Incisor morphology as an aid in the systematics of the South African Leporidae (Mammalia: Lagomorpha)

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Photomicrographs of cross-sections through the principal upper incisors of the South African Leporidae were evaluated for use in species identification. Differences in incisor width and the pattern of the enamel fold provide a reliable means of distinction between *Lepus capensis* and *L. saxatilis*. Incidental comparisons of incisor cross-sections of the South African *L. capensis*, including those from the type locality, and the taxonomically controversial *L. europaeus* reveal marked differences which may be useful in the delimitation of these taxa. Within *Pronolagus*, distinct differences were evident between the incisor patterns of *P. rupestris* and its congeners, *P. crassicaudatus* and *P. randensis*, which are similar with respect to this character. Similarly, striking differences were evident between the incisors of the monotypic *Bunolagus monticularis* and both *L. saxatilis* and, importantly in view of their close phenetic relationship, *L. capensis*.
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Fotomikrograwe van dwarssnitte van die hoof boonste snytande van die Suid-Afrikaanse Leporidae is geëvalueer as taksonomiese hulpmiddel vir die identifikasie van spesies. Verskille in snytandbreedte en die vorm van die emaljevou verskaf 'n betroubare metode om die spesies *Lepus capensis* en *L. saxatilis* van mekaar te onderskei. Vergelyking van snytanddwarssnitte van die Suid-Afrikaanse *L. capensis*, insluitende die afkomstig van die tipe lokaliteit, en die taksonomies betwisbare *L. europaeus* het duidelike verskille tussen hulle uitgewys. Die bevindings kan moontlik in die onderskeiding van die taksa van groot waarde wees. Binne die genus *Pronolagus*, is daar duidelike verskille tussen die snytandpatrone van *P. rupestris* en die ander verteenwoordigers van die genus, nl. *P. crassicaudatus* en *P. randensis*, wat op hul beurt weer eenders in die opsig is. Duidelike verskille is ook aanwesig tussen die snytande van die monotipiese *Bunolagus monticularis* en beide *L. saxatilis* en die feneties naverwante *L. capensis*.
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The enamel folding responsible for the notched appearance of the labial or outer surface of the principal upper incisor and the shape of the tooth in cross-section provide valuable information for use in systematic studies in the Leporidae. Although differences in the enamel patterns of certain species of *Lepus* have been known for some time (Forsyth Major 1898) it would appear that other than Petter's work on African and Asian species of this genus (Petter 1959, 1961, 1963; Petter & Genest 1965), these criteria have not been used widely as major taxonomic characters in leporid systematic investigations.

In the present study, the reliability of characters such as the shape of the incisors in cross-section, the pattern of the enamel invaginations and the presence or absence of cement in this structure are evaluated for use as systematic criteria, particularly with reference to the South African species. It is proposed that the use of this technique will, in most cases, identify species of unknown provenance where neither cranial nor pelage characteristics are available.

Material and Methods

A single principal upper incisor was extracted from the skull of each specimen used in this investigation, embedded in a polyester mounting medium and sectioned using a modified Beuhler Isomet low speed saw (Beuhler Ltd, Evanston, Illinois, USA). Each tooth section was placed on a microscope slide, immersed in a drop of xylene and examined using bright field illumination. The xylene tends to reduce the opacity of the sections, resulting in a more translucent preparation which is suitable for photomicrographic analysis.

The species, number of specimens analysed in each and their localities are presented below (Table 1). Map co-ordinates

Table 1 The respective species utilized in this investigation, their sample sizes and geographic origins presented in tabular form. The localities from which animals were derived are numerically coded and correspond to the annotations used in the Gazetteer

Species	Sample size	Geographic locality code
L. capensis	32	3;7;9;14;16;21 – 22;30 – 31
L. saxatilis	102	1 – 11;13 – 24;26 – 31;33;38;40
P. rupestris	15	14;16;21;24 – 25;28 – 29
P. crassicaudatus	15	26 – 27
P. randensis	14	32;34 – 37;39;41 – 45
B. monticularis	2	12

of these localities were, in most cases, taken with reference to the nearest town using the gazetteers of the United States Board of Geographic Names (South Africa Vols I + II, Division of Geography, Department of the Interior 1954) and Skead's Zoo-Historical Gazetteer (Skead 1973). Where place names were not listed in either of the above sources, use was made of the 1 : 250 000 topocadastrial map series. These data are given in Appendix 1. The geographic origins of the extralimital species used in incidental comparisons in this investigation are omitted from Table 1, but are presented in the text.

Results and Discussion

Variation with age, attrition and between incisors of the same specimen

Although Forsyth Major (1898) proposed that the variation in tooth pattern may reflect an age component in that '. . . species whose incisors show the most complicated pattern in the adult have as yet no trace of this in very young animals, and, *vice versa*, in very old specimens complication tends to disappear again', no evidence of this was found in the test material. Comparisons of incisor cross-sections between skeletally immature and mature specimens (see Robinson 1981; Robinson & Dippenaar 1983 for ageing criteria) failed to reveal any consistent differences, whereas further supportive evidence for the reliability of this character was obtained by sequentially sectioning representative incisors along their entire lengths (Figure 1). This was done to determine whether attrition (and indirectly age, since the incisors in the Leporidae are open rooted) would alter the configurations in any way. Figure 1 illustrates the uniformity in both the enamel fold and presence of cement along the entire length of a *L. saxatilis* tooth. A similar lack of variation in the incisors of the other taxa was also observed.

Preliminary tests revealed that minor differences were sometimes evident between the left and right incisors of a single specimen, thereby confirming earlier observations (Forsyth Major 1898; Petter 1959). However, these differences were never so pronounced that, depending on the tooth sectioned, ambiguous classification of the species could result.

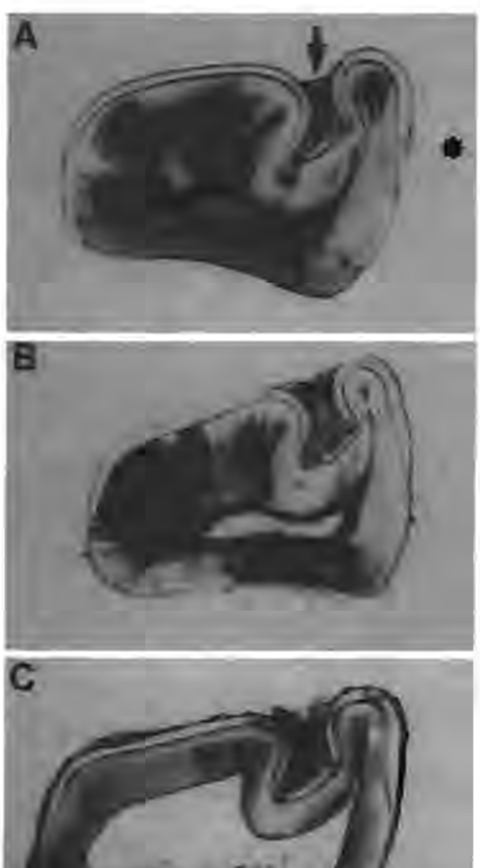

Figure 1 Cross sections through the left principal upper incisor of *L. saxatilis* showing the uniformity of the enamel fold and deposition of cement (arrow) in this structure along the entire length of the tooth. (A) The tooth sectioned near the biting surface, (B) midway down the shaft of the tooth and (C) near the root. The arrow and asterisk indicate the anterior and medial surfaces respectively.

Incisor tooth pattern variation in *L. capensis*

The *L. capensis* incisor tooth pattern provides a reliable means of separating this taxon from the other *Lepus* material. The enamel fold was consistently shallow, always of simple configuration and, without exception, always characterized by the presence of cement. Figure 2 shows the squarish nature of *L. capensis* incisors in cross-section as well as the extent of the individual variation evident in the test material.

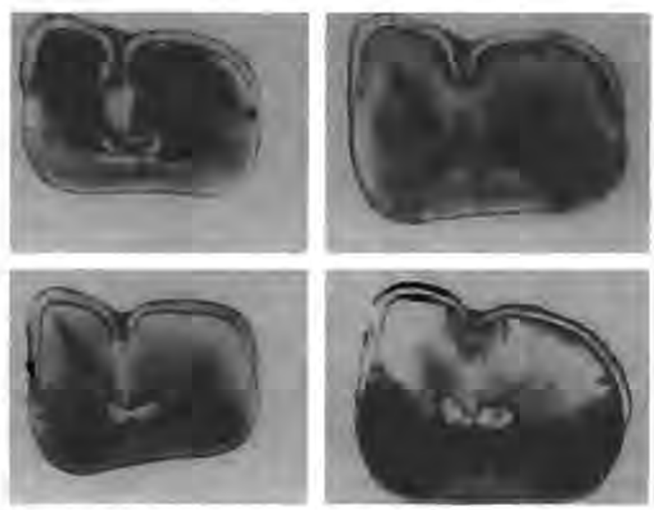

Figure 2 Cross sections through principal upper incisors of South African *L. capensis* showing the extent of variation in the lance-shaped enamel fold and the presence of cement in this structure. Note the squarish appearance of the sectioned teeth.

The enamel fold of the incisors of this species and the presence or absence of cement in this structure has, in the past, had considerable impact on the taxonomy of *L. capensis*. In his earlier work Petter (1959) was clearly of the opinion that, in addition to the simple enamel fold (corroboration of which is provided in this study), the taxon was characterized by the absence of cement in this structure. This confirmed an observation by Forsyth Major (1889) who noted that *L. capensis* 'differs scarcely from *L. europaeus*, Pall. by its minute enamel folding not filled with cement'. In fact, Petter (1961) subsequently concluded that there appeared to be no reliable criteria for the recognition of *L. capensis* from the european or brown hare, *L. europeus* and that, in the palaearctic region, the latter cannot be considered distinct from *L. capensis*. This has led to the synonomysing of the two species (Hewson 1977; Corbet & Hill 1980), a decision not accepted by all workers (Angermann 1972, 1983; Palacios

1983; Schneider & Leipoldt 1983).

However, contrary to Petter's observations (Petter 1961) there does appear to be a very distinct difference in incisor pattern between *L. capensis* from the type locality (Cape province) as well as elsewhere in South Africa (Figure 2) and those of *L. europaeus* (Figure 3A + B). The absence of cement in the enamel fold of *L. europaeus* previously noted by both Forsyth Major (1889) and Petter (1959) is confirmed, while Petter's (1961) conclusions pertaining to the similarity of the condition in *L. capensis*, at least in respect of specimens originating from South Africa, do not hold.

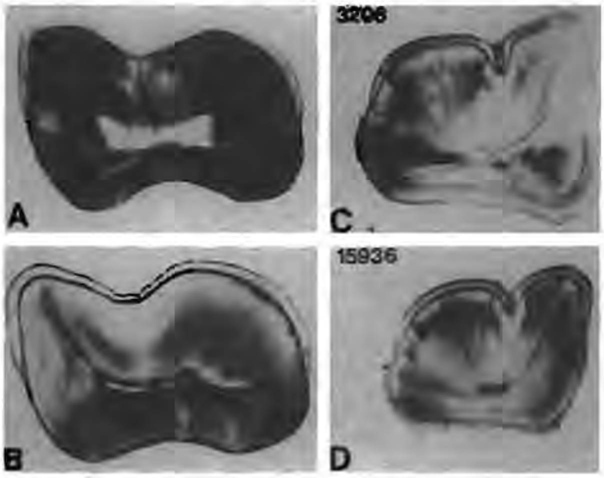

Figure 3 (A + B) Photomicrographs of the cross sections through principal upper incisors of two *L. europaeus* specimens from Scotland showing the morphology of the teeth in cross section and the absence of cement in the broad enamel fold of this species. (C + D) Cross sections through a principal upper incisor of two *L. capensis* specimens from Israel. Specimen 3208 collected in northern Israel and 15936 from the Negev Desert.

Although no reliable data are available on the extent of the variation in the enamel pattern in *L. capensis* outside South Africa, cross-sections through the upper incisors of two specimens from northern Israel and the Negev desert respectively, appear similar in all respects to those of the typical *L. capensis* (Figure 3C + D). The similarity in incisor patterns between specimens of such divergent localities may be indicative of the minor variation present in the incisor pattern of this species and the reliability of this character for the separation of *L. europaeus* from *L. capensis*.

It is possible that the disagreement in the observations of this study and those of Forsyth Major (1898) and Peter (1959) relating to the presence of cement in the enamel fold of *L. capensis* may be attributable to differing techniques. Both authors relied exclusively on superficial macroscopic investigations of the incisors, while tooth sections form the basis of this investigation. Support for this hypothesis was forthcoming by sectioning the teeth used by Petter & Genest (1965) in their study of the morphological variation and distribution of *L. capensis* in Namibia.

The cross-sections through the upper incisors of all the specimens utilized by Petter & Genest (1965) with the exception of TM 8208, 10972 and 9583 which were not available, and TM 4985 and 12610 which lacked incisors, are presented in Figure 4. The presence of cement in the enamel fold of all specimens, including those regarded by them as not showing traces of this substance (for example TM 6926), is clearly illustrated. These results would seem to cast serious doubt on the consistent accurate scoring of cement in this species without the use of sectioned teeth, a trend noted in the preliminary investigations of the present study.

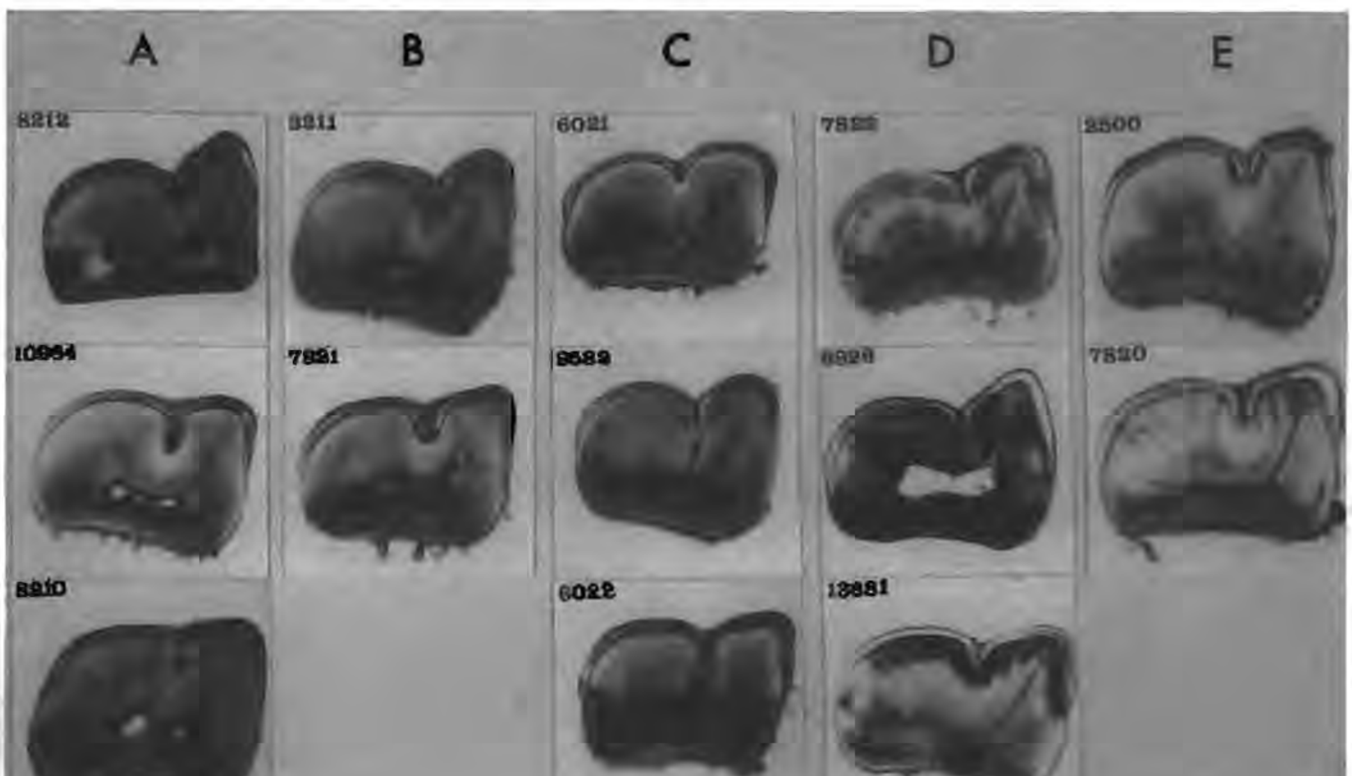

Figure 4 Cross sections through principal upper incisors of *L. capensis* specimens utilized by Petter & Genest (1965) and grouped according to the results of their macroscopic investigation of this material. Specimens in Column A were regarded by these authors as possessing a deep enamel fold characterized by the presence of cement, while those comprising C and D were reported as being of the typical *L. capensis*, not possessing cement (for example 6926 — see Petter & Genest 1965). Specimens grouped in columns B and E were indicated as being intermediate in this character.

In view of these results, an extensive investigation to determine the extent of variation in incisor morphology of *L. europaeus* and the northern forms of *L. capensis*, particularly in the presumed area of sympatry east of the Caspian sea (Angermann 1972), is indicated. Furthermore, a comprehensive attempt to ascertain whether the taxonomic affinities of the palaearctic forms in fact lie with the African *L. capensis*, particularly those from the type locality (Cape province), appears long overdue.

Incisor tooth pattern variation in *L. saxatilis*

Although the shape of the enamel fold in *L. saxatilis* shows far more individual and geographic variation than was evident in *L. capensis*, the use of this criterion nevertheless provides an unequivocal means of separating the two species. The extent of the variation encountered in the South African *L. saxatilis* is illustrated in Figure 5. There appears to be a gradual though not marked tendency towards increasing complexity of the enamel groove, from the south-western parts of the species' geographic range in South Africa north-eastwards, reflecting to some extent a trend illustrated by morphometric analysis of skull data (Robinson 1981; Robinson & Dippenaar 1983).

Specimens from localities in the southern and south-western areas of the Cape Province tend to be characterized by a relatively simple lance-shaped groove (Figure 5A) which does not usually extend deeply into the body of the tooth. However, incisors of specimens originating from the central regions of the Cape Province, the Orange Free State, southern Natal and western Transvaal, were found to possess a more convoluted enamel fold, with the posterior portion of the invagination generally being expanded laterally (Figure 5B + C). In the more north-eastern regions of South Africa (central and northern Natal and the remainder of the Transvaal), the general trend is towards complex invaginations in the majority of specimens (Figure 5D), with a high proportion showing pronounced bifurcations of the fold.

Petter (1959, 1963) is of the opinion that *L. saxatilis* is characterized by a simple enamel groove, while *L. crawshayi* tends to be more complex in this structure. However, the degree of variation in specimens of this study which, using Petter's identification key (Petter 1972), are referable to *L. saxatilis* (principally Figure 5A + B), is so great as to seriously question the use of this criterion in the delimitation of these taxa. In addition, Flux & Flux (1983) record that the enamel groove in *L. crawshayi* in Kenya is complex at low altitudes and simple at high altitudes. This is an interesting parallel with the latitudinal trend, and again casts doubt on the validity of separating *L. crawshayi* from *L. saxatilis* on this character.

Species comparisons and taxonomic conclusions

In cross-section, the principal upper incisors of *L. capensis* can be readily distinguished from those of *L. saxatilis* by their squarish appearance, particularly that part of the tooth which

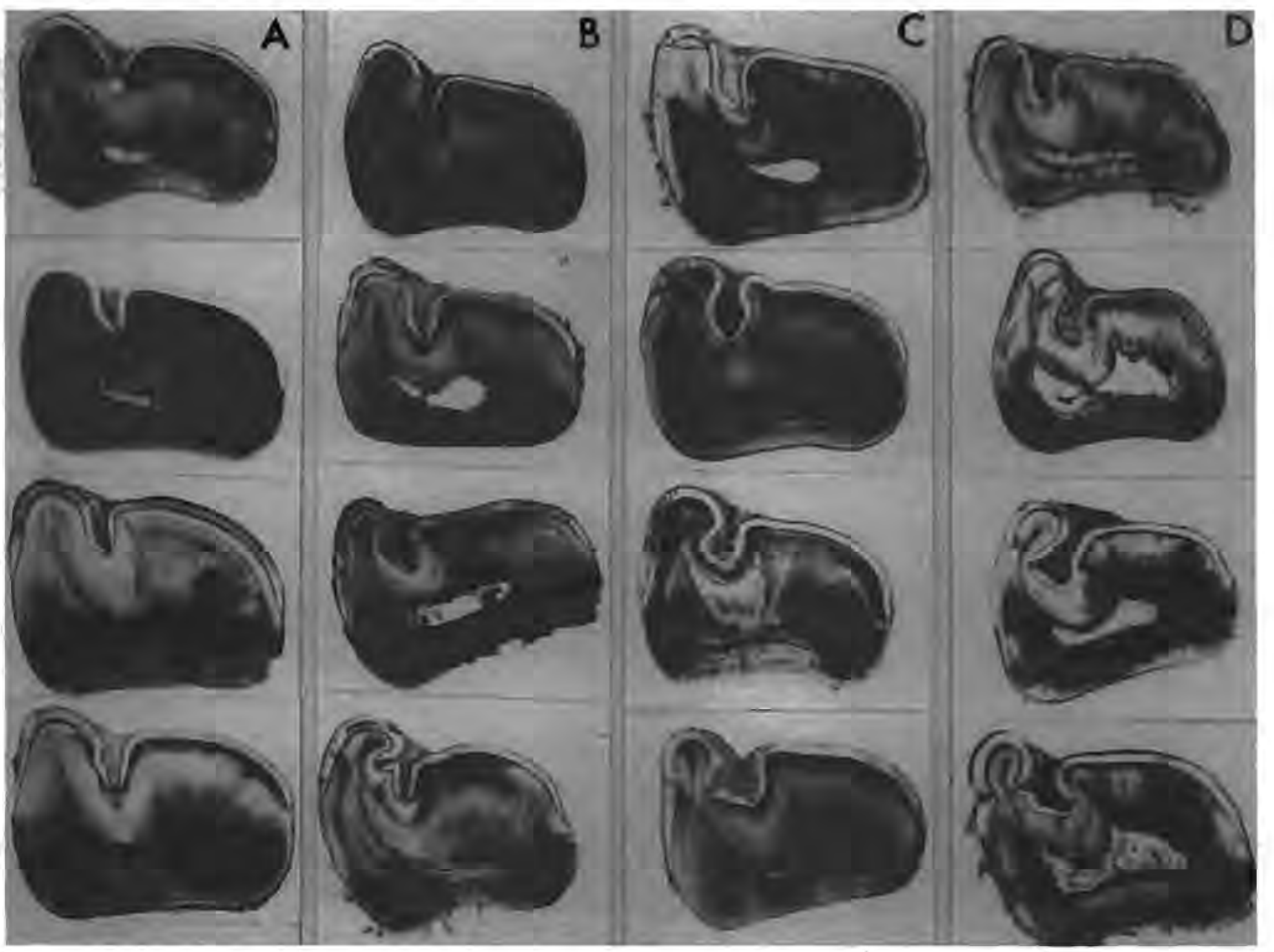

Figure 5 Cross sections through principal upper incisors of *L. saxatilis* specimens showing the extent of variation in the shape of the cement-filled enamel fold and the tendency towards increasing complexity of this structure from the south-western Cape Province, north-eastwards. A = extreme southern and south-western Cape Province; B = central Cape Province; C = Orange Free State, southern Natal and western Transvaal; D = central and northern Natal and remainder of Transvaal.

lies medial to the invagination, and the characteristically more abrupt folding of the enamel layer where it turns into the invagination (Figures 2 & 5). Furthermore, the *L. capensis* incisors are noticably less robust than those of *L. saxatilis*, individual teeth being, on average, narrower ($\bar{x}$ = 2,5 mm; observed range 2,3 – 2,8 mm; n = 32) than those of the latter species ($\bar{x}$ = 3,1 mm; observed range 2,6 – 3,6 mm; n = 102; Robinson 1981). This is particularly striking when dealing with adult material.

Geographic variation in the incisor patterns of *L. saxatilis* is particularly marked when comparisons are made between specimens from the south-western Cape Province and those from the north-easterly regions of South Africa. However, the extent of the variation in specimens referable to both *L. saxatilis* and *L. crawshayi* using Petter's (1972) key, provides no support for the recognition of the smaller northern forms as a species distinct from *L. saxatilis* (Robinson 1981; Robinson & Dippenaar 1983).

Incisor tooth pattern variation in *Pronolagus*

The most striking difference between *Pronolagus* and the South African representatives of the genus *Lepus*, is the absence of cement in the enamel fold of the former taxon. The incisor tooth patterns and the extent of the variation in *P. crassicaudatus*, *P. randensis* and *P. rupestris* are illustrated in Figure 6.

Species comparisons and taxonomic conclusions

In *Pronolagus*, unlike *Lepus*, the major source of variation lies with the shape of the incisors in cross-section and not with the invagination itself. All three taxa are characterized by a simple, shallow enamel groove which is closer in appearance to that of *L. capensis* than *L. saxatilis*, but is characteristically without cement.

Within the respective species of *Pronolagus*, very little interpopulation or individual variation in incisor tooth pattern was evident (Figure 6). However, distinct interspecific differences exist between *P. rupestris* on the one hand, and the remaining taxa, *P. crassicaudatus* and *P. randensis* on the other hand. The obvious disparity in the appearance of the incisors between the two latter species and *P. rupestris* is due largely to the elongation of the tooth lateral to the invagination in the former taxa. This is reflected in the incisor breadth measurements of *P. crassicaudatus* ($\bar{x}$ = 3,2 mm; observed range 2,9 – 3,6 mm; n = 24) and *P. randensis* ($\bar{x}$ = 3,0 mm; observed range 2,6 – 3,4 mm; n = 14) which, on average, are both wider than those of *P. rupestris* ($\bar{x}$ = 2,5 mm; observed range 2,3 – 2,8 mm; n = 14; Robinson 1981). Unfortunately the gross similarities in the size of the incisors and their shape in cross-section in both *P. crassicaudatus* and *P. randensis* effectively negate the usefulness of these criteria in species delimitation.

Incisor tooth pattern variation in *Bunolagus monticularis*

Owing to the rare and endangered status of this species it is poorly represented in museum collections. For fear of slightly damaging the relatively few skulls available during the extraction of the teeth, incisors were removed from only two specimens.

In cross-section the *Bunolagus* incisors are similar to those of the *Pronolagus* species in that the enamel fold is charac-

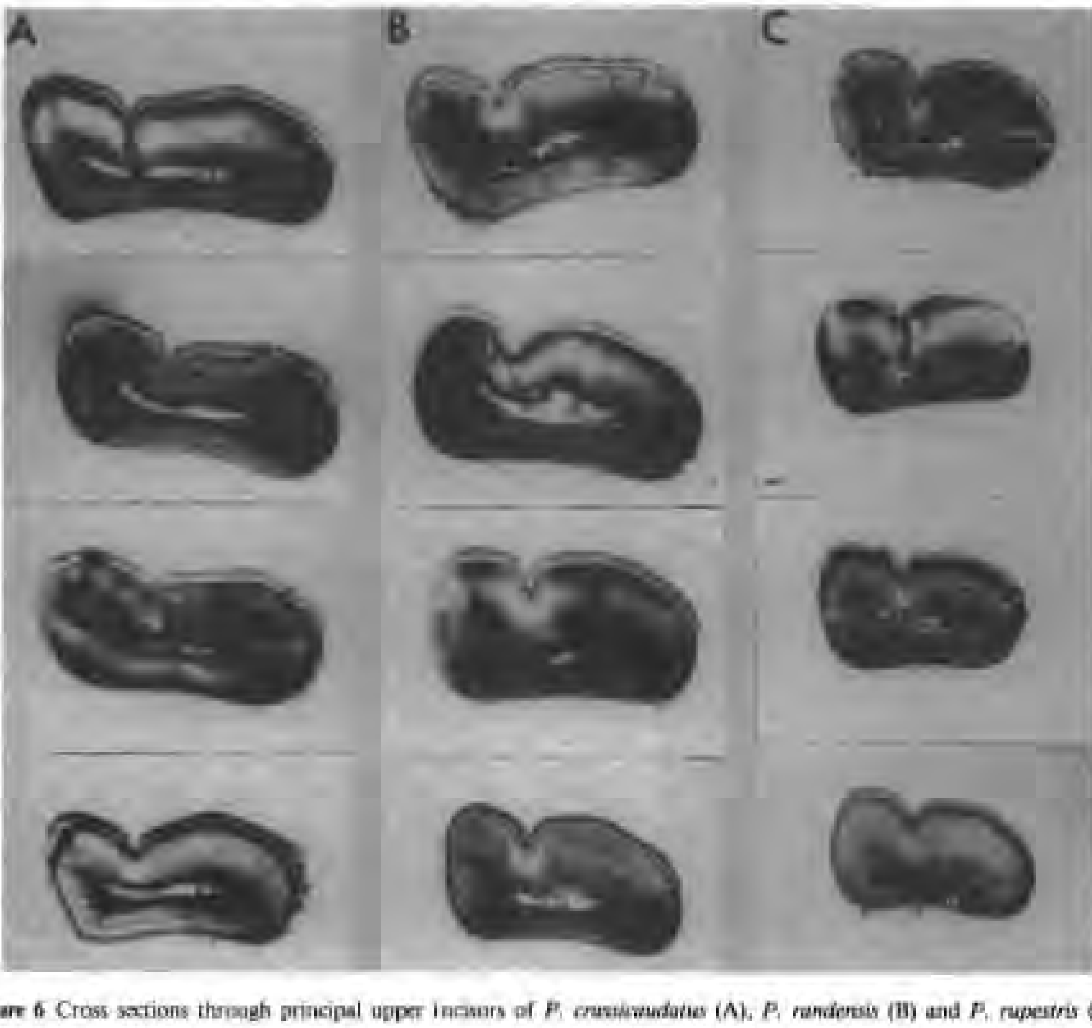

Figure 6 Cross sections through principal upper incisors of *P. crassicaudatus* (A), *P. randensis* (B) and *P. rupestris* (C).

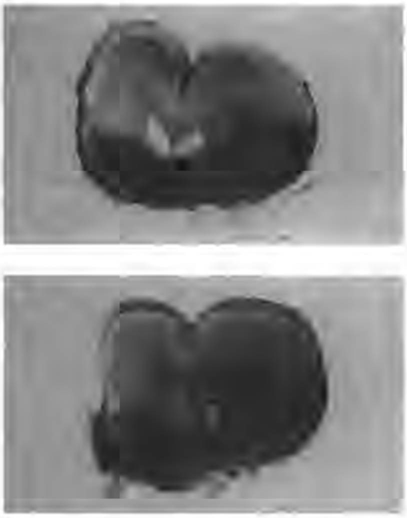

Figure 7 Cross sections through principal upper incisors of two specimens of *B. monticularis* showing the complete absence of cement in the enamel fold, and the roundness of the tooth in section.

terized by the absence of cement (Figure 7). This absence of cement supports Angermann's (1966) observations relating to *Bunolagus*.

Species comparisons and taxonomic conclusions

Striking differences exist in the incisor tooth patterns between the South African *Lepus* and *Bunolagus*. The latter can be clearly distinguished by the absence of cement in the incisive fold, the extreme narrowness of each incisor ($\bar{x}$ = 2,1 mm; observed range 2,0 – 2,2 mm; n = 15; Robinson 1981) and the thinner anterior enamel layer. These criteria provide a highly reliable and practical means of cranially distinguishing *Bunolagus* from the South African *Lepus* and, in particular, *L. capensis* with which it has the closest phenetic affinity (Robinson 1981).

Comparisons of the sectioned *Bunolagus* incisors and those of the three *Pronolagus* species reveal that *P. rupestris* is closer to *Bunolagus* in this character than either *P. crassicaudatus* or *P. randensis*. However, the incisors of the two species differ in shape particularly with regard to that portion of the tooth lateral to the invagination which tends to be more rounded in *B. monticularis* than *P. rupestris*. Although this difference appears particularly evident from the test material, the small *B. monticularis* sample must be considered. With larger sample sizes and possibly greater intraspecific variation in this character than present data suggest, the differences between *B. monticularis* and *P. rupestris* may not be as pronounced.

Acknowledgements

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Appendix 1 Gazetteer

Cape Province. 1 Beaufort West (32°20'S / 22°35'E); 2 Bredasdorp (34°32'S / 20°03'E); 3 Calvinia (31°28'S / 11°50 'E); 4 Cape Agulhas (34°50'S / 20°00'E); 5 Clanwilliam (32°11'S / 18°53'E); 6 Cradock (32°10'S / 25°38'E); 7 Deelfontein (30°59'S / 23°48'E); 8 Grahamstown (33°19'S / 26°32'E); 9 Hutchinson (31°30'S / 23°11'E); 10 Kammanassie (33°39'S / 22°46'E); 11 Lemoenshoek (33°53'S / 22°25'E); 12 Middelpos (31°55'S / 20°13'E); 13 Murraysburg (31°57'S / 23°46'E); 14 Nieuwoudtville (31°23'S / 19°06'E); 15 Prieska (29°40'S / 22°45'E); 16 Springbok (29°40'S / 17°52'E); 17 Sutherland (32°23'S / 20°40'E); 18 Uitenhage (33°46'S / 25°24'E); 19 Wolseley (33°25'S / 19°12'E); 20 Zoetendalsvlei (34°43'S / 19°58'E).

Orange Free State. 21 Boshof (28°33'S / 25°14'E); 22 Rouxville (30°25'S / 26°50'E); 23 Winburg (28°32'S / 27°01'E).

Natal. 24 Babanago (28°22'S / 31°05'E); 25 Estcourt (29°00'S / 29°53'E); 26 Hilton (29°29'S / 30°18'E); 27 Magudu (27°32'S / 31°39'E); 28 Matatiele (30°20'S / 28°48'E); 29 Winterton (28°48'S / 29°32'S).

Transvaal. 30 Bandelierskop (23°19'S / 29°48'E); 31 Bloemhof (27°39'S / 25°36'E); 32 Bon Accord (25°38'S / 28°11'E); 33 Derdepoort (25°43'S / 28°18'E); 34 Hartebeespoort Dam (25°45'S / 27°51'E); 35 Hennop's River (25°51'S / 27°56'E); 36 Jack Scott Nature Reserve (25°52'S / 27°43'E); 37 Johannesburg (26°12'S / 28°05'E); 38 Kaalplaats (25°39'S / 28°11'E); 39 Koster (25°52'S / 26°54'E); 40 Lydenburg (25°06'S / 30°27'E); 41 Messina (22°21'S / 30°03'E); 42 Pafuri (22°27'S / 31°18'E); 43 Silverton (25°44'S / 28°18'E); 44 Waterberg (24°53'S / 27°48'E); 45 Zeerust (25°33'S / 26°05'E).