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GEOLOGY AND PALAEOBIOLOGY OF THE NORTHERN SPERRGEBIET, NAMIBIA

by

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Early Miocene Lagomorpha from the Northern Sperrgebiet, Namibia

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Lagomorph fossils are common at Early Miocene sites in the Northern Sperrgebiet, having been found at Elisabethfeld, Grillental and Langental. A single species, *Austrolagomys inexpectatus* Stromer, 1924, is present, the creation of a second species, *A. simpsoni*, by Hopwood (1929) being based on a combination of measurement error and inadequate illustration of the type species due to its abraded condition. The genus *Kenyalagomys* MacInnes, 1953, is a synonym of *Austrolagomys*. *Austrolagomys* was geographically widespread, having been recorded from Namibia, Kenya, Morocco, Libya, Israel and possibly Uganda. Its age range spans the period a 21 Ma to ca 14 Ma. Relationships to Eurasian Miocene lagomorphs are not clear, but affinities with the Oligocene *Sinolagus* - *Bellatona* group from China are possible, although in some features *Austrolagomys* resembles *Albertona* from Europe.

Introduction

Since 1992, the Namibia Palaeontology Expedition (NPE) has collected lagomorphs from Elisabethfeld, Grillental and Langental. The importance of the new material is that it is better preserved and more abundant than previously available samples (Stromer, 1924, 1926; Hopwood, 1929). All permanent and some deciduous tooth positions are now represented in the sample. A few mandibles and maxillae were collected but much of the material consists of isolated teeth found in disaggregated or intact carnivore scats. The range of variation can now be better assessed, and it is clear that there is only a single species in the Northern Sperrgebiet sites, not two as previously proposed.

Taphonomy: Most of the lagomorphs found by the NPE were preserved in fossilised scats of a jackalsized carnivorous mammal or in small patches of sediment representing disaggregated scats. Few of the specimens show significant digestion attack, although at one fossil concentration the specimens have been altered by salt crystallisation, giving the enamel a flaked, pitted and etched appearance.

Dental nomenclature: Teeth are described using the dental nomenclature of Lopez-Martinez (1986) extended by Sen (2003) for the anteroflexid. The nomenclature of the flexa and flexids in ochotonids has not been applied uniformly by different authors. Lopez-Martinez (1986, fig. 1) defined the metaflexid as the indentation between the metaconid and entoconid, but in the text called this structure the mesoflexid. Sen (2003) called it the metaflexid. Because of its topographic position between the metaconid and entoconid, we refer to it as the mesoflexid. In the upper molars the indentation between the paracone and metacone is called the mesoflexus. It lies in line with the hypoflexus which is between the protocone and hypocone. In our opinion the postero-buccal flexid on

the m/3 is not the paraflexid (Sen, 2003) but is a reduced hypoflexid.

Upper teeth are given in capital letters with a / after the position in the tooth row (D4/ = deciduous upper fourth cheek tooth, P2/ = upper second premolar, M1/ = upper first molar) lower teeth are given in lower case letters with the / before the position in the tooth row (d/4 = deciduous lower fourth cheek tooth etc.).

Systematic descriptions

Order Lagomorpha Brandt, 1855 Family Ochotonidae Thomas, 1897 Genus *Austrolagomys* Stromer, 1924

Type species: *Austrolagomys inexpectatus* Stromer, 1924

Species *Austrolagomys inexpectatus* Stromer, 1924 Synonymy:

- 1924 *Austrolagomys inexpectatus* nov. gen. nov. sp. Stromer, 261.
- 1926 Austrolagomys inexpectatus nov. gen. nov. sp. Stromer, 127-128, Pl. 40, Fig. 16a-16d.
- 1929 *Austrolagomys simpsoni* nov. sp. Hopwood, 2, Fig. 1.
- 2003 *Austrolagomys inexpectatus* Stromer. Mein and Pickford, 175-176.
- 2003 *Austrolagomys simpsoni* Hopwood. Mein and Pickford, 175-176.

Referred material: See list of measurements. Specimens that have not been measured include GT 6'00 right d/3; GT 21'00, right premaxilla with I1/ and I2/; LT 116'99, mandible; LT 160'04; LT 287'99, lower molar; LT 34'01, tooth; LT 101'03, upper molar; LT 182'03, left M1/.

Distribution in Namibia: Elisabethfeld, Grillental, Langental.

Measurements of the teeth: See appendix 1.

Description: The type material in Munich (BSP 1926 X 14) consists of a maxilla and mandible found at Elisabethfeld (Stromer, 1924, 1926). Some of the teeth in the specimens are poorly preserved, having been abraded by wind-driven sand. The poor preservation unfortunately caused inaccuracies in the illustrations published by Stromer (1926, Fig. 16a-16d) (Mein and Pickford, 2003). The new material from the Northern Spergebiet is better preserved, in particular the fossils from Langental.

Maxilla: EF 207'01 is a poorly preserved, fragmental skull and mandible with most of the teeth (Fig. 1). The diastema between I2/ and P2/ is 10.2 mm long (Fig. 1b) and the length of the right cheek tooth row from P2/ to M2/ is 10.7 mm. The premaxillomaxillary suture is about half way along the diastema and anteriorly there is an elongated incisive foramen. The zygomatic arch departs abruptly from the maxilla opposite P3/ and curves backwards abruptly to run almost parallel to the tooth row. There is a distinct vertical crest of bone on the lateral surface of the maxilla above the anterior lobe of P3/ which joins the base of the zygomatic process. The lateral surface of the zygomatic arch is concave. The palate opposite the P3/ and P4/ is deeply vaulted, but damage prevents any observations of fenestra.

In GT 130'04, more of the palate is preserved (Fig. 2b). Laterally the maxillary crest above the P3/ is sharp, and separates the facial fossa in front from the remainder of the maxilla behind. In palatal view the palatine is seen to extend as far as the front of M1/, the suture separating it from the maxilla being curved. The rear edge of the maxillary fenestra is abraded but its position can be guaged by the vaulting in the maxilla. The posterior nares open opposite the front of M1/.

<u>Mandible</u>: The mandible of EF 207'01 (Fig. 1e) shows a diastema of 7.5 mm between the i/1 and p/3. The ventral part of the mandible is abraded, revealing the bases of the cheek teeth which extend ventrally beyond the incisor, the latter tooth lying lingual to the p/3, p/4 and m/1, terminating before m/2. The coronoid foramen is behind and slightly lateral to the m/3, and connects to the internal mandibular foramen on the medial side of the jaw about 3 mm behind the m/3.

<u>Upper dentition</u>: The upper central incisor is represented by several specimens. It has a deep, wide anterior groove, the bottom of the groove being closer to the mesial side (Fig. 1b1). The mesial ridge is sharp, but the distal one is rounded. The upper second incisor is tucked in immediately behind the I1/, close to the premaxillary suture (Fig. 1b1). Its section is oval with the long axis of the oval transversely oriented. The P2/ is an oval pillar, the long axis of the oval being transversely oriented. In little worn specimens the occlusal outline is oval with an anterior groove but in advanced wear the lingual side develops a crest and the anterior groove fades out, eventually to disappear about 1 mm from the radicular apex. The tooth is longitudinally curved, concave distally, so that its radicular end lies above the occlusal surface of the P3/. The alveolus of the P2/ in GT 130'04 shows the orientation well. The occlusal surface of the tooth broadens and lengthens as it wears which accounts for the large range of variation in the measurements. There is no root in any of the permanent cheek teeth.

The P3/ has a triangular occlusal outline. In worn teeth the paraflexus is elongated and curves distally near the centre line of the tooth. In several specimens the internal termination of the paraflexus is almost in the middle of the tooth, and not towards the buccal side. The hypoflexus forms a shallow groove on the lingual side of the tooth.

An extremely juvenile specimen of P3/, GT 54'06, has the paraflexus opening anteriorly and curving buccally as it enters the occlusal surface of the crown (Fig. 2d) but seen from its radicular end the paraflexus has a lateral opening. There is a shallow mesoflexus to the buccal side of the opening of the paraflexus, marked by two crests of enamel that converge towards each other. With wear this structure disappears completely, as it is absent in more worn examples of P3/ and is not visible in the radicular view of GT 54'06 (Fig. 2c). On the occlusal surface of this juvenile tooth the hypoflexus is weakly indented whereas at the radicular apex of the tooth it is more deeply invasive, showing that the dimensions of the hypoflexus also change with wear.

In conclusion, with increasing wear the detailed enamel outline of the occlusal surface of the P3/ of *Austrolagomys* changes dramatically until the teeth are moderately worn after which the form stabilises, but not the dimensions which continue to change.

The P4/ is bilobed, rectangular in occlusal outline (Fig. 1a, 1d, 2b). In the juvenile specimen, GT 54'06, the occlusal surface is very lightly worn, and shows the original structure well. There is a well developed but shallow paraflexus that extends from the buccal surface to a point across the centre line of the tooth. With about 1 mm of wear this structure would disappear completely. The hypoflexus is moderately indented in this specimen, and with wear would invade the crown more deeply, as seen from the radicular end. The protoloph is lightly worn exposing dentine in an arc between the protocone and paracone. Between the protoloph and the mesoflexushypoflexus axis, there is a shallow arc-shaped fossette bordered on the disto-lingual side by a low cusp. This fossette opens into the hypoflexus via a low sill. The small accessory cusplet behind and lingual to the anterior fossette has a posterior crest reaching towards the precrista of the hypocone, but separated from it by a shallow incision which connects the hyEarly Miocene Lagomorpha from the Northern Sperrgebiet, Namibia

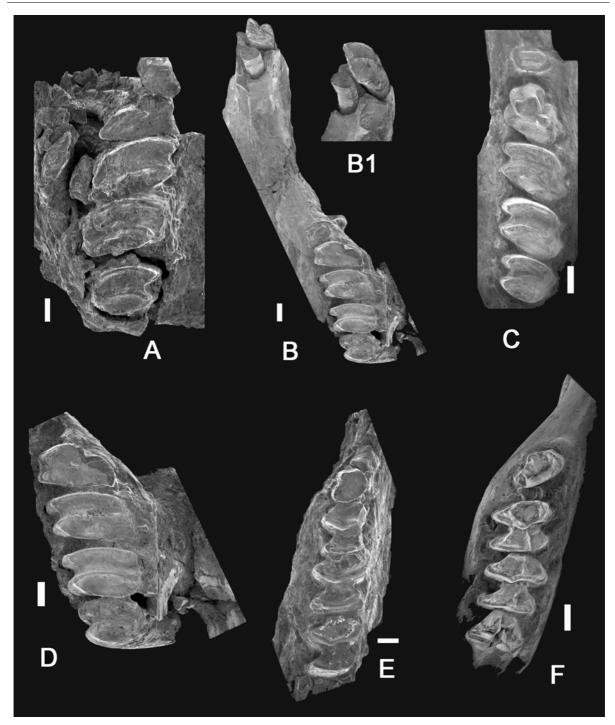


Figure 1: Austrolagomys inexpectatus from the Northern Sperrgebiet, Namibia. A) EF 207'01 right maxilla with P4/-M2/;
B) EF 207'01, left maxilla and premaxilla with 11/-12/, P3/-M2/;
B1) EF 207'01, enlargement of upper left incisors;
C) LT 453'96, left maxilla with P3/-M2/ and root of P2/;
D) EF 207'01 left maxilla with P3/-M2/ (enlargement of Fig. 1B);
E) EF 207'01, left mandible with p/3-m/1;
F) LT 160'04, left mandible with p/3-m/2 (damaged) (scale bars : 1 mm).

poflexus to the posterior fossette. The posterior loph is unworn and shows a shallow crescentic fossette which is confluent with the anterior fossette in the middle of the tooth and which at its buccal extremity connects to the mesoflexus via a narrow slit.

In worn P4/s, the superficial occlusal structures disappear and the hypoflexus, which is concave pos-

teriorly, comes to dominate the occlusal surface, penetrating almost to the buccal side of the crown. The mesoflexus, in contrast, almost disappears, remaining as an undulation in the buccal surface of the crown.

The M1/ is constructed along the same lines as the P4/, at least as far as concerns worn teeth (Fig. 1a,

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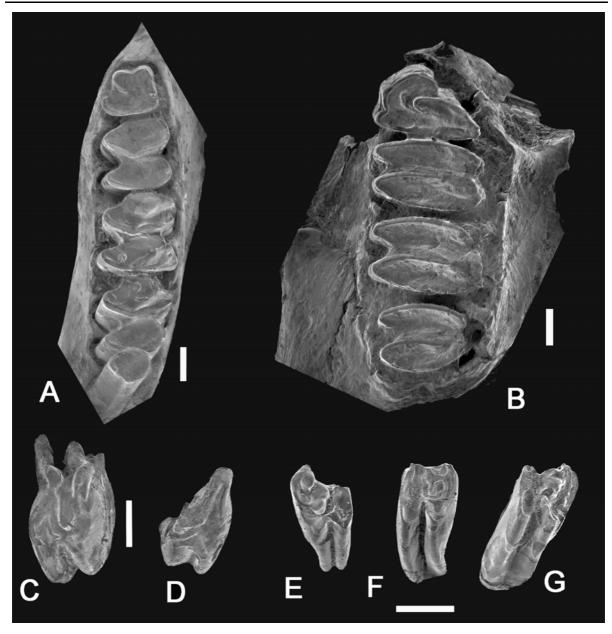


Figure 2: Austrolagomys inexpectatus from the Northern Sperrgebiet, Namibia. A) LT 34'05, left mandible with p/3-m/3; B) GT 130'04, left maxilla with P3/-M2/; C) GT 56'04, left P4/; D) GT 56'04, left P3/ (C-D are from a single individual); E) EF 102'05, right D2/ or D3/; F) EF 102'05, left D4/; G) EF 102'05, right D4/ (E-G are probably from a single individual) (scale : 1 mm).

1b, 1c, 2b). The posterior loph is narrower buccolingually than the anterior one. The M2/ is a smaller version of the M1/.

The deciduous upper teeth are represented by several specimens in various wear stages. The D2/, D3/ and D4/ are bilophodont teeth with roots (Fig. 2e, 2f, 2g). The hypoflexus is more or less invasive depending on the wear stage, and the paraflexus and mesoflexus are either well developed (in little worn teeth) or leave small fossettes on the occlusal surface (in lightly worn teeth) or are obsolete in worn teeth.

Lower dentition: The i/l has a flattened anterior surface and a rounded lingual one. Its internal apex ter-

minates on the lingual side of the radicular end of the m/1.

The d/3 is trilobed with a single triangular anterior cusplet connected to the second lophid by a central isthmus of enamel. The protoflexid and paraflexid are well developed. In material from Elisabethfeld and Grillental the second and third lophids are connected by a central isthmus of enamel, but two specimens from Langental show the third lophid separated from the second one by cementum. The rear portion of these teeth thus resemble the morphology of permanent molars.

The d/4 is bilophid with a slightly trapezoidal occlusal outline. It has no posterior basal pillar and in

the only available specimen from Langental, LT 84'97, there is no sign of a flexid, perhaps due to the advanced stage of wear. There is no connection between the enamel of the anterior and posterior lophs, the two being joined by cementum.

The p/3 is broader than long with two flexids on the anterior side, a small anterior one near the lingual end and a larger one invading the occlusal surface near the buccal end. The lingual side has a slight flexid.

The p/4, m/1 and m/2 are bilophid with the two columns joined by cementum (Fig. 1e, 1f, 2a). The m/3 is a single pillar which is strongly curved, the radicular end terminating close to the mandibular foramen slightly lower than the occlusal surface of the cheek teeth. It has a very slight postero-buccal flexid (the hypoflexid (paraflexid of Sen, 2003)).

Discussion

In the Arrisdrift monograph, Mein and Pickford (2003) showed that the species Austrolagomys simpsoni was a synonym of A. inexpectatus, the morphological characters listed in the diagnosis by Hopwood (1929) not differentiating the type specimen from Stromer's (1926) material which was poorly preserved and as a result, was inaccurately illustrated. The supposed size difference between the species was due to measurement error. There is, however, a d/3from Langental that shows no enamel connection between the second and third lophids, unlike specimens from Elisabethfeld which do. The Langental population may thus have been somewhat more evolved than the Elisabethfeld one, although individual variation cannot be ruled out to explain the difference

The upper central incisor section of Austrolagomys inexpectatus closely resembles that of Kenyalagomys rusingae (MacInnes, 1953, text-fig. 5). The occlusal morphology of the upper cheek teeth of Kenyalagomys mellalensis (Janvier and de Muizon, 1976) fall within the range of variation of Austrolagomys inexpectatus the slight differences in occlusal morphology being due to differences in wear stage rather than to fundamental differences in morphology. There can be little doubt that the various species of Kenyalagomys should be transferred to Austrolagomys, as was concluded by Mein and Pickford (2003).

<u>Relationships of *Austrolagomys* to other ochotonids</u>: There is at present no general agreement about ochotonid classification, some authors accepting a single family (Lopez-Martinez, 1986; Sen, 2003) and others up to three families (Erbaeva, 1988).

In her cladistic analysis, Lopez-Martinez (1986) found three broad groups of ochotonids, but these do not correspond to the three families proposed by Erbaeva (1988). In Lopez-Martinez's study, *Kenyalagomys* grouped with the genera *Sinolagomys* from the Oligocene of China, *Bellatona* from the Middle Mio-

cene of Asia and *Bohlinotoma* from the Oligocene of Asia. *Albertona balkanica* from Aliveri, Greece (MN 4) grouped with *Marcuinomys*, *Lagopsis*, *Alloptox* and *Titanomys*, while *Piezodus*, *Prolagus* and *Amphilagus* formed a third group.

Given that *Kenyalagomys* is a synonym of *Austrolagomys*, the latter genus would appear to have affinites with lineages from the Oligocene and Middle Miocene of China rather than with Middle Miocene forms from Europe. However, as Lopez-Martinez (1986) pointed out, there are some similarities between the teeth of *Kenyalagomys* and those of *Albertona* from Greece, such as the morphology of the P3/ and the degree of molarisation of the P4/, but the former differs from the latter by having a relatively smaller P2/ with one flexus only, the absence of a mesoflexid in adult p/3, and its very shallow centroflexid. There is also a size difference, *Kenyalagomys* being larger than *Albertona*.

The p/3 of *Austrolagomys* is shorter than broad and it has no mesoflexid, which differentiates it from *Bellatonoides eroli* from Sinap, Turkey (Sen, 2003) which possesses an enlarged and prolonged anteroconid and two flexids (called the centroflexid and metaflexid in Sen, 2003, which we call the centroflexid and mesoflexid) on the buccal aspect of the tooth. The Turkish species is smaller than *A. inexpectatus*.

<u>Biogeography</u>: *Austrolagomys* was widespread in Africa and, under the name *Kenyalagomys*, has been reported from the Early Miocene of the Middle East (Tchernov *et al.*, 1987) and the Middle Miocene of Morocco (Janvier and De Muizon, 1976; Lavocat, 1978). It is present in basal Middle Miocene deposits of Libya (Mein and Pickford, 2003; Wessels *et al.*, 2003) and is common in some Early Miocene deposits of Kenya such as Rusinga (MacInnes, 1957) while an unidentified ochotonid has recently been reported from the Middle Miocene of Bukwa, Uganda (Winkler *et al.*, 2005). The known stratigraphic range of *Austrolagomys* is from ca 21 Ma at Elisabethfeld, Namibia, to about 14 Ma at Beni Mellal, Morocco.

In Europe, ochotonids arrived during the Upper Oligocene and were abundant throughout the Miocene and Plio-Pleistocene, eventually going extinct in historic times. At many localities they are the dominant micromammal. In contrast, in Africa, ochotonids arrived later and died out sooner and, apart from one or two localities in Kenya, were seldom abundant, always being greatly outnumbered by rodents.

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Breadth Breadth Catalogue Tooth Length anterior posterior N٥ loph loph EF 102'05 GT 130'04 d/3 1.85 1.46 M2/ 2.13 3.08 EF 102'05 d/3 1.67 1.48 GT 95'04 M2/ 1.92 3.47 EF 71'96 d/3 2.08 1.72 LT 231'98 M2/ 1.88 2.98 EF 71'96 d/3 1.88 1.52 LT 453'96 M2/ 1.99 2.86 2.52 GT 6'00 d/3 2.20 1.85 GT 95'04 0.70 p/2 1.15 <u>p/2</u> LT 84'97 d/3 1.74 1.29 GT 95'04 0.90 1.43 <u>p/</u>2 LT 84'97 d/3 1.70 1.57 LT 34'05 1.45 1.95 LT 84'97 d/4 2.07 1.55 1.55 EF 207'01 <u>p</u>/3 1.66 1.60 EF 102'05 D3/ 1.28 2.53 <u>p</u>/3 1.26 1.96 GT 16'03 EF 102'05 D3/ 1.34 2.43 LT 232'98 <u>p</u>/3 1.32 1.97 EF 102'05 D4/ 1.28 2.85 LT 34'05 <u>p</u>/3 2.20 2.34 2.48 EF 102'05 D4/ 1.18 1.32 EF 207'01 <u>p/4</u> 2.07 2.10 EF 102'05 D4/ 1.25 2.20 EF 55'01 p/4 2.08 2.22 1.94 EF 102'05 D4/ 1.08 1.64 EF 71'96 1.90 1.90 p/4 1.77 EF 102'05 D4/ 1.25 2.05 GT 16'03 p/4 2.30 2.30 EF 207'01 i/1 1.80 1.85 LT 84'97 2.25 2.60 p/4 EF 207'01 I1/ 1.72 2.07 EF 71'96 2.20 2.20 1.90 p/4 or m/1 1.95 p/4 or m/1 EF 70'96 I1/ 1.53 GT 95'04 2.34 2.52 2.26 1.90 EF 70'96 I1/ 1.49 EF 102'05 P2/ 1.05 1.68 GT 95'04 I1/ 1.25 2.26 EF 102'05 P2/ 1.13 1.50 EF 207'01 I2/1.01 1.59 EF 102'05 P2/ 1.22 1.90 GT 95'04 I2/1.34 1.50 EF 33'96 P2/ 0.60 1.10 EF 112'01 2.00 2.20 GT 130'04 P2/ 1.10 2.20 m/12.25 EF 207'01 2.28 2.47 LT 230'98 P2/ 0.91 1.25 m/1EF 55'01 2.44 2.35 2.29 EF 207'01 P2/ 1.33 1.85 m/1EF 71'96 1.87 1.60 EF 102'05 P3/ 1.74 4.05 m/1EF 71'96 2.00 2.16 1.60 EF 207'01 P3/ 1.76 3.55 m/1LT 34'05 2.62 2.43 2.48 EF 33'96 1.58 m/1P3/ 3.80 EF 112'01 2.25 2.40 EF 70'96 1.43 2.77 m/2P3/ EF 207'01 2.62 2.50 2.10 EF 70'96 1.42 m/2P3/ 2.66 EF 55'01 2.63 2.38 1.87 EF 70'96 1.28 2.23 m/2P3/ EF 71'96 GT 130'04 2.43 2.02 1.94 2.25 m/2P3/ 3.60 LT 34'05 2.50 2.53 2.45 2.25 GT 95'04 P3/ 3.60 m/2EF 102'05 1.22 1.02 GT 95'04 P3/ 1.88 2.65 m/31.52 EF 102'05 1.16 2.27 m/3LT 453'96 P3/ 3.30 EF 55'01 0.90 0.85 GT 54'06 P3/ 1.10 2.00 m/3EF 71'96 1.10 1.00 1.90 m/3LT 231'98 P4 3.97 GT 3'97 0.95 1.89 m/3 1.18 LT 231'98 P4 GT 95'04 m/3 1.13 1.42 1.85 EF 207'01 P4/ 3.20 3.35 GT 95'04 m/3 0.96 1.30 EF 32'96 P4/ 2.00 3.50 LT 231'98 1.15 0.75 EF 33'96 P4/ 2.05 3.55 m/3 1.27 LT 34'05 1.25 EF 70'96 P4/ 1.79 3.15 m/3 EF 207'01 2.93 3.14 2.95 M1/ EF 70'96 P4/ 1.60 3.45 EF 32'96 2.10 3.80 M1/ GT 130'04 2.05 3.95 P4/ 3.85 EF 33'96 1.95 3.30 M1/ GT 54'06 P4/ 1.72 2.95 2.89 EF 70'96 M1/ 1.82 LT 453'96 P4/ 1.89 3.18 3.50 3.93 GT 130'04 2.25 3.90 GT 130'04 P4/? 2.78 M1/ 1.65 2.63 GT 95'04 2.01 3.67 M1/ LT 231'98 1.99 M1/ 3.60 LT 453'96 2.32 3.27 3.15 M1/ 2.77 EF 207'01 2.42 M2/ 1.85 EF 70'96 1.75 2.87 M2/

Appendix 1. Measurements (in mm) of the teeth of *Austrolagomys inexpectatus* from the Northern Sperrgebiet, Namibia (EF = Elisabethfeld, GT = Grillental, LT = Langental).

EF 70'96

1.79

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M2/