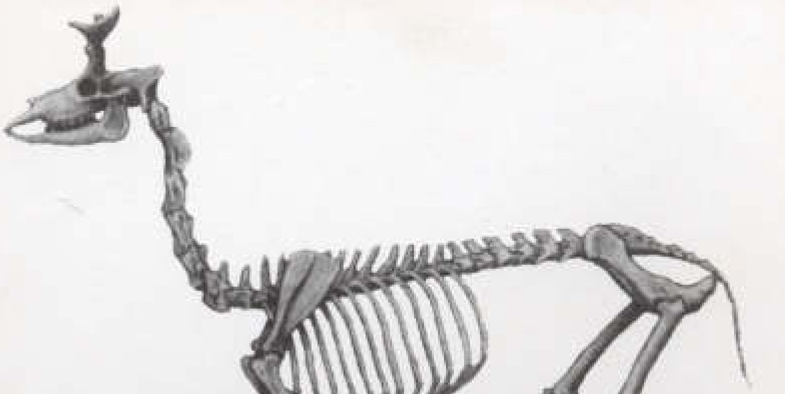

Orangemeryx hendeyi

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Reconstructing fossil mammals from Arrisdrift (17-17.5 Ma), Namibia

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Anatomical restorations of selected mammalian taxa from Arrisdrift (17-17.5 Ma), Namibia, were prepared using a methodology that combines comparative and functional anatomy with phylogenetic considerations. These reconstructions were then incorporated into a palaeo-environmental setting created with data about the ancient topography, vegetation and climate of the area around the site.

Résumé français

Les reconstitutions appropriées des mammifères fossiles dans leur aspect vivant fournissent des informations sur l'anatomie et la biologie des espèces disparues et servent également à transmettre ce savoir au grand public. Pour accomplir cette reconstitution il faut suivre une méthodologie rigoureuse qui tient compte des données fournies par différentes branches de la science dont l'anatomie comparee et l'anatomie fonctionnelle ainsi que l'éthologie des espèces actuelles et bien sûr une figuration artistique.

Cette approche est appliquée à la reconstruction de quelques formes disparues du site d'Arrisdrift en Namibie. Ce site présente une opportunité intéressante pour l'artiste paléontologue car bien des espèces de ce gisement sont connues par des restes relativement complets comprenant à la fois des crânes et des éléments du squelette et bien des espèces y sont mieux représentées qu'àilleurs où ne sont connues que de cette localité.

Le travail consiste à reconstituer l'anatomie des espèces sélectionnées puis de les placer dans leur environnement recréant des aspects de leur comportement possible et montrant également des détails de la topographie et de la végétation locale.

Introduction

Accurate reconstructions of the life appearance of fossil mammals are a useful means of providing a package of information about the anatomy and palaeobiology of extinct species, and also serve to transmit this knowledge to the general public. In order to accomplish these goals, the reconstruction process must follow a precise methodology, which combines information From various fields of knowledge, including comparative and functional anatomy, as well as the ethology of modern species and, of course, artistic drawing.

In this contribution I intend to summarise the essentials of this methodology, as applied to the reconstruction of some of the fossil mammal species From the Miocene site of Arrisdrift in Namibia. This site offers an especially interesting opportunity for the palaeontological artist, because many of the species present at the site are represented by relatively complete material, including both cranial and post-cranial remains, and several of these species are known only, or best, From Arrisdrift.

The first step is to create anatomically accurate restorations of selected mammalian species From Arrisdrift, and then an attempt is made to reconstruct the animals in their environment, recreating aspects of their possible behaviour, and also showing details of the topography and vegetation around the site.

History and methods of reconstruction

The basics of the anatomical reconstruction of fossil mammals were established as early as the late nineteenth century, when artists such as C. R. Knight and B. Horsfall worked in collaboration with vertebrate palaeontologists including E.D. Cope, H. F. Osborn and W.B. Scott, to produce remarkable renditions of extinct mammals (Czerkas & Glutt 1982). In his book "A History of Land Mammals in the Western Hemisphere", W.B. Scott (1937) briefly discussed the process of reconstruction. He wrote: "The form and proportions of an animal are chiefly determined by its muscular system and this may be accurately deduced From the skeleton, for the muscles that are important for the work of restoration are attached to the bones and leave their unmistakable marks upon them. The intimate relation between bone and muscle is made clear in every treatise on anatomy, and it is shown how every attachment of muscle, tendon and ligament is plainly indicated by rough lines, ridges, projections and depressions. With the skeleton before him, any competent anatomist can reconstruct the muscles in sufficient detail" (Scott 1937: 65). Scott went on to discuss how other aspects of the appearance of fossil mammals, including coat patterns, can be reconstructed. Although more than 60 years have passed since publication of the revised edition of his book, the essentials of the methodology remain valid, and many of the restorations by Knight and Horsfall published in it are still among the best ever produced.

The 1990s saw a renewed interest in the reconstruction of unpreserved attributes in fossil vertebrates, and some of the problems which the early artists faced using their intuition, were studied with a more analytic approach (Bryant & Russell 1992; Bryant & Seymour 1990; Witmer 1995).

To summarise the process of anatomical reconstruction, we can divide it in two stages. First, we need to reconstruct the skeleton in a feasible posture. Then we add the soft tissues, proceeding From the inside out, as in a reversed dissection (Antón 1996, 1998, 1999, in press; Antón *et al.* 1998).

The difficulty of the first stage of course depends on the preservation of the fossils. In the exceptional cases where fossil skeletons are found articulated and complete, reconstruction is much facilitated, but more usually we have to work from fragmentary remains. Articulated skeletons are unknown at Arrisdrift, and even the best known mammals From the site are represented by isolated remains of different animals. In such cases, we need to combine bones From different individuals taking into account any apparent size differences, then reconstruct unknown parts on the basis of closely related species where the morphology of missing parts is known. Obviously, the more distantly related the species used for reference, the less reliable the reconstruction will be, but at the same time we need to bear in mind adaptive considerations, which may imply that the most closely related species available is not the best model for reconstruction if it has evolved different locomotor or feeding adaptations (Bryant & Russell 1992). Once the missing bones are restored, the skeleton has to be assembled into a credible posture. The shape of the articular areas provides information about the range of flexion and extension of each articulation, showing, for example, whether an animal stood on crouched or extended limbs, or whether the back was normally held straight or was strongly curved.

The second stage, the reconstruction of the soft tissues requires an examination of the muscle attachment areas in the bones. While muscle insertion areas are relatively difficult to recognize in the bones of reptiles and birds, on the bones of mammals a high proportion of muscles leave clear markings, making them an easier group to work with in this respect (Bryant & Seymour 1990). For other soft tissues which leave no mark on the bone, such as cartilage, fat, skin and fur, we need to make inferences based on functional and phylogenetic criteria. We can apply some general rules (herbivores have larger guts, mammals living in cold climates have smaller ears, forest-dwelling predators have coat patterns that provide camouflage, etc.), but such functional reasoning has to be combined with phylogenetic considerations, and when there is doubt about some relevant but unpreserved attribute, the extant phylogenetic bracket (Witmer 1995) can provide the necessary phylogenetic grounds upon which to base a decision.

Reconstructing Arrisdrift mammals

Artiodactyls. Among the Arrisdrift artiodactyls, one of the most interesting in terms of reconstruction is the giraffoid *Orangemeryx hendeyi* (Fig. 1). The species is known on the basis of good skeletal material, including cranial and mandibular fragments with dentitions, complete limb bones, and several vertebrae. Missing portions of the skull were restored on the basis of the related genus *Sperrgebietomeryx*, from the Namibian site of Elizabethfield, although the latter animal did not have cranial appendages. Even though the limb bones were not found articulated, they correspond to animals of broadly similar size, and give a good idea of relative limb proportions, with elongated legs that were not, however, highly specialised for speed. Two well-preserved anterior cervical vertebrae show that the neck was elongated and powerful. As inferred from the shape and position of insertion areas, the muscle masses of *Orangemeryx* would have followed the general pattern of modern, long limbed ruminants, with fleshy portions of limb muscles concentrated on the proximal sections of limbs, and only tendons reaching the distal parts. The neck would have been well muscled but elegant and gently curved. In life, the animal would have vaguely resembled a modern gerenuk in general body proportions, although, with a shoulder height of about 1.2 metres, it was considerably larger. The appearance of the head, with its strange bony appendages, would have been of course unique.

Another ruminant species described from Arrisdrift is small homed bovid *Namacerus gariepensis*. As in the case of *Orangemeryx*, we have cranial and mandibular fragments, and several complete limb bones which give a fair idea of size

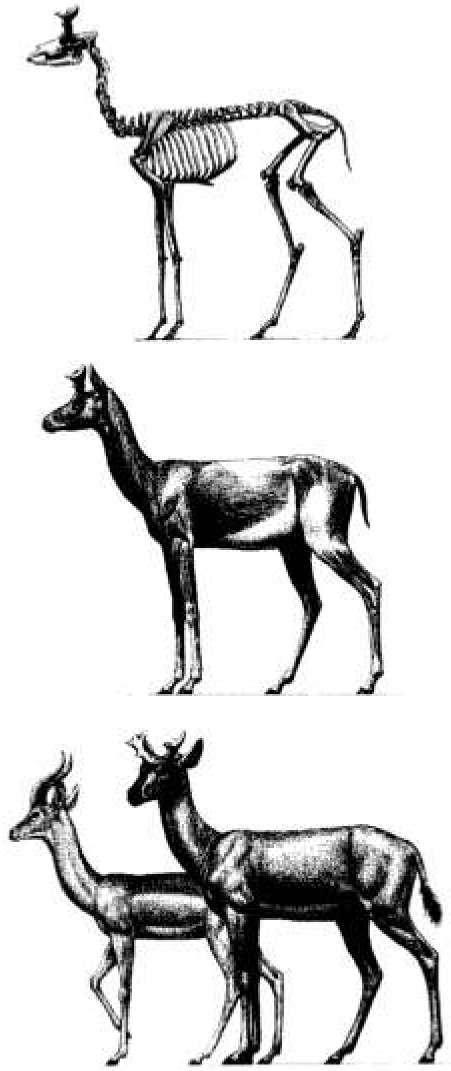

Figure 1: Sequential reconstruction of the giraffoid *Orangemeryx hendeyi*, showing the restored skeleton (top), the muscular masses (centre) and the reconstructed life appearance drawn to scale with a modern gerenuk, *Litocranius walleri*. Reconstructed shoulder height of *Orangemeryx*: 120 cms.

and limb proportions. With an approximate shoulder height of 40 cms, it was a small ruminant, considerably smaller than a steenbok (*Raphicerus campestris*), for instance, and with somewhat different body proportions (Fig. 2). Effectively, its Hindlimbs were longer relatively to the forelimbs, as is the case in modern duikers (Cephalophini), suggesting a similar jumping mode of locomotion among shrubs and thickets. During the 1998 field season of the Namibia Palaeontology Expedition, after the first preliminary reconstruction of this animal had been drawn, additional fossil material was found at Arrisdrift, including cranial fragments with small appendages that indicate that *Namacerus* was a homed ruminant.

Hyraxes. One of the most abundantly represented mammal species at Arrisdrift is the giant dassie *Prohyrax hendeyi*. Known from very complete cranial and mandibular remains, as well as from abundant limb bones, *Prohyrax* reveals itself as a rather different animal from modern hyraxes, such as the rock-dassie (*Procavia capensis*) shown in Fig. 3. Not only was it larger with a shoulder height of about 36 cms, but it also differed in posture and locomotion. The elbow articula-

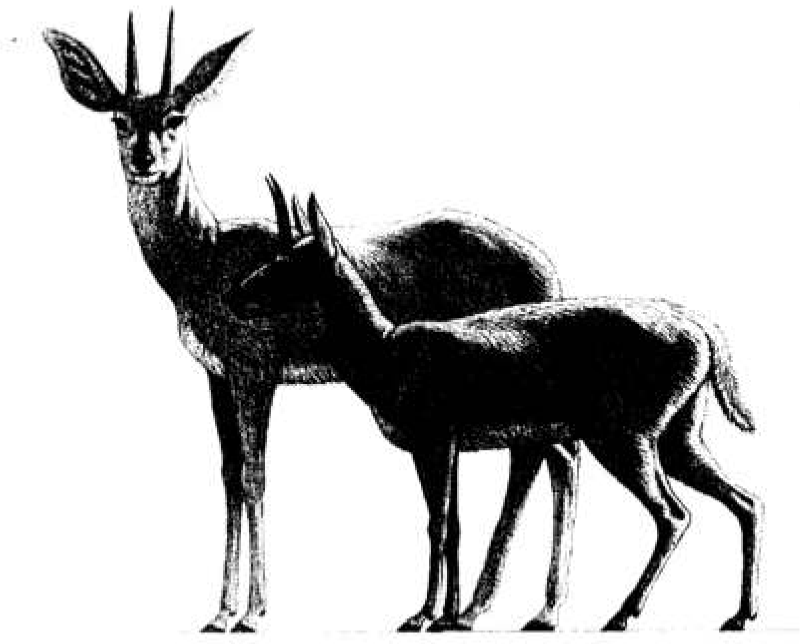

Figure 2: Reconstructed life appearance of the bovid *Namacerus gariepensis*, drawn to scale with a modern steenbok, *Raphicerus campestris*. Reconstructed shoulder height of *Namacerus*: 40 cms.

tion was more stable in an extended position, indicating that the animal stood on straightened forelimbs. The knee articulation was also better adapted for movement along the sagittal plane, showing adaptation for more efficient walking on hard ground. All this shows that the animal stood and walked in an upright posture, rather than the rabbit-like crouch of modern dassies.

Proboscideans. Elephant-like animals are represented by fragmentary fossils at the site, but enough is preserved to allow identification at the generic or specific level. The deinothere, *Deinotherium hobleyi* is well represented at the Libyan site of Gebel Zelten (Harris, 1973), and the Namibian animal is reconstructed on the basis of the North African material which is similar in size.

Mastodons of the species *Afromastodon coppensi* were similar in overall body proportions to well-known European species of the genus *Gomphotherium* (Göhlich 1999), but differed in their larger size and in the shape of their mandible and lower tusks. With shoulder heights of around two metres, the Arrisdrift deinotheres would be dwarfed by a modern elephant, especially by a large African elephant bull as shown for comparison in Fig. 4, while *Afromastodon* would have been a very large animal.

Carnivores and Creodonts. While mammalian predators are a relevant part of the Arrisdrift palaeoecosystems, and several of them belong to species new to science, the anatomical rep-

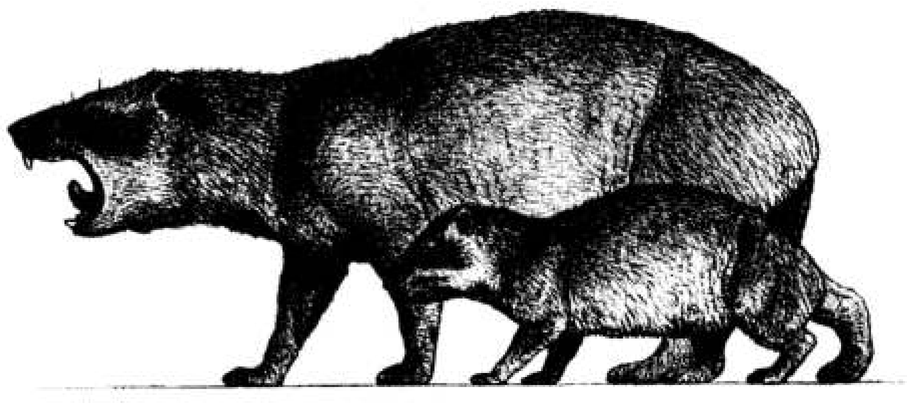

Figure 3: Reconstructed life appearance of the giant dassie *Prohyrax hendeyi*, drawn to scale with a modern rock dassie, *Procavia capensis*. The giant dassie is shown with a gaping display gesture typical of modern hyraxes. Reconstructed shoulder height of *Prohyrax*: 36 cms.

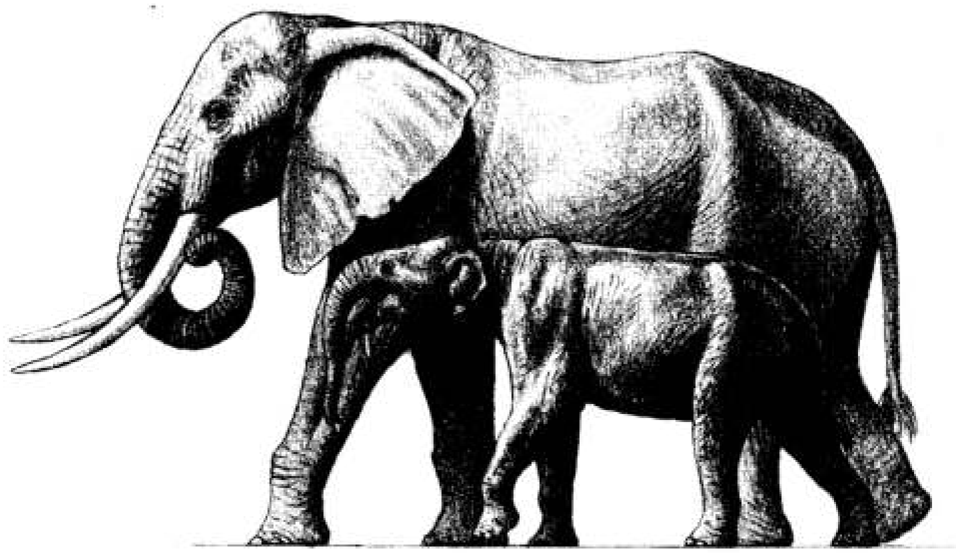

Figure 4: Reconstructed life appearance of the primitive deinothere *Deinotherium hobleyi*, drawn to scale with a modern bull African elephant, *Loxodonta africana*. Reconstructed shoulder height of *Deinotherium*: 2 m.

resentation of these animals from the site is rather poor, as is the case in most fluvial fossil sites. Most of the carnivore and creodont fossils from Arrisdrift correspond to fragments of mandibles and maxillae, dentitions, or isolated postcranial bones which are difficult to identify at the species level. Even so, we have attempted to reconstruct some of these animals on the basis of the preserved remains and with reference to material from other sites.

The giant creodont *Hyainailouros sulzeri* is represented at Arrisdrift only by dentitions and mandibular fragments, but excellent skeletal remains of this animal are known from the French site of Chevilly (Ginsburg, 1980), so we have reconstructed the animal from Arrisdrift with similar body proportions (Fig. 5). Comparing the dental and mandibular measurements of the Namibian and French fossils, it is evident that the former belonged to comparatively smaller animals, which nonetheless would have been impressive, with shoulder heights slightly above 1 metre and relatively huge heads.

The giant bear-dog, *Amphicyon giganteus*, is likewise represented by teeth and mandibular fragments at Arrisdrift, but more complete remains of this and related species of *Amphicyon* are known from several sites in Europe (Ginsburg & Telles Antunes, 1968; Bergounioux & Crouzel, 1973). Using the European material as a reference, the Namibian bear-dog is reconstructed as a bear-sized beast with a shoulder height of around 90 cms. (Fig. 5). Although *Hyainailouros* and *Amphicyon* would be animals of comparable mass in life, they would look strikingly different because the former "had a pro-

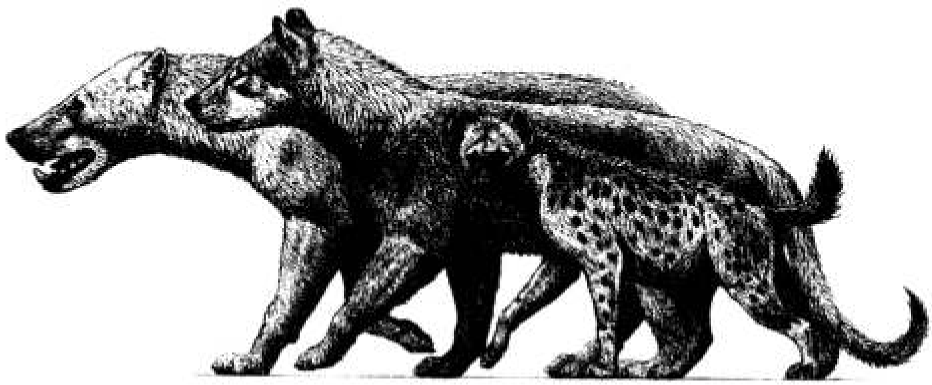

Figure 5: Reconstructed life appearance of the giant creodont *Hyainailouros sulzeri* (left) and the bear-dog *Amphicyon giganteus*, (centre) drawn to scale with a modern spotted hyaena, *Crocuta crocuta*.

portionally much bigger head, while in the latter the proportion between skull size and body size would not have been much different from a modern bear. It is interesting to show both giant predators drawn to scale with the modern spotted hyaena, *Crocuta crocuta* (Fig. 5), because the dentitions of all three animals show adaptations to both eating meat and crunching bones. However, while the spotted hyena is at present the largest mammalian predator in the African continent to occupy the "meat eating-bone crunching" niche, the Miocene ecosystems included at least two species of gigantic size that competed for those resources. While a carcass in the present-day African savannah is usually disputed by lions, spotted hyenas and jackals, the scene around a cadaver in Miocene Namibia would have been rather more spectacular with giant creodonts and at least two species of bear-dogs to dispute the spoils.

Among the smaller carnivores from Arrisdrift, the catlike *Diamantofelis* is an especially interesting but somewhat frustrating subject for reconstruction. It was originally described on the basis of teeth and mandibles, which reveal that it was a precociously specialised hyper-carnivore, with a strongly shearing cheek dentition and a shortened muzzle, just as in modern cats. Such mandibular proportions make it clear that the head must have looked rounded and rather cat-like. But the absence of any complete skull and the paucity of post-cranial remains (only a phalanx and a *proximal ulna* have been recovered thus far) turn any attempt at a reconstruction into an exercise in speculation. Classified by its discoverers within the family Felidae, *Diamantofelis* would be an early member of the cat group, and thus we can expect it to display a typical generalised feliform anatomy: a long body and tail, flexible and well-muscled legs of medium length with the Hindlimbs considerably longer than the forelimbs, and re¬tractable claws, all wrapped in a furry coat with some sort of camouflaging pattern. This is a purely probabilistic ap¬proach to what the unknown anatomy of Diamanto{etis would look like, but only the discovery of more complete fossils will prove if these assumptions were right.

Environmental reconstruction

A further step in the process of reconstruction is to show the animals behaving naturally in their environment. The nature of the fossiliferous sediments in Arrisdrift clearly shows the fluviatile nature of the accumulation, but the presence of numerous clay drapes indicates that the channel had water flowing through it only now and then, and that for the rest of the time it was a quiet, shallow pool. Some elements of the fauna, such as the abundant crocodiles and the giant tortoises, point to a more tropical climate in the area than that of the present day.

Fossil wood found at Arrisdrift, and most especially at the slightly older site of Auchas (Pickford *et al.*, 1995) provides useful information about the vegetation around the site in the early and middle Miocene. The identified trunks correspond to trees of the genera *Combretum* and *Terminalia*, which suggest the presence of an open woodland as occurs today in southern Africa in dry areas with sandy soils, but always in places with

Figure 6: Environmental reconstruction of the area around the site of Arrisdrift about 17 ma. From left to right there can be seen a group of deinotheres, *Deinotherium hobleyi*, and a single mastodon, *Afromastodon coppensi*; a group of hyraxes, *Prohyrax hendeyi*; a group of giraffoids, *Orangemeryx hendeyi* approach the pool to drink, but are aware of the presence of a resting crocodile, *Crocodylus gariepensis*; and in the right foreground, a carnivore of the species *Diamantofelis ferox* is seen attacking a family group of bovids, *Namacerus gariepensis*.

more soil water than is available at present in the lower Orange River drainage.

The resulting picture (Fig. 6) is of an abandoned meander of the proto-Orange river, which would attract many animals to drink, or to eat from the surrounding greenery, during the dry season.

Many of the visitors to the area would be browsing mammals, including those shown in the reconstruction: the proboscideans *Deinotherium* and *Afromastodon*, the hyracoid *Prohyrax* the giraffoid *Orangemeryx*, and the bovid *Namacerus*. Some of these animals would be attacked and devoured by the abundant crocodiles of the species *Crocodylus gariepensis*, as testified by the common occurrence of tooth marks in the fossil bones. Mammalian predators would hide among the vegetation around the pools, waiting for suitable prey to come by. The hyper-carnivorous *Diamantofelis*, for instance, would ambush small prey such as the diminutive bovid, *Namacerus*. With the rainy season, water would flow again, if briefly, through the channel, transporting the bones of dead animals and burying them in sediment.

Conclusions

The mammalian fossils from Arrisdrift allow for a series of anatomical restorations of species never reconstructed before, such as the giraffoid *Orangemeryx*, the bovid *Namacerus*, and the giant dassie *Prohyrax*. Other species of fossil mammals have a poorer anatomical representation at Arrisdrift, and they are reconstructed with abundant reference to specimens from other sites, or to better known, closely related species. That is the case of the proboscideans and mammalian predators. The results of these anatomical restorations, combined with data about the topography, vegetation and climate, allow the preparation of a landscape reconstruction, where several of the mammalian species from the site are shown in their palaeoenvironment. Such reconstructions, based on firm palaeontological evidence, provide a useful package of information about the palaeobiology and ecology of fossil mammals and their environments, both for the specialist and for the general public.

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