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Orangemeryx hendeyi

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Fossil picas (Ochotonidae, Lagomorpha, Mammalia) from the basal Middle Miocene of Arrisdrift, Namibia

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Lagomorpha from the Proto-Orange deposits at Arrisdrift are assigned to the genus *Austrolagomys*. Better samples of this genus from the type locality, Elisabethfeld, reveal that it is similar to *Kenyalagomys*, the perceived differences between the genera being due to damage to the material available to Stromer (1926). *Kenyalagomys* MacInnes, 1953, is thus a synonym of *Austrolagomys* Stromer, 1926. The Arrisdrift specimens are assigned to a new species of *Austrolagomys*.

Résumé français

Les picas sont des petits lagomorphes. Le bon échantillon d'ochotonidés du Miocène moyen basal d'Arrisdrift résoud plusieurs problèmes d'ordre systématique. Connu par un crâne et plusieurs mandibules *Austrolagomys hendeyi* nov. sp. est suffisamment différent de l'espèce type *A. inexpectatus* pour justifier la création d'une espèce nouvelle. L'espèce d'Arrisdrift, placée auparavant dans le genre *Kenyalagomys* par Hendey (1978) est en fait proche d'*Austrolagomys*. L'examen de nouveaux spécimens d'*A. inexpectatus* de la localité type (Elisabethfeld, Namibia) montre que certains caractères signalés et figurés par Stromer (1926) sont inexacts, établis sur un matériel érodé où cassé. Les différences supposées avec *Kenyalagomys* utilisées par MacInnes (1953) quand il créa le genre Est- Africain ne sont donc plus réelles et il est maintenant évident que ces deux genres sont synonymes. Les différences entre les formes de Namibie et du Kenya ne sont pas d'ordre spécifique. En plus l'espèce *A. simpsoni* érigée par Hopwood (1939) à partir du spécimen de Langental est synonyme d'*A. inexpectatus*; la différence de taille supposée résulte d'une erreur dans la mesure des fossiles. Il n'y a aucune différence morphologique avec le nouveau matériel récolté à Elisabethfeld.

Introduction

Hendey (1978) described several lagomorph specimens from Arrisdrift, and pointed out that they were closer morphologically to *Kenyalagomys minor* than to *Austrolagomys inexpectatus*. The material fell outside the range of variation of the known species of *Kenyalagomys*, (*K. rusingae*, which is larger than the Arrisdrift species and *K. minor*, which is the same size but differs in some features of the dentition). Hendey proposed that the Namibian fossils represented a new species of *Kenyalagomys*, but he did not name it.

Arrisdrift has yielded some important ochotonid material including a partial skull and several mandibles.

Systematic descriptions

Order Lagomorpha Brandt, 1855
Family Ochotonidae Thomas, 1897
Genus *Austrolagomys* Stromer, 1926

Emended diagnosis: Upper P2/ reduced, upper P3/ with single flexus (mesoflexus) with deep enamel fold antero-externally; upper P4/ molarised; lower incisor root extends backwards to terminate as a swelling on the lingual surface of the mandible near the rootward end of m/1; lower m/3 unilobed. Dental formula upper 2-0-3-2 : lower 1 0 2 3*

*NB MacInnes (1957) reported that 8 specimens of *Kenyalagomys minor* possessed alveoli for a lower p/2, but only one of them retained a tooth fragment, a partial root. None of the Namibian material shows any sign of an alveolus anterior to p/3, neither do any of the specimens assigned to *K. rusingae* by MacInnes. Without re-examining the specimens of *K. minor* we cannot exclude the possibility that the alveoli interpreted by MacInnes as being for a p/2 may perhaps be where a deciduous tooth was emplaced, and that if the individuals had lived longer, then the alveoli may have disappeared. If MacInnes is

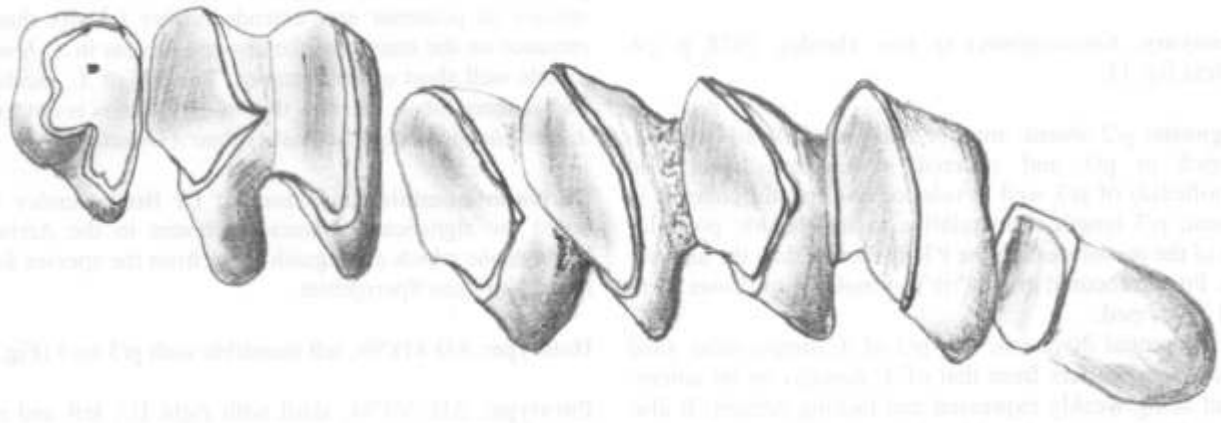

Figure 1: AD 418'99, *Austrolagomys hendeyi* sp. nov., left mandible, occlusal view of the cheek teeth.

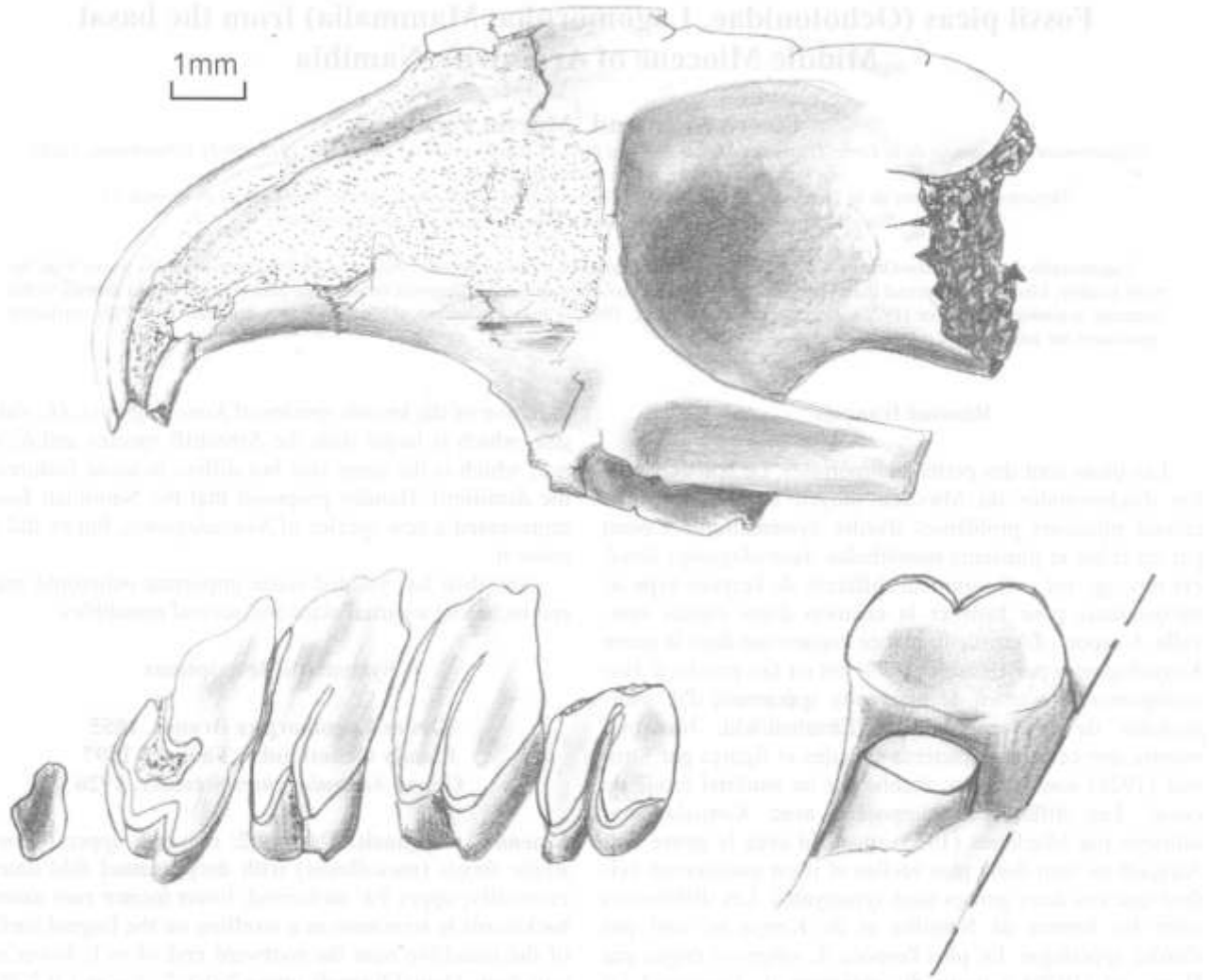

Figure 2: AD 261'94, *Austrolagomys hendeyi* sp. nov., snout with dentition, a) left lateral view; b) left cheek teeth occlusal view; c) right upper incisors internal view.

right about these alveoli, then it suggests that there may well be a second genus of ochotonid in East Africa the dental formula of which would be upper 2-0-3-2 : lower 1-0-3-3, but such a revision is outside the scope of this paper.

Type species: *Austrolagomys inexpectatus* Stromer, 1926

Species: *Austrolagomys hendeyi* sp. nov.

Synonymy: *Kenyalagomys* sp. nov. Hendey, 1978, p. 29-31, text fig. 13.

Diagnosis: p/2 absent; anterior fold (anteroflexid) well developed in p/3 and covered in cement; labial fold (hypoflexid) of p/3 well developed and mostly covered in cement; p/3 length short relative to its breadth; posterior arm of the mesoflexus in the P3/ is shorter than the anterior arm. Postprotoconid crista ('rib') of molariform lower teeth well developed.

Differential diagnosis. The p/3 of *A. inexpectatus* (and *A. simpsoni*) differs from that of *A. hendeyi* by its anteroflexid being weakly expressed and lacking cement. It also differs by its greater breadth relative to its length. The hypoflexid in p/3 of *A. inexpectatus* is present but has no cementum. *A. hendeyi* differs from *A. minor* by its superior size (mandibular depth below p/3 is 6.5-6.6 mm in *A. minor* and is 8.3-8.85 mm in *A. hendeyi*). It differs from *A. rusingae* by its less well developed hypoflexid in the p/3, its smaller size (P3/-M2/ in *A. rusingae* is 9.25-9.5 mm, whereas in *A. hendeyi* it is 8.9 mm) and narrower skull. The P3/ of *A. mellalensis* differs from that of *A. hendeyi* by its weakly developed hypostria and the extremely elongated posterior arm of its mesoflexus. In the Beni Mellal species its posterior arm extends further labially than its entrance on the margin of the crown whereas in *A. hendeyi* it ends well short of the entrance. The P2/ of *A. mellalensis* has three lobes, whereas that of *A. hendeyi* is not lobed. *A. mellalensis* is slightly smaller than *A. hendeyi*.

Derivatio nominis: In honour of Dr Brett Hendey who noted the significant characters present in the Arrisdrift lagomorphs which distinguish them from the species found in the Northern Sperrgebiet.

Holotype: AD 418'99, left mandible with p/3-m/3 (Fig. 1).

Paratype: AD 261'94, skull with right I1/, left and right I2/, right P3/-M1/: left P3/-M2/ (Fig. 2).

Remainder of hypodigm: PQAD 813, left mandible with m/1-

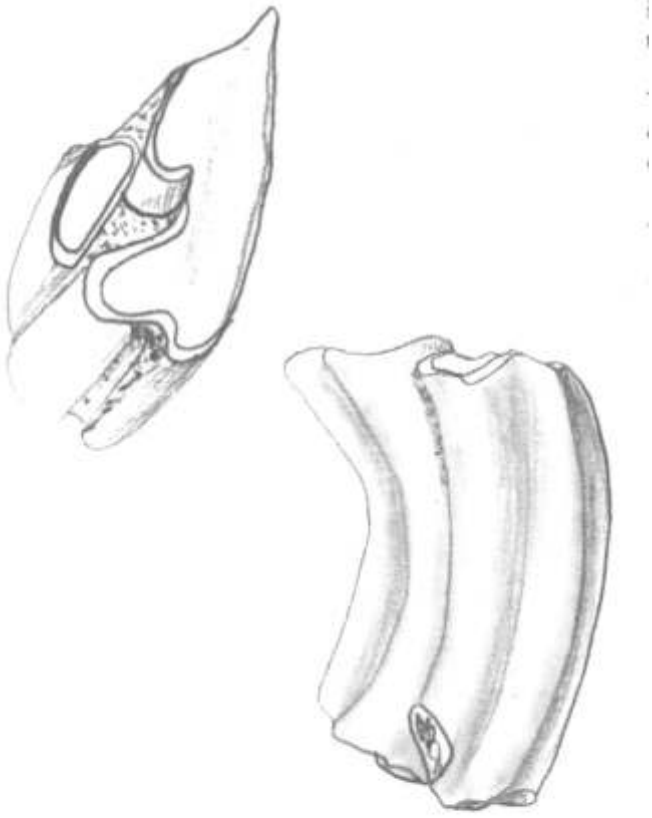

Figure 3: PQAD 1185, *Austrolagomys hendeyi* sp. nov., left upper P3/, a) occlusal view; b) mesial view.

m/2; PQAD 1185, left P3/ (Fig. 3); PQAD 1135, left mandible with p/4-m/3; PQAD 1684, left maxilla with P3/-M1/; PQAD 2118, left mandible with m/1-m/3; AD 262'94, right mandible with incisor and p/3-m/1; AD 263'94, left mandible with p/4-m/3; AD 63'95, right mandible with p/4-m/1; AD 226'97, right mandible with incisor and p/4-m/2; AD 411'97, molariform left lower cheek tooth, probably p/4; AD 18'98, right P4/; AD 418'00, right M1/; AD 503'00, right mandible with p/4-m/2; AD 680'00, left mandible with p/4-m/1; AD No number, left lower incisor (may be the same individual as PQAD 1135).

Description: Mandible. The depth of the mandible is relatively great compared with other species of the genus. The ascending ramus is not preserved in any of the Arrisdrift specimens, but its root suggests that it was probably nearly vertical. The swarm of nutritive foramina on the lingual side of the body is well preserved in AD 226'97 and there is a low swelling representing the incisive jugum which ends below the m/1. Unfortunately, the jaw AD 418'99 is broken and distorted in this region. In material from Elisabethfeld, the incisive jugum ends vertically below the m/2 which corresponds to the rootward end of the m/1, the molars sloping forwards from their roots to their occlusal surfaces. The position of the incisive jugum is thus similar in *A. inexpectatus* and *A. hendeyi* as well as in Kenyan material of the genus (MacInnes, 1957, text fig. 4). Note that MacInnes described the position of the distal end of the swelling as being "approximately below the posterior end of the m/2" which, taken at face value would suggest a difference from the Namibian species, but it is below the occlusal surface of the m/2, and not its root, the molars sloping backwards and downwards into the jaw. Thus its position is precisely as in the Namibian fossils.

The lower incisor has an equilateral triangular section. The enamel is thicker on the labial surface than on the other two sides. There is a shallow open groove on the lateral surface, as in *A. rusingae* and *A. minor*.

All the cheekteeth are hypsodont and there is no trace of roots in any of the teeth.

The p/3 is almost vertical in the jaw (in lateral view the tooth is slightly convex anteriorly), with a flat occlusal surface which is wider at the rear than at the front. It is covered by abundant cement which completely fills the flexids. There are two flexids, an anterior one which is moderately deep (the anteroflexid) and a labial one which is deeper. The posterolabial lobe (hypoconid) is well developed.

The p/4, m/1 and m/2 are approximately similar in size. The breadth of the posterior lobe is greater than that of the anterior lobe in p/4 but it is narrower than the anterior lobe in m/2. These molariform teeth present two lozenge shaped lophs (trigonid and talonid). The postprotoconid crista (posterior trigonid rib) of molariform lower cheek teeth is strongly developed, as was noted by Hendey (1978).

The p/4 is completely molariform with two subequal lobes (the anterior one is slightly longer in occlusal view than the posterior one). The enamel is thicker on the posterior and labial surfaces than it is on the anterior and lingual surfaces. In occlusal view, the trigonid has a fold in the enamel on its anterolabial contour where the enamel thickness diminishes anteromesially. This fold is present throughout the height of the tooth. The labial ends of the lobes have pointed enamel outlines, whereas the lingual ends are rounded in outline. The enamel on the posterior side of the anterior lobe is developed into a 'rib' in the midline of the crown but it does not meet the posterior lobe. Thus the two lobes (trigonid and talonid) are independent of each other but are held together by cement. The tooth is almost straight in lateral view and is almost vertical in the jaw. Because of this, the occlusal surfaces of the p/3 and p/4 are in contact, but their alveoli are separated by a short gap. The occlusal surface of p/4 is not flat, but wears into two transverse ridges, higher posteriorly than anteriorly. The talonid ridge is equal in height throughout, but the trigonid ridge descends towards the 'rib' from both ends.

The m/1 is similar to the p/4 in most respects save that the posterior rib of the protoconid is less well pronounced and, in lateral view, the tooth is lightly curved and slopes gently to the rear from its occlusal surface rootwards. Thus its rootward end is vertically below the occlusal surface of m/2. Because of this slight curvature, the talonid is lower than the protoconid, even if, at the occlusal surface they appear to be at the same height. The breadths of the two lobes are almost equal. The anterolabial fold in the enamel is more marked than it is in the p/4.

The m/2 is like the m/1 except for its narrower talonid relative to the trigonid, and its slightly greater curvature from occlusal surface rootwards.

In AD 418'99, the m/3 is single lobed and slopes strongly to the rear, so much so that in lateral view the rear of the occlusal surface is higher than its front. On the postéro-lingual corner of the crown there is a low enamel crest which descends the entire height of the tooth. Apart from that, the occlusal outline of the tooth is oval with slightly flattened an-

Table 1: Measurements of the teeth, skull and mandible (in mm) of *Austrolagomys hendeyi* sp. nov. from Arrisdrift, Namibia (e = estimated measurement).

Specimen	length	anterior breadth	posterior breadth
Upper dentition and skull			
PQAD 1185, P3/	1.63	2.92	3.50
PQAD 1684, P3/	1.70	2.87e	
PQAD 1684, P4/	1.89	4.09	3.55
PQAD 1684, M1/	1.96	3.68	3.22
PQAD 1684, length P3/-M1/	6.07		
AD 261'94, right I1/(ap x tr)	1.41	2.36	
AD 261'94, left I2/ (ap x tr)	1.32	1.53	
AD 261'94, right I2/ (ap x tr)	1.22	1.55	
AD 261'94, left P3/	1.77		3.87
AD 261'94, left P4/	1.82	3.80	3.50
AD 261'94, left M1/	2.13	3.60	3.41
AD 261'94, left M2/	1.94	--	2.70e
AD 261'94, zygomatic breadth		2 x 11.8 = 23.6	
AD 261'94, breadth interorbital constriction		2 x 3.8 = 7.6	
AD 261'94, length I1/-M2/	27.2		
AD 261'94, length diastema	11.5		
AD 261'94, length P2/-M2/	11.35		
AD 261'94, length P3/-M2/	8.9		
AD 261'94, external palatal breadth at P4/		17.5e	
AD 261'94, internal palatal breadth at P2/		5.3e	
AD 261'94, internal palatal breadth at M2/		2 x 3.7 = 7.4e	
AD 261'94, height of skull at M1/	19.7		
AD 18'98, rt P4/	1.76	3.86	3.70
AD 418'00, M1/	2	2.9	2.9
Lower dentition and mandible			
PQAD 813, depth of mandible	8e		
PQAD 1135, p/3	1.20	1.87	
PQAD 1135, p/4	1.93	1.94	2.70
PQAD 1135, m/1	2.30	2.23	2.24
PQAD 1135, m/2	2.24	2.33	2.05
PQAD 1135, length p/3-p/2	7.04		
PQAD 2118, m/1	2.16	2.18	2.38
PQAD 2118, m/2	2.50	2.13	2.18
PQAD 2118, m/3	0.70	1.31	
PQAD 2118, length m/1-m/3	5.45		
PQAD 2118, mandible depth at p/3	8.3		
AD 262'94, p/3	1.31	1.93	
AD 262'94, p/4	2.35	1.90	1.90
AD 263'94, p/4	1.75	2.40	2.00
AD 263'94, m/1	2.20	--	--
AD 263'94, m/2	2.60	2.05	1.83
AD 263'94, m/3	2.04	1.10	
AD 263'94, length p/3-m/2	6.95		
AD 63'95, p/4	2.5	2.1	2.65
AD 63'95, m/1	2.6	2.6	2
AD 411'97, ?m/2	2.30	2.20	2.06
AD 226'97, incisor (ap x tr)	2.09	1.91	
AD 226'97, p/4	2.28	2.05	2.17
AD 226'97, m/1	2.20	2.18	2.18
AD 226'97, m/2	2.28	2.12	1.85
AD 226'97, length p/4-m/2	6.68		
AD 226'97, mandible depth at p/3	8.85		
AD 418'99, p/3	1.25	2.05	
AD 418'99, p/4	2.08	1.97	2.25
AD 418'99, m/1	2.50	2.32	2.44
AD 418'99, m/2	2.56	2.32	2.25
AD 418'99, m/3	0.80	1.53	
AD 418'99, length p/3-m/2			8.75
AD 418'99, length p/3-m/3			10.15
AD 503'00, p/4	2.1	2.3	2.3
AD 503'00, m/1	2.3	2.6	2.25
AD 503'00, m/2	2.7	2.4	2.5
AD 680'00, p/4	2.05	2.0	2.15
AD 680'00, m/1	2.3	2.4	2.75
AD No number, incisor (ap x tr)	2.05	1.95	

terior and posterior surfaces. In AD 263'94, the low enamel crest is more distal in position.

Skull. In the palate, between the incisive foramina and the posterior choanae, there are several accessory foramina. The anterior palatal foramen is located in the maxilla near the tooth row opposite the lingual roots of P3/-P4/ and a second foramen is located on the maxillo-palatine suture about a third of the distance across the palate opposite the rear of P4/. The positions of these foramina are similar to those of *Austrolagomys rusingae* (MacInnes, 1957, text fig. 2). In AD 261'94 the posterior root of the zygomatic arch is located above the rear of M1/, as in *A. mellalensis* (Janvier & de Muizon, 1976), but different from *A. rusingae* in which it is located further backwards above the rear of M2/.

There is a large inferior antorbital foramen in front of the anterior root of the zygomatic arch and there are several accessory foramina in front of it. Much of the upper part of the skull in front of the orbits has broken away, but the preserved parts appear to be similar to *A. rusingae*.

The upper central incisor has a wide and deep groove on its labial surface, the base of the incision being closer to the mesial side of the tooth than to the lateral edge. The anteroposterior breadth is greater on the lingual side than the lateral one, as in *A. rusingae*. The posterior surface of the tooth is flat.

The second upper incisor is tucked in behind the central incisor and is much smaller than it. It is longitudinally curved and its section is almost circular.

The upper P2/ is not present in the Arrisdrift collection, but the skull AD 261'94 has alveoli immediately in front of the P3/s. The alveolus is wider than long and has a posterior margin with a re entrant in its outline and uniformly curved anterior border.

The upper P3/ has a trapezoidal occlusal outline, with long posterior and labial sides, and short anterior and lingual ones. The posterior margin has a shallow, wide groove near its labial end. The lateral surface also has a shallow, wide groove near the postero-labial extremity of the crown, which contributes to the pointed appearance of this corner (the most lateral part of the post-lobule of Lopez Martinez, 1989). In anterior view the tooth is curved from its occlusal surface rootwards. There is a deep groove between the anterior and labial surfaces which marks the entrance to the mesoflexus. The lingual flexus immediately behind it is deep and is covered by cement. In occlusal view the mesoflexus is narrow near the lateral margin, but widens towards the centre of the tooth before turning backwards and laterally in a short extension which ends about the midline of the tooth. The length of the posterior arm of the mesoflexus does not change with wear, as shown by its termination in the radicular view of PQAD 1118. Because of this morphology, *A. hendeyi* is considered to be specifically distinct from *A. mellalensis* which has a posterior arm of the mesoflexus which extends much closer to the labial edge of the tooth (Janvier & de Muizon, 1976).

In the P3/ there is a shallow fold in the enamel at the lingual end of the mesial surface between the mesial hypercone and the mesial hyperloph. In P3/ number PQAD 1118, in occlusal view there is a very narrow connection between this fold and the mesoflexus, which thereby separates the mesial hyperloph from the mesial hypercone. In AD 261'94, in contrast, the mesial hyperloph and mesial hypercone are joined by a continuous band of dentine which separates the mesoflexus from the anterior margin of the tooth. This difference could be due to the relatively unworn state of the former tooth and the more worn condition of the P3/s in AD 261'94. Nevertheless there is a constriction in the enamel outlines which reveals where these two cusps used to be separated when unworn. In its morphology the P3/ of *Austrolagomys* resembles that of Lagopsis from Europe (Lopez Martinez, 1989).

The P4/-M2/ are completely molariform and resemble each other. They are typical ochotonid teeth, with two lobes. It has a hypoflexus which traverses two thirds of the tooth. This flexus is concave distally. The enamel is thicker on the anterior surfaces of each lobe as well as on the lingual margins than it is posteriorly and labially. The labial side of each lobe terminates in a point, the distal one being better developed than the anterior one. The P4/ is the widest of the cheek teeth. The hypoflexus is filled with cement which extends lingually well past the enamel.

The M1/ has a slightly longer hypoflexus than the P4/, but is otherwise similar to it. The M2/ is the smallest of the molars and its hypoflexus is more curved than in the preceding teeth.

Discussion: The differences between *Austrolagomys* and *Kenyalagomys* listed by MacInnes (1953) are subtle and some were even based on the supposed accuracy of Stromer's (1926) figures. We now have augmented samples of *Austrolagomys inexpectatus* from the type locality, Elisabethfeld, and other sites such as Langental and Grillental in the northern Sperrgebiet. It is now clear that in some respects, the figures in Stromer (1926) are defective, mainly due to damage to the specimens available to him. It is also evident that some of the supposed differences between the genera are due to differences in wear stages of the dentitions. The columns of enamel in the cheek teeth are slightly wider at their bases than at their summits, and thus measurements of the occlusal surface may yield a misleading view of variability in the samples.

MacInnes (1953) listed five dental characters and one mandibular one which he took to separate the two genera. We have examined each of these characters and find that none of them holds up against the new collections.

1. The upper second premolar of *Austrolagomys* possesses a shallow fold on its anterior surface, and is not convex as reported. In this it is similar to *Kenyalagomys*.

2. In the upper third premolar of *Austrolagomys* there is a deep, narrow V-shaped fold in the external surface of the enamel. Stromer's (1926) figure shows a slight fold, but other material shows a deep fold, as in *Kenyalagomys*.

3. The hypostria of the upper molariform teeth of *Austrolagomys* extend almost 4/5 of the way across the crown, as in *Kenyalagomys*.

4. The external enamel fold in the lower p/3 of *Austrolagomys* is present, even if not as deep as in *Kenyalagomys*. We consider that this feature is variable and its expression at the occlusal surface could vary with the stage of wear of the tooth. It may be of specific value, but is not, in our opinion, useful for separating genera.

5. The 'rib' which descends the posterior surface of the trigonids of the molariform lower cheek teeth is indeed marked in *Kenyalagomys* and material from Arrisdrift, as pointed out by Hendey (1978), but such ribs are not absent in *Austrolagomys*, they are more subtly expressed as a slight swelling in the posterior wall of the trigonid. This difference is not one of

kind, but of degree, and it is easy to see how the slight swelling in the posterior surface of the trigonids of *Austrolagomys* could give rise to the 'ribs' in *Kenyalagomys*. These ribs do not meet the talonids behind them as suggested by MacInnes (1953) - the trigonids and talonids are separated from each other by cementum throughout their entire height.

6. The ascending ramus of *Austrolagomys* is almost vertically oriented, as in *Kenyalagomys*. The figure in Stromer (1926) suggests a posteriorly sloping ascending ramus, but the specimen is damaged. Other samples from Namibia show a more vertical ramus.

Thus none of the characters that were used by MacInnes (1953) to diagnose and define *Kenyalagomys* as a separate genus from *Austrolagomys* holds up under scrutiny of the new material from the type locality of *A. inexpectatus*. *Kenyalagomys* MacInnes, 1953, is thus a synonym of *Austrolagomys* Stromer, 1926.

Hopwood (1939) erected the species *Austrolagomys simpsoni* on the basis of three dental characters which he took to separate it from the type species. These were the deep external fold in the p/3, the marked angulation or 'rib' on the posterior surface of the anterior loph of each lower molar, and the squared outline of the m/3. In addition he reported that his species was slightly smaller than the type species.

New material from the type locality at Elisabethfeld reveals that the depth of the external fold in the p/3 does not differ significantly between the two species. The posterior 'rib' in lower molariform teeth is present in Elisabethfeld specimens, but it is subtle, and not markedly different from the Langental specimens available to Hopwood. The m/3s from Elisabethfeld are similar to those from Langental and possess a shallow posterior concavity in the enamel outline. Because the m/3 slopes strongly to the rear, as wear progresses the occlusal outline can and does change markedly from almost circular to oval to squarish with rounded corners. Thus the squared outline of the m/3 in *A. simpsoni* is due to its wear stage, and not to a fundamental difference in morphology from *A. inexpectatus*. The differences in size are possibly due to different ways of measuring. We have compared casts of the specimens directly, and observe that the two holotypes are not very different (p/4-m/2 is 6.3 mm in the type specimen of *A. simpsoni* and is 7.5 mm in the type of *A. inexpectatus*). Hopwood (1929) gives the measurement of p/4-m/3 as 6.1 mm, but this is erroneous. The two species are thus likely to be synonyms.

Janvier & de Muizon (1976) described *Kenyalagomys mellalensis* from Beni Mellal, Morocco which differed from *K. rusingae* by its slightly smaller size, by the presence of a trilobed P2/ and hypostriae which extend almost to the labial wall of the upper molars. It should probably be transferred to the genus *Austrolagomys*.

Tchernov *et al.*, (1987) recorded *Kenyalagomys* from Israel, but it should probably be transferred to *Austrolagomys* as it is reported to be similar to *K. rusingae*. The genus is also present at Gebel Zelten although it was first reported as Ochotonidae indet., in Savage, (1990). A cast of a P3/ from Gebel Zelten présented to PM by O. Fejfar belongs to *Austrolagomys*.

Conclusion

A derived species of *Austrolagomys* occurs at Arrisdrift, where it is represented by a skull and several jaws and isolated teeth. The main difference from the Early Miocene species *Austrolagomys* inexpectatus resides in the better developed posterior 'rib' on the trigonid of each molariform lower molar. In some respects the Arrisdrift species is closer to the species *A. minor* from East Africa, but in others, such as absence of lower p/2, it differs from it. The genus appears to have been widespread, because it occurs in Namibia, East Africa, Libya, Morocco and possibly Israel.

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