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GEOLOGY AND PALAEOBIOLOGY OF THE NORTHERN SPERRGEBIET, NAMIBIA

by

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Taphonomy of the fluvio-paludal deposits of the Sperrgebiet, Namibia

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The mammalian collections from the northern Sperrgebiet are dominated by micromammals, with abundant medium sized specimens, and exceptionally few large mammals. Taphonomic conditions appear to have favoured the burial and preservation of small specimens, and tended to filter out large material, the few specimens found being in poor condition due to lengthy subaerial exposure prior to burial. Aspects of the taphonomy of the region are discussed, including the important role of carnivores in concentrating small mammal remains. Depositional, geochemical and meteorological aspects are also examined for their effects on the fossils.

Introduction

The vertebrate fossils from the northern Sperrgebiet comprise abundant microfauna (small reptiles, rodents, macroscelidids, lagomorphs, insectivores), with fewer medium-sized species (ruminants, suids, hyracoids, carnivores) and extremely rare occurrences of large mammals (proboscideans, rhinocerotids, anthracotheres). This paper examines some aspects of the taphonomy of the fossiliferous localities at Elisabethfeld, Fiskus, Grillental and Langental. It is surmised that one of the most important features of the deposits that played a preponderant role in the taphonomic processes, is the fine-grained, low energy deposition that took place, with rapid burial of small specimens, but with generally slow burial of larger specimens.

Recent geochemical and meteorological conditions have played an important role in determining what specimens survive the processes of natural exposure, with fog and wind being the most important. Fog brings salt and weak sulphuric acid into the inner Namib (the strip nearest the coast) with the result that the sediments are extremely salty and have important deposits of superficial gypsum. Both the salt and the gypsum have affected many fossils, sometimes to the point of total destruction, but in some cases, such as Elisabethfeld, the fossils are well preserved although many of them should not be placed in water for any length of time, otherwise they will dissolve. At Langental, but also to some extent at Elisabethfeld, the *in situ* fossils are soft and friable, whereas those that have eroded out naturally under a cover of soft superficial sediment, are case hardened and in good condition. In this case, many cycles of exposure to the effects of fog which precipitates onto the soil and dampens it to a depth of a few cm, removes some salt and gypsum from the fossils, but only if they are not exposed to the action of the boisterous winds that typify the sites. This is one reason why exposed outcrops of *in situ* sediment yield few fossils, whereas similar deposits with a thin cover of superficial sediment such as sand or weathered sediment under a thin salt crust tend to be rich in well preserved fossils.

At Elisabethfeld, large patches of red marly sediment are rich enough in lime to be classed as impure limestones. Fossils in these deposits tend to be exceptionally well preserved, and are easily freed from their matrix by bathing them in weak acetic acid (10%). In salty marls at the same site, in contrast, fossils can be extracted using water, but they should not be left in water for more than a few minutes or sometimes even seconds, otherwise they fall to pieces or dissolve entirely.

Agents of concentration of fossils

Stromer, 1926, thought that the small mammals at Elisabethfeld might have been concentrated by nocturnal or diurnal raptors. His was the first attempt to determine what would today be referred to as the taphonomic conditions responsible for generating the fossil record of the northern Sperrgebiet. His raptor hypothesis is probably not correct, since it is more likely that many of the small mammals at Elisabethfeld passed through the digestive tract of small carnivores (Pl. 1, fig. 2, 4) rather than those of raptors, because they show signs of chewing and digestion typical of such mammals (Pickford and Senut, 2000). Nevertheless, Stromer's hypothesis is of historical interest, because he was endeavouring to explain why the faunas he studied were dominated by small mammals.

We now know that there were several independent factors or processes involved in generating the Early Miocene fossil record of the northern Sperrgebiet, among which both geological and biological ones are important. Some specimens were eaten by carnivores, some died in their burrows, and some died on the land surface and became mummified before being buried. Others were partly destroyed by larger carnivores, while large mammal remains gen-

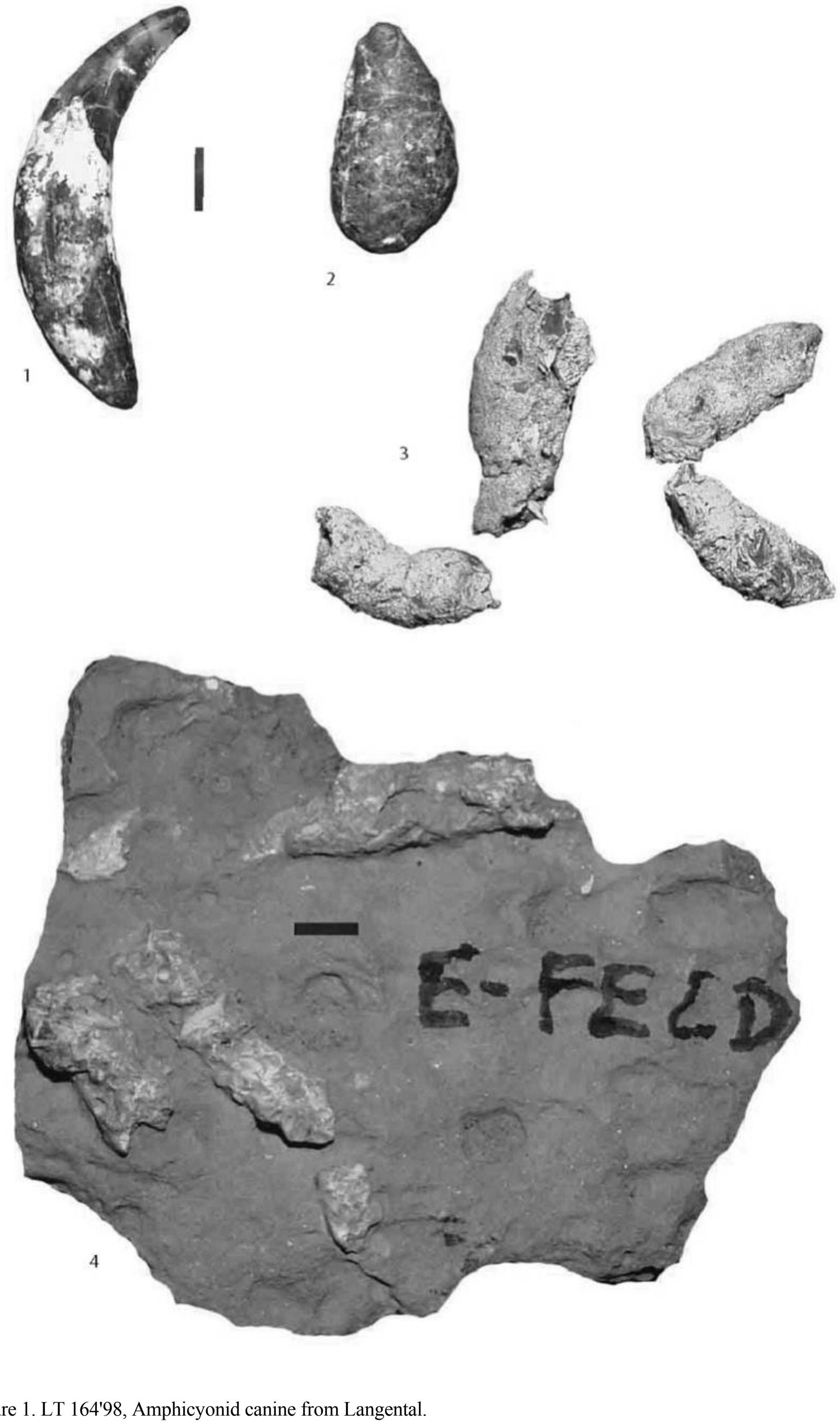


Plate 1.

Figure 1. LT 164'98, Amphicyonid canine from Langental.

Figure 2. LT 9'97, Carnivore coprolite containing micromammalian bones from Langental.

Figure 3. Extant scats of Black-backed Jackal (*Canis mesomelas*).

Figure 4. Carnivoran coprolites in impure limestone, Elisabethfeld (Scale: 10 mm).

erally disintegrated under the influence of subaerial exposure before they could be buried.

There are abundant signs of fluvial activity in the deposition of the fossiliferous sediments of the northern Sperrgebiet, yet there is little evidence that water was a significant agent in concentrating fossils, unlike the deposits at Arrisdrift in the Orange River Valley (Pickford and Senut, 2000). The taphonomic processes active during the Early Miocene in the nascent Namib were thus many and varied.

A large concentration of skeletons at Elisabethfeld : In 1993, an area of about 50 x 50 cm and some 30-40 cm deep yielded an amazing concentration of skeletons of small mammals. Particularly prevalent were *Protypotheroides beetzi* (at least 13 individuals), *Diamantomys luederitzi*, and *Myohyrax oswaldi*, with some teeth of *Prohyrax tertiarius* and *Namibiomeryx senuti* and a lower jaw of *Miorhynchocyon*. The occurrence was a small pocket of fossil-rich green sediment in otherwise azoic red silts, and it may represent the den of a small carnivore. Some of the remains had not been chewed and skeletal parts were sometimes articulated, suggesting that whatever concentrated these specimens together brought most of them in as cadavers rather than as scats.

A similar rich occurrence of micromammalian remains was found at GT Carrière in 2004. An area about 50 cm in diameter and 20 cm deep yielded hundreds of bones and teeth of rodents and macroscelidids, almost all of which had been broken (presumably by chewing prior to ingestion) but not etched by digestive acids.

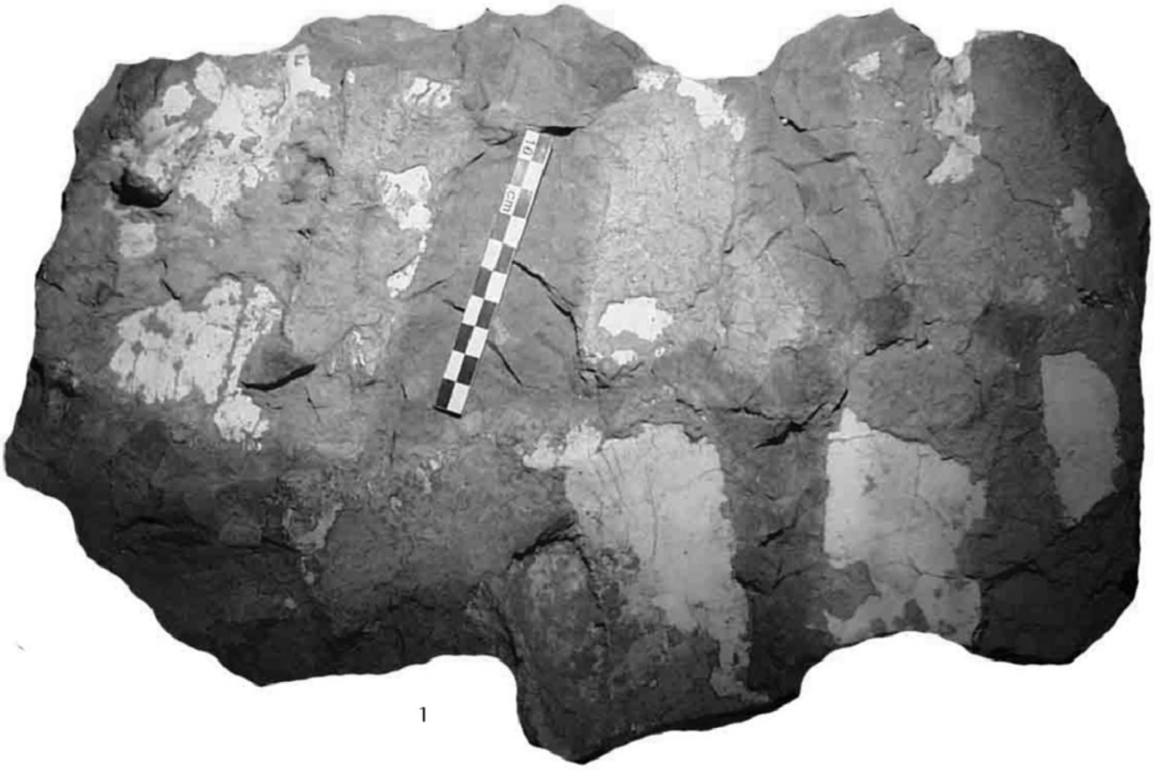
In 2005, a thin layer of red silts yielded hundreds of jaws and teeth of micromammals from an area less than a square metre surrounded by sediment devoid of fossils. While prising open the sediment layers, the deposit split naturally along a bedding plane exposing abundant carnivore scats fossilised in various stages of decomposition. The bones, teeth and jaws were eroding from these scats, which probably represent a latrine of a small carnivore about the size of a black backed jackal.

Tortoises : Several places at Elisabethfeld have yielded concentrations of tortoise carapaces, some of which are complete to sub-complete. In other instances, rich scatters of tortoise scutes occur. The former specimens were undoubtedly buried rapidly, whereas the latter had time to disaggregate before burial (Pl. 2, Fig. 1). The more or less complete carapaces were always plastron down, suggesting that they died at or close to where they were found, and were not transported post-mortem. These concentrations could be explained by tortoises gathering around drying up water holes, and eventually dying there.

Scats : At Elisabethfeld, coprolites of a jackal-sized carnivore are extremely common, and they frequently contain fossil bones and teeth (Pickford and Senut, 2000). Concentrations of coprolites occur in discrete patches (Pl. 1, Fig. 3, 4), suggesting that the carnivore responsible was habitually defecating at specific spots, presumably to mark its territory just as extant carnivores do. Some of the coprolites are hard and preserve their original shape, but many disaggregated before becoming fossilised and released the bones and teeth that they contained onto and into the surrounding sediments (Pl. 2, Fig. 2). With time some incredibly rich concentrations of small mammals were formed by this process. At Langental, several coprolites were collected, (Pl. 1, Fig. 2) but in most cases the contents had been well digested, leaving little for the palaeontologist to study. Some specimens do contain bones and teeth, but the coprolites are too hard to break down unless acid is used.

The predominance of small and medium mammals over large : It is evident from previous works on faunas from the northern Sperrgebiet that large mammal remains are rare, whereas there is an abundance of small mammals. The only large mammal that Stromer (1926) described was a rhinocerotid mandible from Langental (Heissig, 1971). The NPE found three isolated, poorly preserved proboscidean teeth at Elisabethfeld (Pickford, 2003a), and some rhinocerotid remains at Langental (Guérin, 2003) including a metacarpal, a phalanx, a humeral shaft and a fragmented skull with seven teeth. At Glastal and Grillental isolated rhinocerotid metapodials and phalanges were collected, and at GT1 a partial skeleton of a juvenile rhinocerotid was discovered in 2004. Corvinus recovered a talus of *Brachyodus* from Grillental (Pickford, 2003b) and a vertebral body of the same genus was discovered by the NPE. Finally, at Fiskus some rhinocerotid remains were found including an upper molar, a proximal metacarpal III and a femur shaft.

Bones and teeth of medium sized mammals are more common in the northern Sperrgebiet, being well represented at most sites. The species present include *Propalaeoryx austroafricanus*, *Sperrgebietomeryx wardi*, *Prohyrax tertiarius*, *Nguruwe namibensis*, *Diamantohyus africanus*, *Namibiomeryx senuti* and *Dorcatherium songhorensis*. There are also some poorly preserved carnivore fossils (amphicyonids). By far the lion's share of the mammalian fossil record in the northern Sperrgebiet is however, comprised of rodents and macroscelidids, with rarer lagomorphs, tenrecids, erinaceids and small creodonts. The taphonomic reasons for the paucity of large mammals are not immediately evident, but from the few specimens available, it would appear that large bones tended to get buried relatively slowly, so that they had time to disintegrate or become badly fissured before burial. Medium and small mammal remains however, were usually rapidly buried and are well preserved. Furthermore, many of the small mammals, especially those from Elisabethfeld, occur in carni-



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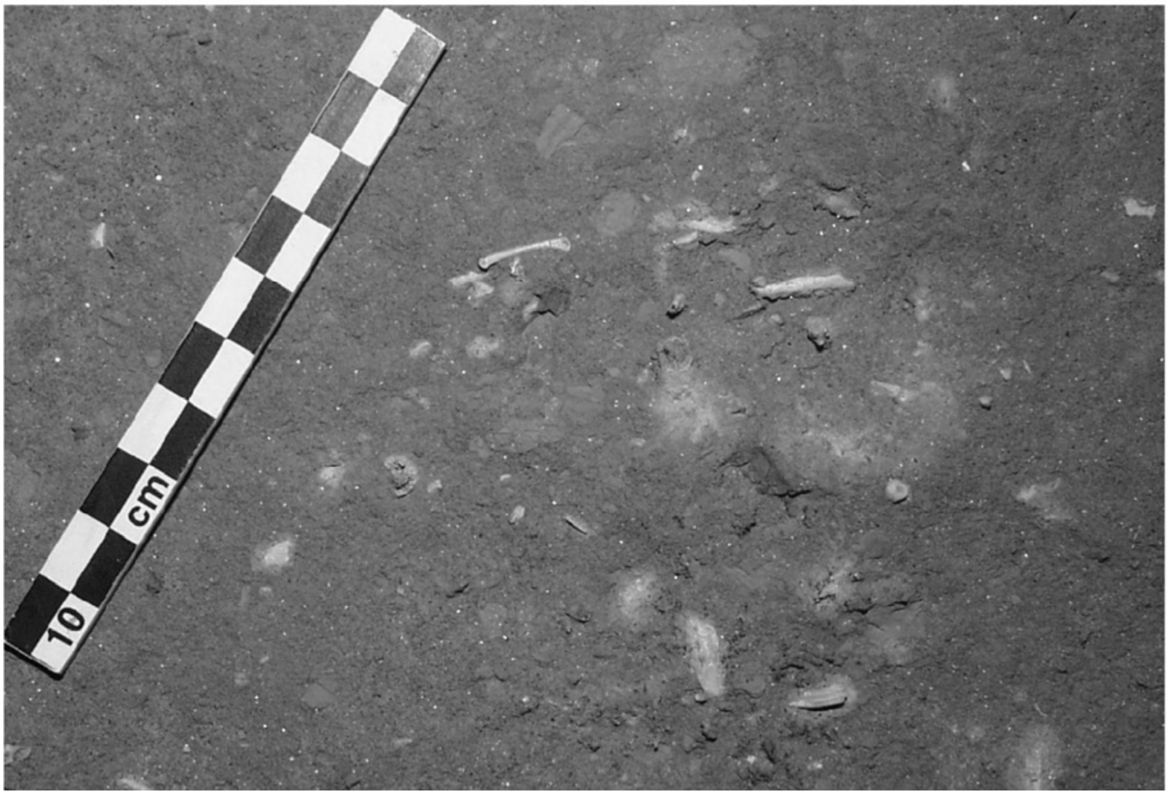

Plate 2.

Figure 1. Disaggregated tortoise carapace, Elisabethfeld.

Figure 2. Disaggregated carnivore scats and coprolites containing micromammalian bones and teeth from Elisabethfeld.

vore scats. Other individual rodents and macroscelidids appear to have been buried in their burrows.

There was thus a variety of taphonomic factors that disfavoured the preservation of large skeletal remains, contrasting with conditions that promoted the preservation of small remains. The fact that many of the sediments are fine grained overbank deposits (Elisabethfeld, parts of the Grillental succession, some of Langental) or palaeosols (much of Langental, Glastal) helps, in part, to explain this bias, since small specimens are more easily buried in such depositional environments than large bones are. An alternative explanation could be that large mammals were rare in the region, and thus had low potential for being preserved as fossils.

Preburial damage to fossils

Rodent gnawing : Among the many hundreds of bones collected from the Sperrgebiet, there are a few cases of bones being gnawed by rodents (Pl. 3, Fig. 2). One such specimen from Langental is a proximal metacarpal of a ruminant (*Propalaeoryx*), another from Grillental 6 is a fragment of a rhinocerotid metapodial. This paucity of rodent action on bones is remarkable when comparison is made with contemporaneous East African Early Miocene localities such as Songhor and Napak, at which a relatively high proportion of bones has been gnawed.

Carnivore chewing : Apart from bones preserved in scats, few of the fossils from the northern Sperrgebiet show evidence of tooth marks (Pl. 3, Fig. 1, 2, 3, 4, 5, 6). Indeed, the only obvious specimens affected by puncture marks comprise two specimens from Grillental and some ruminant bones from Langental. In these specimens the puncture or gnawing marks were evidently made by quite a small carnivore, perhaps one the size of a jackal or a medium-sized amphicyonid (Pl. 1, Fig. 1).

General lack of articulated specimens (excepting specimens of *Sperrgebietomeryx*, *Propalaeoryx*, *Bathyergoides*, *Parapedetes*, *Myohyrax*, *Austrolagomys*) : Throughout the Sperrgebiet, it is rare to find articulated skeletal remains of mammals. A few exceptions were found however. The holotype of *Sperrgebietomeryx wardi* was found in a semi-articulated concentration in a channel deposit of green sands. Parts of the skeleton originally poked out of the surface of the sediment at the time of deposition, and these were weathered away before the channel deposit was itself buried. In this case it appears that a cadaver became incompletely buried in sands before it could be devoured by carnivores or dispersed while lying unprotected on the surface. At Elisabethfeld and Langental several fore-limbs of *Propalaeoryx austroafricanus* were found with the carpals, metacarpals, and phalanges in connection. This would suggest that the tendons binding the distal forelimb elements together were strong, elevating the chances of the bones staying together until burial. Several partial skeletons of *Bathyergoides neotertiarius* were found, not only at Langental, but also at Grillental. It is likely that this was a burrowing rodent, and that occasionally it died within its burrow and was thus not subjected to any predatory activity. Similarly, a partial skeleton of *Parapedetes namaquensis* found in anatomical connection possibly indicates death within a burrow. Stromer (1926) described an almost complete skeleton, the holotype of the species, that was found articulated in a block of red limey silt, indicating the same thing. At Elisabethfeld, some complete skeletons of *Myohyrax oswaldi* and *Austrolagomys inexpectatus* and a partial skeleton of a tiny creodont were found in a deposit that yielded some complete tortoise carapaces. The skeletons were in flattish nodules almost as though they were encased in dehydrated skin prior to burial. It is possible that they were mummified by dessication and then buried as complete, but dried up cadavers. At Elisabethfeld eight snake vertebrae were found in connection in red limey siltstone. At Grillental, a block of green silty sand contained many disarticulated snake vertebrae, probably representing a single individual, the bones of which drifted apart from one another but remained concentrated in a small area prior to being buried. In 2004, GT1 yielded a partial juvenile rhinocerotid skeleton in coarse fluvial sands. However, instances of articulated or closely associated skeletal remains are rare in the Northern Sperrgebiet.

A much more common association of skeletal parts in the Sperrgebiet occurs in fossilised carnivore scats, but the bones are usually disarticulated, even though close together. However, in some cases some parts of the skeleton have remained in articulation, in particular the distal tibia and talus, the distal humerus and proximal radio-ulna, and sometimes phalanges. In general, the bones of small mammals found in scats are broken into only a few pieces, indicating that they were not subjected to prolonged chewing before being swallowed. It is usual to find two or more small mammal skeletons in a single scat, or sometimes a mixture of micromammal and small reptile (snake, lizard) remains. At Elisabethfeld, the carnivore scats are about the same size as those made by extant jackals, *Canis mesomelas*.

Bones as sediment particles

Bones vertical in sediment : Bones that are oriented vertically in sediment deposits are often remarked on because of their peculiar positioning. A popular explanation for such occurrences is that trampling of specimens in soft mud has led to some specimens being upended. Whilst this idea does appear to apply

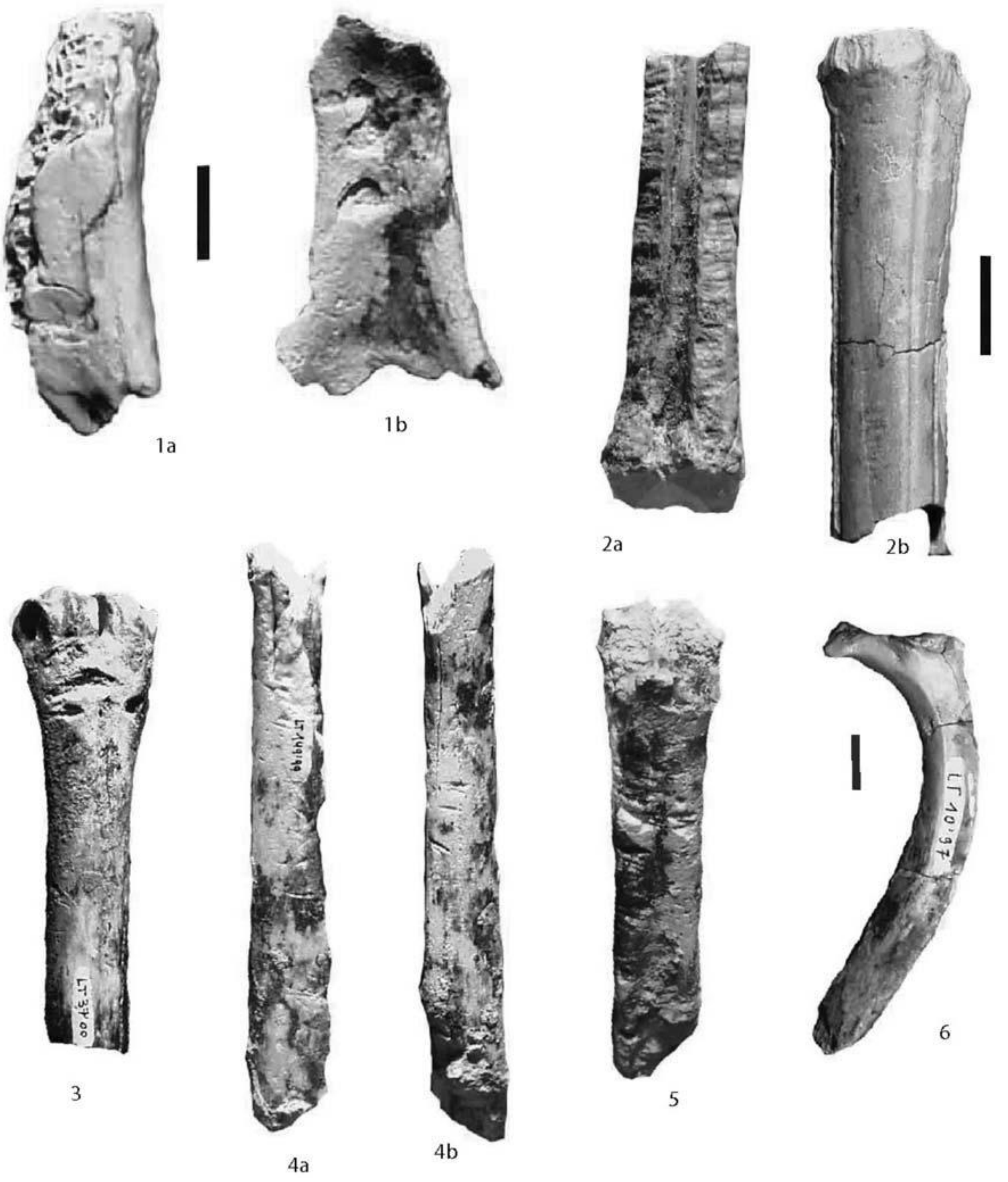

Plate 3.

Figure 1. Bones with tooth puncture marks from Langental, a) LT 510'96 with single puncture mark, b) LT 519'96 with three puncture marks.

Figure 2. EF 5'03, ruminant metapodial from Elisabethfeld with extensive gnawing marks made by rodents.

Figure 3. LT 37'00, Ruminant metapodial from Langental with tooth marks at distal end, possibly made by a carnivore.

Figure 4 and 5, LT 149'99, ruminant metapodial diaphysis from Langental with carnivore tooth marks.

Figure 6. LT 10'97, Ruminant rib from Langental with tooth puncture mark near proximal end.

in many localities, especially Arrisdrift, Namibia, (Pickford and Senut, 2000, 2003) it does not seem to be the case at Langental. At this locality several jaws of *Protypotheroides* and rodents were vertical in the sediment, and metapodials of ruminants are often angled in the sediments. Given that the deposits at Langental were subjected to pedogenesis soon after deposition, with the formation of calcareous nodules and the development of mottled texture, it seems that a more likely explanation of the vertical orientation of small fossils is that they fell into cracks developed in the soil during dry periods. Even today, the Langental palaeosols crack open during dry weather forming fissures several cm wide, tens of cm long in hexagonal patterns, and 10 to 20 cm deep. Fossils and pebbles on the surface near these fissures are easily scuffed into the cracks by passing animals such as jackals, hyaenas and antelopes, or they fall in naturally during strong winds. A similar process appears to have functioned during the Early Miocene, suggested by the fact that some of the vertical fossils are embedded in carbonate nodules formed at that time.

Fossils in pedogenic carbonate nodules : At Langental, there are many fossils preserved in carbonate concretions of pedogenic origin. At Glastal the same kind of preservation occurs but is less common. Small bones and teeth are usually well preserved, but sometimes with fissures filled with calcite that has expanded and moved the fragments apart. Large fossils can also be well preserved, but they are usually greatly affected by expansion with fissures being filled with large amounts of calcite. A rhino skull at Langental with detached teeth was in such a condition, and only the teeth could be partly preserved by careful excavation. Some parts of this specimen had been destroyed by gypsum attack, which had turned teeth, especially dentine, into brown powder. Enamel embedded in calcite is, in contrast, well preserved.

Post-burial alteration to fossils

Penecontemporaneous alterations

Ferruginised fossils : At Grillental 6 there is a patch of marly, sandy sediment that has abundant ferruginised nodules and thin plates of ironstone Laterally the marls become more pure and the influence of iron salts diminishes, eventually disappearing altogether. Fossil gastropods and mammal bones (Pl. 4, Fig. 5) in the sediments that contain iron nodules are coated in a durable mass of iron oxide overgrowths, gastropods in particular being covered in irregular growths of knobbly nodular ironstone (Pl. 4, Fig. 1, 2, 3). A similar deposit occurs at Elisabethfeld (Pl. 4, Fig. 6). Laterally, the iron only makes a thin coat on the fossils, more of a superficial rust colour than an overgrowth. Even further laterally fossils have no rusty colouration at all (Pl. 4, Fig. 4). The most encrusted specimens are aquatic, indicating that ferruginisation was strongest in the wettest depositional environment.

Colour differences between fossiliferous and non-fossil bearing sediments : At Elisabethfeld, the most areally extensive deposits are bright red. However, almost invariably, bones and teeth in these beds are surrounded by a thin coating of greenish silt, indistinguishable in terms of grain size from neighbouring sediment, but more easily disaggregated in water. The colour difference appears to be due to the valence of the iron oxides, reduced ferrous oxides in proximity of the fossils being green and ferric oxides in the rest of the deposit being red. This colour difference is a great aid to prospecting, as well as for extracting fossils from the sediment.

At Langental the sedimentary deposits are mottled greens and greys with calcareous nodules of pedogenic origin. Bones from the mottled palaeosols are themselves mottled browns, blacks and pale yellow to white. Bones occurring in calcareous nodules tend to be black or dark grey, whereas specimens in yellow limestone nodules and masses tend to be white or pale yellow, almost the same colour as the limestone, and thus extremely difficult to see especially if encrusted in the same material. The fossils in the American Museum of Natural History from "South of Lüderitz" most probably came from Langental on the basis of the colour scheme and preservation characters. They certainly did not come from Elisabethfeld, Grillental or Fiskus.

At Glastal, most of the fossils, and they are few and far between, occur in light pink pedogenic carbonate nodules which occur in patches within green silts and sands, the nodules themselves being with or without thin veins of darker calcite. Bones are white and gastropods pink.

At Grillental, the richest fossil deposits are green to grey silts and fine sands. Bones are usually white or grey although teeth are often dark brown and egg shells dark grey.

At Fiskus, bones occur in green sands and silts, most bones being white and the teeth brown or mottled brown, black and yellow.

Pleistocene to Recent alterations

The cool fog desert extends about 40 km inland from the coast (Selby, 1977) beyond which is the alternate fog desert (40 to 60 km inland) and the desert steppe (from 60 km inland to the base of the great escarpment). Precipitation from the fog can reach 0.7 mm per event, but the usual figure is about 0.1 mm. Since the fog incorporates tiny droplets of sea spray and H_2S emanating from coastal muds, it is a weak solution of sulphuric acid containing minute quantities of sodium chloride. Over geological time periods, the precipitation of fog near the coast has led to the development of saline soils, the so-called "salt Namib" (White, 1986), and it has produced vast quanti-

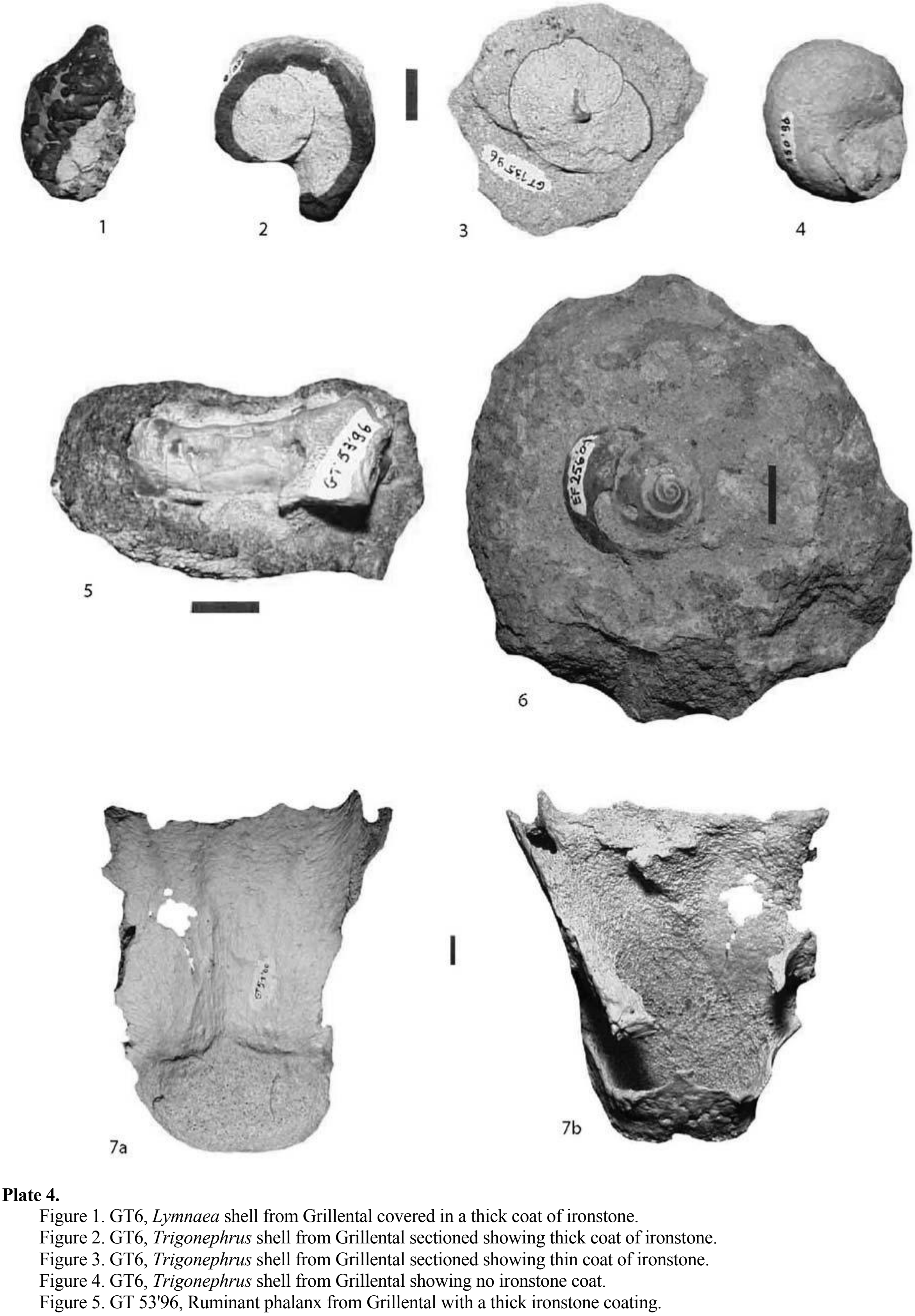

Plate 4.

Figure 1. GT6, *Lymnaea* shell from Grillental covered in a thick coat of ironstone.
Figure 2. GT6, *Trigonephrus* shell from Grillental sectioned showing thick coat of ironstone.
Figure 3. GT6, *Trigonephrus* shell from Grillental sectioned showing thin coat of ironstone.
Figure 4. GT6, *Trigonephrus* shell from Grillental showing no ironstone coat.
Figure 5. GT 53'96, Ruminant phalanx from Grillental with a thick ironstone coating.
Figure 6. EF 256'01, *Trigonephrus* shell from Elisabethfeld with ironstone coating.
Figure 7. GT 51'00, Severely sand-blasted anthracothere vertebra from Grillental.

ties of gypsum as the sulphuric acid reacted with calcium carbonate in the soils and sediments. These two factors have had a preponderant effect on the fossil record of coastal Namibia.

Salt preservation : At Elisabethfeld, some deposits are so richly impregnated with salt that fossils are replaced to a large extent by this soluble mineral. Wet screening of such deposits has to be done expeditiously, otherwise the fossils simply dissolve away, leaving minute flakes of bone and enamel. During natural exposure fossils from these deposits usually disintegrate, and it is only by excavation that they can be recovered.

At Langental, in contrast, the most resistant fossils are those that have weathered out naturally just beneath a surface scatter of sand and granules. Many of the *in situ* fossils are extremely fragile, partly because they are heavily impregnated with salt, but also because of the growth of fibrous gypsum in the surface layers of sediment. The latter process tends to fragment the fossils. However, if the same fossils are protected in the uppermost few cm of sediment beneath a thin cover of sand or granules, the salt and gypsum are gently and slowly removed by many cycles of condensed fog which dampens the ground to a depth of a few cm, and the fossils become case hardened and much more resistant than their *in situ* counterparts. For example, several fossils found cropping out at the surface with parts of the bone deeply buried in unaltered sediment were invariably harder where exposed than the *in situ* bone of the same specimen.

Gypsum damage to fossils : When fog containing weak sulphuric acid condenses, the acid reacts with carbonates in the soils forming gypsum, often of a fibrous nature, most abundantly just below a surface crust of sediment developed on underlying deposits. Fossils within this zone are often broken apart by the gypsum growth, and bones or teeth can be replaced by gypsum, and thus eventually destroyed completely. This type of damage is particularly prevalent at Langental.

Sand blasting of fossils : Once they emerge from their protective sand or sediment cover, fossils in the Sperrgebiet quickly become sand blasted and break into pieces (Pl. 4, Fig. 7). At Elisabethfeld, a mandible of *Sperrgebietomeryx* exposed in green sands, lost almost 2 cm of teeth and bone in four months of sand blasting.

Conclusions

Fossils in the northern Sperrgebiet have passed through several taphonomic processes. Carnivores are responsible for concentrating much of the micromammalian assemblages at Elisabethfeld, mainly in the form of fossiliferous scats. Other specimens died in burrows. Some medium sized specimens such as the long bones of ruminants were chewed by rodents or carnivores before burial, but this kind of damage is rare. Large bones tended to disintegrate before burial, the few specimens found generally being in terrible condition, with abundant cracks, powdery surfaces and neighbouring fragments not in contact with each other. Pedogenesis, especially at Langental has affected many specimens, with some being preserved in calcareous nodules, while others have been damaged by nodule formation, because fissures filled with calcite expanded and separated the fragments from each other.

More recently, salt deposition, gypsum formation and sand blasting have weakened, damaged or destroyed innumerable fossils. At Langental case hardening of fossils in a thin layer of weathered sediment under a surface crust has occurred, preserving fossils that are extremely fragile when *in situ* in unweathered deposits. Specimens that are hard and well preserved at outcrop can be fragile and poorly preserved in their *in situ* parts.

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