
The bovid *Pseudoeotragus seegrabensis* nov. gen., nov. sp. from the Aragonian (Miocene) of Seegraben near Leoben (Austria)

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ABSTRACT

A new bovid, *Pseudoeotragus seegrabensis*, n. gen., n. sp., from the Aragonian of Seegraben near Leoben (Austria) is described. In the past this animal has been ascribed to *Eotragus*. *P. seegrabensis* differs from the genus *Eotragus* by having longer and more slender horn pits that are inclined more backwards and are closer to the rim of the orbit and it has a different skull architecture. The molars of *P. seegrabensis* are more hypsodont and have flatter lingual walls. *P. seegrabensis* also has a shorter premolar row. The species *E. sansaniensis* is larger than the species *P. seegrabensis*.

Pseudoeotragus seegrabensis is also compared with '*Antilope*' *cristata*, which is smaller, has less hypsodont teeth and has a different skull structure. *Caprotragoides stehlini* has more hypsodont teeth and has horn cores that are curved backwards and has a different skull structure. A small *Miotragocerus* has different horn cores, larger premolars and larger last molars; its premolars are also more elongated.

The new species is found in MN 4 and MN 5.

INTRODUCTION

There are two sites near Leoben (Styria, Austria) where mammalian fossils are found in lignites: Seegraben and Münzenberg. Both sites are about the same age and are known in literature as 'Leoben'. Faunal lists for the Styrian sites have been compiled by Mottl (1970). 'Leoben' is placed in MN 5 (Mein, 1975).

Some bovid material from Seegraben described and figured by Thenius (1952) as *Eotragus sansaniensis* shows differences with the *Eotragus* material from Sansan. The material from Seegraben was restudied; there proved to be two species: *Eotragus* aff. *sansaniensis* (it is a little smaller than *E. sansaniensis*) and

a species that does not belong to *Eotragus*. This second species will be compared to other bovids of about the same age (MN 4, 5 and 6). In Europe only few bovid species of about this age were described, some others were erroneously placed in the Bovidae. The following taxa were described:

Cervus haplodon Von Meyer, 1846

Cervus lunatus Von Meyer

Antilope Martiniana Lartet, 1851

Antilope sansaniensis Lartet, 1851

Antilope clavata Gervais, ?1852

Antilope cristata Biedermann, 1873

Caprotragoides stehlini Stehlin, 1951

Eotragus artenensis Ginsburg & Heintz, 1968

Miotragocerus sp. Moyà Solà, 1983

In 1923 Schlosser made the genus *Eocerus* for *Antilope Martiniana*, *Antilope sansaniensis*, *Antilope clavata*, *Antilope cristata*, *Cervus lunatus* and *Cervus haplodon*. *Cervus lunatus* is no bovid; it is synonymous with *Amphimoschus artensis*. The name *Eocerus* was pre-occupied. Pilgrim (1939) renamed the genus *Eotragus*. *Eotragus martiniana*, *E. sansaniensis* and *E. clavata* are based on material from Sansan and are synonymous; the name *E. sansaniensis* has priority (Ginsburg & Heintz, 1968). *E. sansaniensis* is considered a junior synonym of *E. haplodon* (Moyà Solà, 1983 and Astibia, 1985 & 1987).

The species *Cervus haplodon* was made by Von Meyer (1846) for some teeth from Neudorf Sandberg. He never published figures of the teeth, nor did he describe them well or publish numbers under which they are stored in a museum. The only figures of bovid teeth from Neudorf Sandberg known to me are those published by Thenius (1952b). They resemble in morphology and size *Eotragus sansaniensis* from Sansan (but figures frequently do not have the right dimensions; as far as I know no dimensions were ever published). A lectotype probably never was appointed and it is not clear whether the material described by Thenius included the material mentioned by Von Meyer. The material described by Thenius is scarce, does not include horn pits, and it is scattered over 8 collections of which 4 are private collections. In the following *C. haplodon* is ignored because it is a problematic species (no type, insufficiently described, little material) and because it is probably synonymous to *Eotragus sansaniensis*.

Eotragus artenensis is smaller and older than *E. sansaniensis* and is thought to be its ancestor. *Eotragus* is considered to be a lineage characterized by size increase (Ginsburg & Heintz, 1968). *Antilope cristata* was described by Biedermann in 1873 on material from Veltheim (Switzerland). Biedermann mentioned the possibility that his species would prove to be synonymous with one of the Sansan species. This suggestion was picked up by Thenius (1952) who, after studying the holotype stated that this species was indeed synonymous with *E. sansaniensis*. Thenius probably did not study the extensive Sansan collection in the Muséum national d'Histoire naturelle: the species from Veltheim is certainly not

synonymous to *Eotragus sansaniensis*. '*A.*' *cristata* is not an *Antilope* but it is not the purpose of this paper to discuss the affinities of '*A.*' *cristata*.

Caprotragoides stehlini Thenius, 1951 is known from Austria, but also from Paracuellos (Morales & Soria, 1985) and from Arroyo del Val and Manchones in Spain.

A *Miotragocerus* sp. from Puente Vallecas is described by Moyà Sola (1985). A more detailed description of this material is in preparation (Moyà Solà & Morales).

The bovid from Seegraben differs from the remaining five species. A detailed comparison with *E. artenensis* from Artenay, the intermediate *Eotragus* from Seegraben, *E. sansaniensis* from Sansan, '*Antilope*' *cristata* from Veltheim and *Caprotragoides* from Manchones and Arroyo del Val will be made. The comparison with the *Miotragocerus* sp. from Puente Vallecas will be less detailed, as I did not study all this material.

There are some more European bovids that are close in age to the Seegraben material, for instance in Arroyo del Val and Manchones, but as this material is not yet described, it will not be included in this study.

The material described in this paper from Seegraben, Labitschberg and Göriach is stored in the Joanneum in Graz, the material of *Antilope cristata* is stored in the museum in Winterthur and the material of *E. sansaniensis* from Sansan is stored in the Museum national d'Histoire naturelle in Paris. The material from Arroyo del Val and Manchones is stored in the Instituut voor Aardwetenschappen in Utrecht and in the Rijksmuseum voor Geologie en Mineralogie in Leiden. The material from Paracuellos is stored in the Museo de Ciencias Naturales in Madrid.

Literature on the Seegraben bovids

The Seegraben bovid material was first published by Hofmann, Redlich and Zdarsky in a series of articles written as the collection grew: Redlich, 1898, Hofmann & Zdarsky, 1904, Redlich, 1906 and Zdarsky, 1909. The material comprises abundant dentition, two horn pits and a skull fragment of *Pseudoeotragus seegrabensis* n. gen., n. sp. and several fragments of horn pits and some dentition of *Eotragus*. Redlich described some mandibles of *Pseudoeotragus seegrabensis* as *Antilope* cf. *sansaniensis*. In his second paper he expressed the opinion that all bovid material from Leoben was *Antilope cristata*. Hofmann and Zdarsky identified the horn pits of *Eotragus*, the skull fragment of *P. seegrabensis* and all the dentition as *A. cristata*. Zdarsky (1909) described a horn pit as *Antilope* sp. ind.. In a revision of the Bovidae from Styria, Thenius (1952) separated the horn pits of *Eotragus*: some of them were described as *E. haplodon* and others as *E. sansaniensis*. The *Eotragus* dentition was described as *E. haplodon* since it resembled the material of this species from Neudorf Sandberg. Because the dentition of *Pseudoeotragus seegrabensis* was different it was assigned to *E. sansaniensis*. Thenius probably considered the Seegraben horn pits of *Pseudoeotragus seegrabensis* and of *Eotragus* to be *E. sansaniensis* (he did not give the numbers of the horn pits).

SYSTEMATICS

Family Bovidae Gray, 1821

Pseudoeotragus nov. gen.

Type species: *Pseudoeotragus seegrabensis* nov. sp.

Derivatio nominis

This bovid resembles *Eotragus* in certain characters and has long been taken for *Eotragus*, but it is different. The holotype comes from Seegraben.

Holotype

3678 a fragmentary skull with a palate with all cheek teeth, parts of the bases of the horn pits, parts of the frontalia and parietalia. It is stored in the Joanneum in Graz. It is figured by Hofmann and Zdarsky, 1904, plate XVI, fig. 2.

Paratype 1

59.605 a right horn pit, which is stored in the Joanneum.

Paratype 2

3715 a left mandible with P₂-M₃, which is stored in the Joanneum. It is figured by Zdarsky, 1909, plate VIII, fig. 10 & 11.

Paratype 3

3707 a right maxilla with P³-M³.

Paratype 4

3702 a right maxilla with P³ and P⁴. It is figured by Hofmann & Zdarsky 1904, plate VIII, fig. 2 & 3.

Type locality

Seegraben near Leoben in Austria. The site is placed in MN 5, which is Aragonian.

Synonymy

1888 *Antilope cristata*; Hofmann, Table VIII, fig. 7 & 8

1898 *Antilope* cf. *sansaniensis*; Redlich, Table II, fig. 3-8

1904 *Antilope cristata*; Hofmann & Zdarsky, text figure p. 509, Table XV, fig. 19-20, Table XVI, fig. 1-3 & 6-14

1909 *Antilope cristata*; Zdarsky, Table VIII, fig. 10-13 & 18

1909 *Antilope* sp. ind.; Zdarsky, Table VIII, fig. 21-22

1952 *Eotragus sansaniensis*; Thenius, fig. 7-10

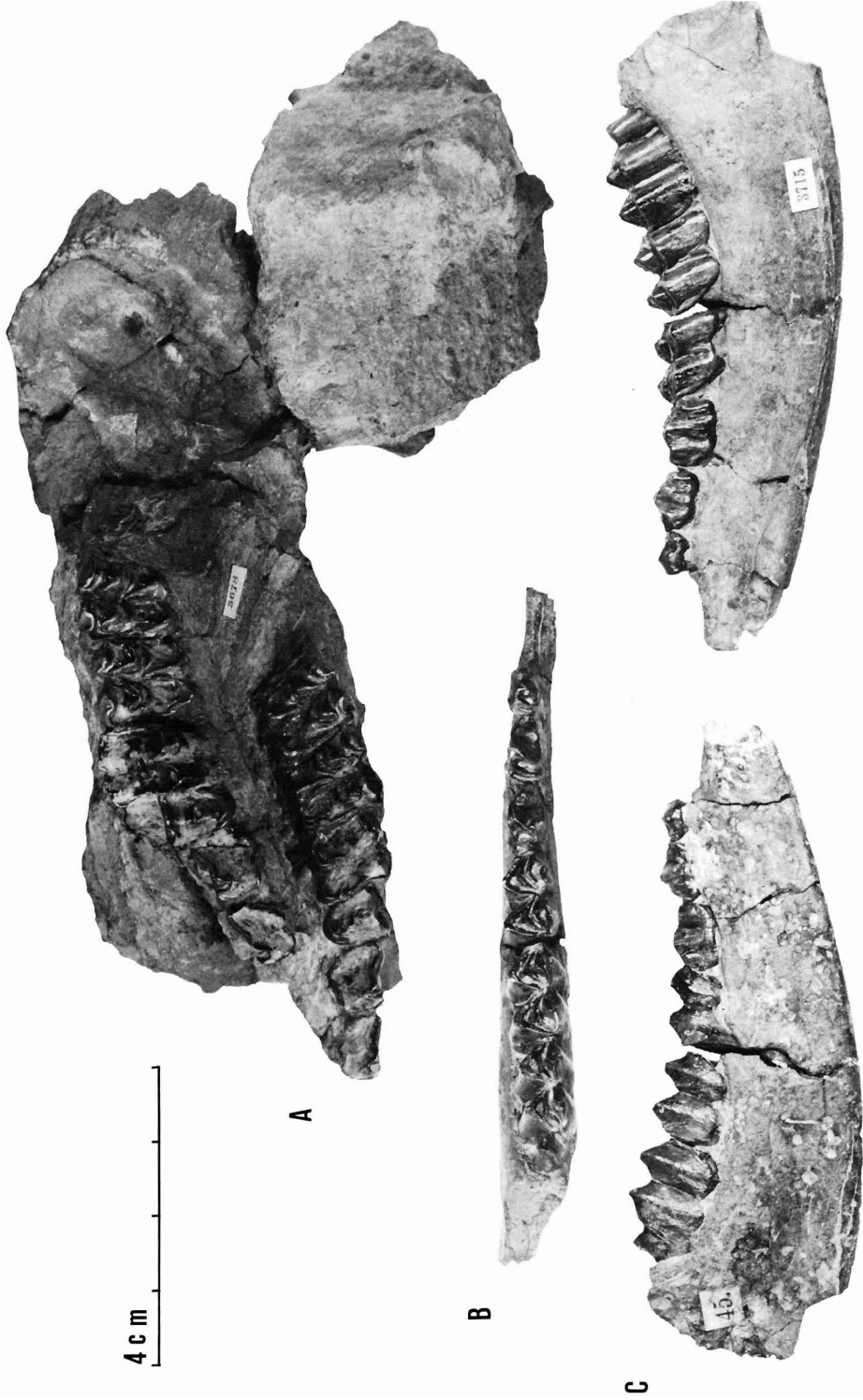


Plate I. *Pseudoeotragus seegrabensis*, Seegraben near Leoben, Austria. No. 3678, holotype; ventral view (a). No. 3715, mandible with P₃ to M₃; occlusal (b), lingual (c) and buccal (d) views. Joanneum, Graz.



2 cm

Plate II. *Pseudoeoitragus seegrabensis*, Seegraben near Leoben, Austria. No. 3678, holotype; close-up of frontalia and parietalia. Joanneum, Graz.

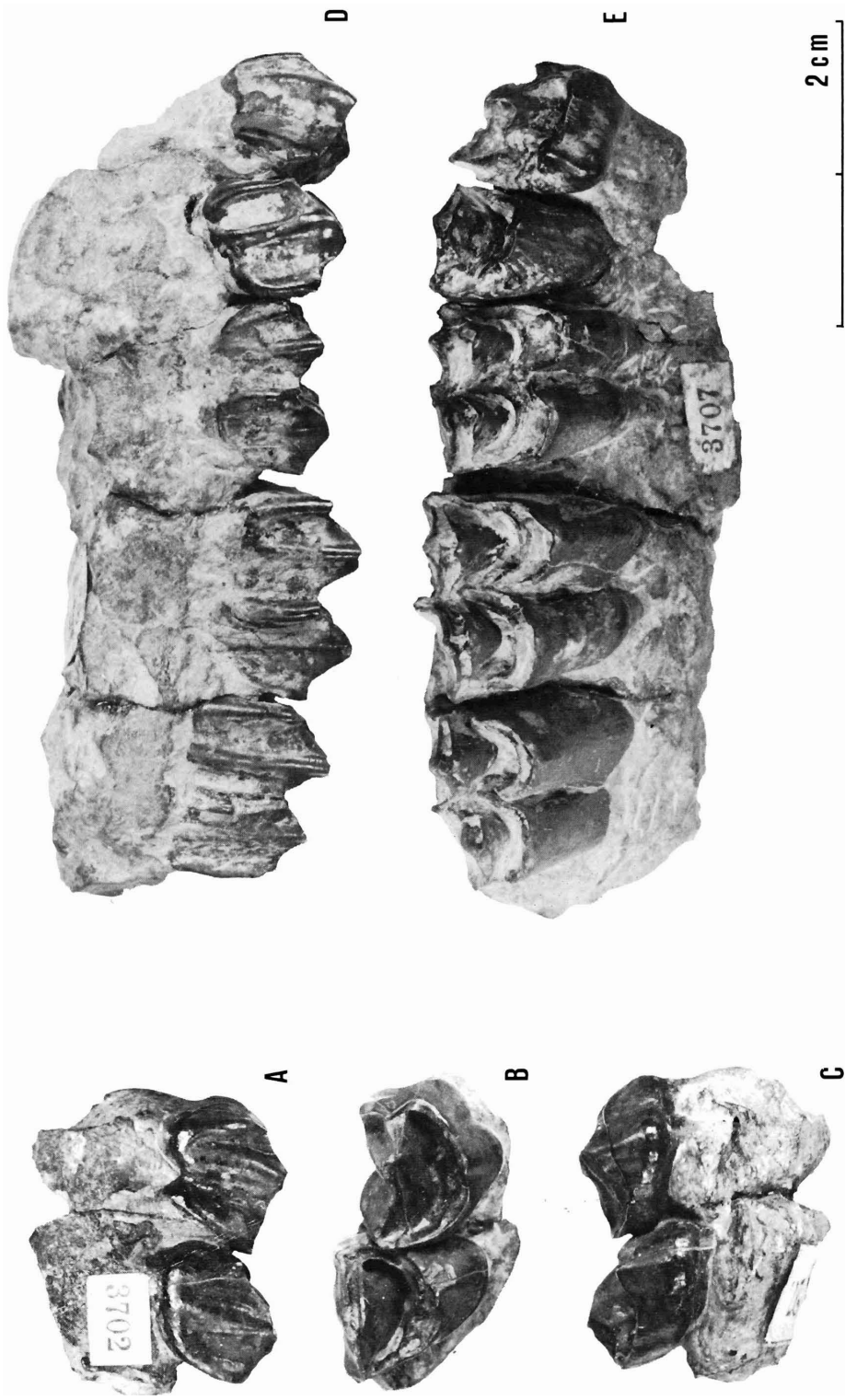


Plate III. *Pseudoeotragus seegrabensis*, Seegraben near Leoben, Austria. No. 3702 maxilla with P³ and P⁴; buccal (a), occlusal (b) and lingual (c) views and no. 3707, maxilla with P³ to M²; buccal (d) and occlusal (e) views. Joanneum, Graz.

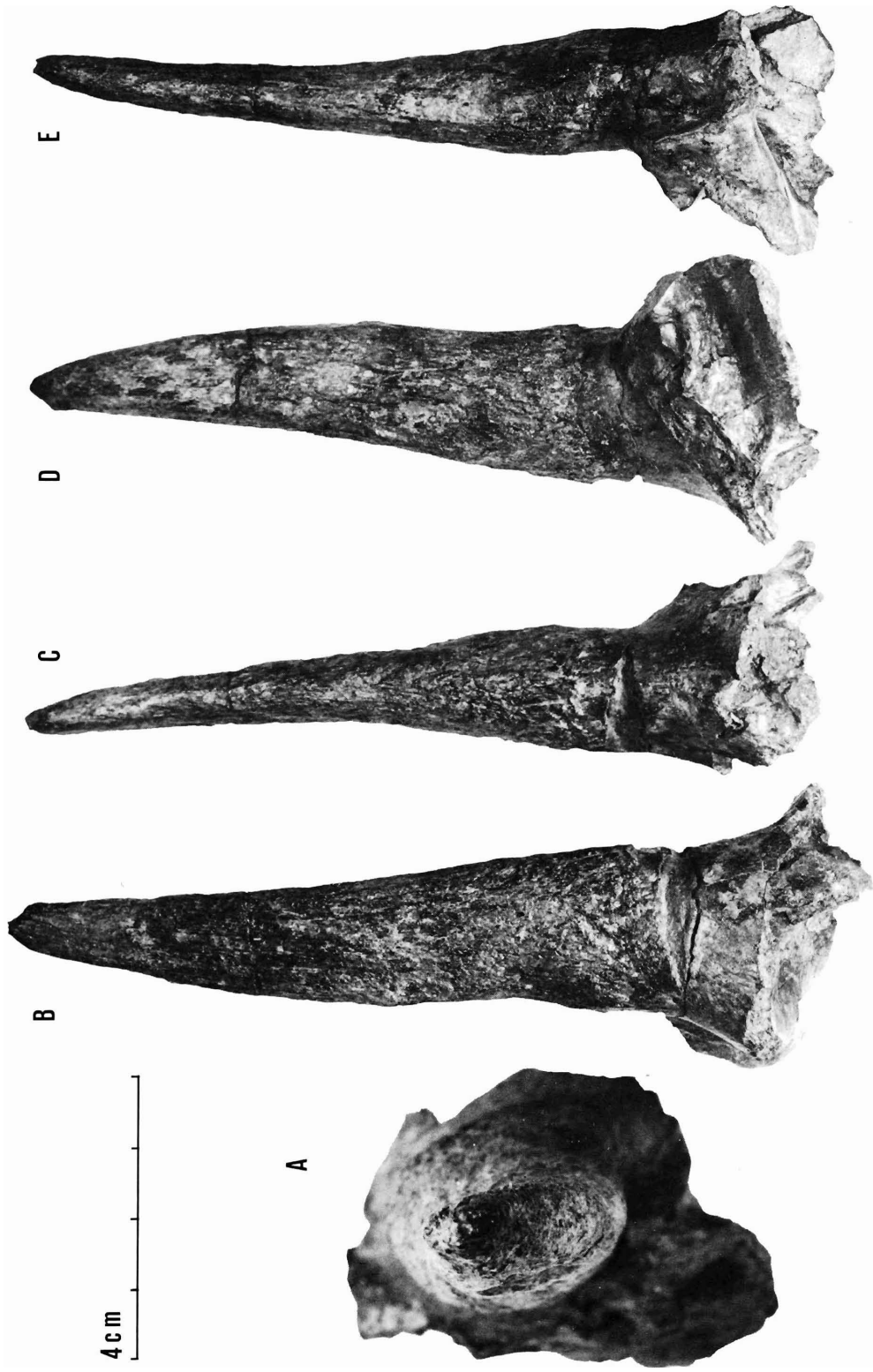


Plate IV. *Pseudoeotragus seegrabensis*, Seegraben near Leoben, Austria. No. 59.605, horn pit seen from the apical (a), external (b), anterior (c), internal (d) and posterior (e) sides. Joanneum, Graz.

1985 *Eotragus* aff. *aplodon*; Astibia, fig. 25a, b & c.

1987 *Eotragus* aff. *aplodon*; Astibia, fig. 15 a, b, & c; plate 3, fig. 9 a & b.

Diagnosis

As *P. seegrabensis* is the only species in the new genus *Pseudoeotragus* it is not possible to separate the diagnosis of this new form into a diagnosis for the genus and a diagnosis for the species.

Pseudoeotragus seegrabensis is a small bovid with molars that have height/length ratios usually below 0.9. The premolars are long considering their width. The horn pits are nearly straight, have an oval section, are inclined strongly backwards and slightly externally and are at the edge of the orbit. The tips of the horn cores are curved slightly forward. The axis of the frontal zone makes a small angle with the axis of the parietal zone. The skull has wide and short parietals, that curve down distally.

Differential diagnosis

Pseudoeotragus differs from *Eotragus* by its short and down-curved parietals; its molars are more hypsodont; the lower molars have flatter lingual walls and the horn pits are longer and are inclined more backward. The horn cores are wider apart and nearer the rim of the orbit, flaring out. In addition *Pseudoeotragus seegrabensis* differs from the species *E. sansaniensis* in particular in that the mean size of the dentition is smaller.

P. seegrabensis differs from *A. cristata* in having short and down-curved parietals and by having dentition with a greater mean size, greater hypsodonty and by horn pits that are inclined backward, flare out and that are wider apart.

P. seegrabensis differs from *Caprotragoides stehlini* by the smaller size of the dentition, narrower P₃ and P₄, lesser hypsodonty and by horn pits that are not curved backwards and are further apart.

P. seegrabensis differs from *Miotragocerus* sp. from Puente Vallecas in not having horn cores with a triangular section, in having smaller M₃ and in having shorter (and equally wide or wider) P₃ and P₄.

Material

- 3678 partial skull with a palate with all cheek teeth, parts of the bases of both horn pits, parts of the frontalia and parietalia (figured by Hofmann & Zdarsky, 1904, plate XVI, fig. 1, 1a).
- 3679 a left maxilla with P³-M²
- 3680 a left maxilla with P²-M³ (figured by Zdarsky, 1909, plate VIII, fig. 13)
- 3701 a left maxilla with P²-M³
- 3702 right P³-P⁴ (figured by Hofmann & Zdarsky, 1904, plate XVI, fig. 2 & 3)
- 3706 a right maxilla with P²-P⁴

- 3707 a right maxilla with P³-M³
3709 a right maxilla with P²-M³
3712 a left P₄ (figured by Hofmann & Zdarsky, 1904, plate XVI, fig. 12-14)
3714 a left mandibula with P₃-M₃ (figured by Hofmann & Zdarsky, 1904, plate XVI, fig. 10)
3715 a left mandibula with P₂-M₃ (figured by Zdarsky, 1909, plate VIII, fig. 10 & 11)
3716 a left mandibula with M₁-M₃
3719 a left mandibula with M₃ (figured by Hofmann & Zdarsky, 1904, plate XV, fig. 19 & 20)
3720 a left mandibula P₂-M₁ and a fragment of M₃
3721 a left mandibula with P₄-M₃
3722 a left mandibula with M₂ and a fragment of M₃
3723 a left mandibula with P₄-M₃
3725 mandibula with P₄ in alveolus and P₃
3726 a right mandibula with M₁-M₃
3727 left M₁-M₃
3731 a right mandibula with P₄-M₃
3732 a right mandibula with P₄-M₃
3633 a right mandibula with M₂ & M₃
3735 M₁-M₂
3737 mandibula with M₂-M₃
3738 a right mandibula with P₂-M₁ (figured by Hofmann & Zdarsky, 1904, plate XVI, fig. 11)
3739 a right mandibula with P₃-M₃
3740 a right mandibula with P₃-M₃
3742 isolated lower premolars and molars: 1 left P₃, 2 right P₃, 1 left P₄, 1 right P₄, 2 left M₁, 1 right M₁, 3 left M₂, 1 right M₂, 2 left M₃ (stored under the same number are 2 right M₃, 1 right M₁ of *Eotragus* and 2 left M₁ and an M₁ and a left M₂ belonging together, but it is not clear to which species they belong)
3743 isolated upper premolars and molars: 1 left P³, 1 left P⁴, 2 right P⁴, 1 left M¹, 3 right M¹, 2 left M², 1-doubtful left M², 3 right M², 3 left M³, 2 right M³ (under the same number are stored several fragments of teeth and 2 M^x that are probably of *Eotragus*)
3744 right horn pit (figured by Zdarsky, 1909, plate VIII, fig. 21, 22)
56.882 isolated molars and premolars: left P₄ & M₁ belonging together, 2 right M², 1 left M², 1 right M³
59.605 right horn pit

Description

The skull is crushed, later it was cut by a fracture in the clay in which it was imbedded. The area of the palate is laterally compressed and the right tooth row is displaced forward. Parts of the roof of the craneum however do not seem to

be laterally compressed. There is a transverse fault running from behind the left horn pit to the anterior part of the right horn pit. Along this fault much of the bone is missing. The part behind the fault is rotated with respect to the part in front of the fault. The occipitals seem to have been broken off at or near the site of the suture between the occipitals and parietals. The part of the skull between the palate and the parietals is covered by sediment.

The skull seems to have been slightly wider at the position of the eyes than at the braincase. The distance between the median plane and the most external preserved part of the frontal is 36.1 mm. The distance between the median plane and the most external preserved part of the parietal is 31 mm. The temporal lines are visible on the convex parietals. The minimum distance between the left and right temporal line is about 11 mm. The horn pits are wide apart and above the eyes, the external part of the base of the horn pit extends almost as far outward as the edge of the orbit. As far as can be judged the section of the horn pits is oval, with no sharp angles (the expression of a keel in a section). The distance between the bases of the horn pits was approximately 36.6 mm. The supraorbital foramen is situated at the base of the horn pit, just to the inside of the horn pit. Between the horn pits the frontals are concave upwards in transverse section. The posterior part of the base of the horn pit protrudes externally and ends free above the coronoid process of the mandible. The orientation of the horn pit on the skull can be reconstructed with the help of the two complete horn pits. The horn pit is inclined backwards. The angle between the frontals between the horn pits and the anterior side of the horn pits is 25° or a little less. The angle between the posterior side of the horn pit and the antero-posterior axis of the brain case in the parietal zone is 40 to 50° . The angle between the anterior and posterior sides of the horn pit is about 10° . The parietal axis must have had an inclination of about 5 to 15° with respect to the frontal axis. The horn pits flare out; if seen from the anterior they make an angle of about 40° to 60° with each other. Between the last molars the width of the palate was probably 28.6 mm before deformation. In the sagittal plane the palatine bone extends at least 11 mm posteriorly beyond the last molar. The curvature inwards of the palatine bones between the pterigoids and the last molar extends as far forwards as the distal end of the M^3 .

The horn pits of *Pseudoeotragus seegrabensis* have an oval section. There are no keels. They curve externally and anteriorly. The surface is smooth. There is no sinus in the pedicle. The base of the rugose part of the horn pit is about as wide as the pedicle. Horn pit number 59.605 shows that there are no sinuses in the frontalia. This horn core is still 80.8 mm long but must have been longer. The basal section is 22.9×17.6 mm². No. 3744 is approximately 9.5 cm and also must have been longer. Its basal section is 25.3×19.8 mm².

No P_2 has a fully formed anterolingual conid. The oblique crest is straight and becomes rapidly lower. The posterior stylid and the ridge directed to the posterolingual conid are parallel and transverse. In fact no such posterolingual conid is formed: the ridge has no swelling here. In another specimen these ridges are oblique and shorter. There is some variation in crown height.

The P_3 has the same structure, but is larger. All ridges are more clearly defined. At the end of the oblique cristid there is only a very faint swelling which might be called the mesolingual conid. The anterolingual conid is not well developed.

The P_4 has roughly the same structure as the P_3 . The anterolingual conid is better developed, although its higher part does not extend much lingually. There is a shallow valley between the anterolingual conid and the anterior styloid. A mesolingual conid is developed. It is much lower than the mesolabial conid and it is placed more distally. A posterolingual cristid originating from the mesolingual conid tends to fuse with the posterolingual conid (a more accurate description being a transverse ridge at the place of the posterolingual conid). The anterior valley is wide. In the large Sansan sample this morphology occurs in addition to several others.

The M_1 and M_2 have flat lingual walls. The metastyloid is not well developed. The parastyloid is always clearly visible and dips 60 to 80°. The metaconid and entoconid ribs do not protrude much and are only clearly visible in their upper parts. Parastyloids and entostyloids do not protrude much anteriorly and posteriorly. Ectostyloids are generally not higher than 3 mm. An anterolingual styloid is present, but not very pronounced. In its upper part the prehypocristid is fused to the postprotocristid near the spot where this crest fuses with the lingual wall of the tooth. In its lower part the prehypocristid may be fused with the pre-entocristid. The post-metacristid is fused to the pre-entocristid, thus closing the anterior fossa. The premetacristid is well fused to the preprotocristid.

The anterior part of the M_3 has the same structure as the anterior molars. There is a talonid consisting of a hypoconulid which is connected to the posthypocristid by a curved ridge. Lower down the concave lingual side of the crest becomes convex: the talonid has a circular base. In several specimens there is a low crest at the place of the entoconulid. This crest partly or completely closes a talonid fossa.

The anterior style of the P^2 is well developed, as is the rib of the labial cone. There is a deep gully between them.

The P^3 has almost the same structure as the P^2 , but is somewhat wider. The lingual wall is semicircular; in the middle of it the base of the lingual cone typically protrudes. A little higher up the lingual cone does not protrude so much.

The P^4 has well-developed anterior and posterior styles and the rib of the labial cone is narrow, clearly defined and has a constant width. The three structures are roughly parallel.

The upper molars often have parallel labial styles and ribs. The rib of the metacone may be very feeble or absent. No ectostyles are developed. One specimen has a well-developed cingulum along the base of the metaconule. The precrista of the metaconule is not always fused with the postparacrista.

Table 1 Measurements (in mm) of the lower dentition of *Pseudocorragus seegrabensis*. In premolars it is not always possible to measure the transverse diameter of the anterior lobe (DTa) because of the rounded shape of the tooth. In some cases the crown-height (h) and the depth of the mandible (d) could be measured; these values are given on the line below the DAP and DT values.

no.	P ₂ DAP h	DTa d	DTp	P ₃ DAP h	DTa d	DTp	P ₄ DAP h	DTa d	DTp	M ₁ DAP h	DTa d	DTp	M ₂ DAP h	DTa d	DTp	M ₃ DAP h	DTa d	DTp	DTpp	
3712				11.1 >7.8	5.0	5.3														
3714		14.5		8.7 +17.8	3.9 +17.8	>4.8	9.7	4.7 18.0	5.8	10.3	6.6 19.9	7.3	11.0	7.7 20.7	8.3	16.3	7.4 23.2	7.7	4.4	
3715	6.3 3.1	4.1 15.9	4.1	9.0 4.4	3.5 15.2	5.1	9.6 >7.3	— 15.7	5.5	11.3 —	6.8 17.9	7.4	12.1 >9.2	7.9 19.9	8.0	17.0 >11.1	7.7 22.9	7.5	4.0	
3716										11.0	6.9 +17.6	6.9	12.7 >9.2	7.5 19.3	7.6	17.5	7.7 22.3	8.0	5.0	
3719										9.8	6.8	7.7	11.7	8.4	8.1	17.9	8.1 21.4	7.5	3.8	
3720				8.3	15.9	5.0	9.3	15.5	5.6	10.0	7.0 17.7	7.7				—	—	—	—	
3721							10.2 >6.8	5.2 +17.7	5.2	10.9	6.7	—	12.2	8.0	7.9	18.0	7.7 >10.0	7.4	4.1	
3722													11.5	8.3 +21.0	>8.1	—	—	—		
3723							—	—	+5.5	10.2	6.2	7.3	12.0	7.2	8.1	16.6	—	7.3	4.0	
3725				10.1 6.5	4.4	5.0	— >7.9	—	6.0											
3726										—	6.2	7.9	12.4 >9.3 20.2	8.7	8.7	—	8.6	—	—	
3727										10.7	6.1	6.8	12.1	6.8	7.3	17.3	7.1	7.5	4.6	
3731							—	—	—	10.5	7.1	7.9	12.6	8.5	8.5	17.5	8.3	7.4	3.9	
3732							10.8	5.8 17.7	6.5	—	6.7 18.7	—	—	—	8.6	18.8	8.2 25.7	8.8	4.8	
3733													11.3	7.5	7.7	18.1	7.5	7.8	4.5	
3735										9.9	6.6	7.2	11.9	8.0	8.5					
3737													—	—	7.8	—	7.1	—	—	
3738	6.1 4.6	13.8	3.3	9.2 6.5	15.3	5.2	10.7 8.0	14.8	6.3	— >8.1	>5.0 18.5									
3739				—	—	4.4	8.8	4.3	5.2	9.9	6.2	6.7	10.8	7.5	7.5	16.6	7.3	7.2	3.6	
3740		14.3		9.3	3.9 15.0	4.7	10.0	4.6 15.7	5.4	10.5	6.8 18.3	7.3	11.9	8.0 —	8.4	17.5 >10.1	8.0 24.0	8.4	4.4	
3742				9.9	—	4.6														
				9.1	—	5.2														
				8.7	—	4.6														
							10.2	—	5.1											
							10.6	—	5.8											
										10.2	6.3	7.8								
										10.3	6.3	7.3								
										10.7	6.0	6.6								
													12.6	8.2	8.3					
													11.5	6.9	7.2					
													12.1	7.8	7.8					
													>9.2							
													11.5	7.9	8.4					
																—	7.8	7.5	—	
																>11.1				
																—	7.6	7.9	—	
																>11.3				
56.882							9.5	—	5.2	9.9	6.6	7.8								
																18.1	8.5	7.7	4.8	

COMPARISON WITH OTHER BOVIDS

In the following section *Pseudoeotragus seegrabensis* will be compared with *Eotragus sansaniensis* from Sansan, *Eotragus aff. sansaniensis* from Seegraben, *Caprotragoides* from Arroyo del Val and Manchones, *Miotragocerus* sp. from Puente Vallecas and *Antilope cristata* from Veltheim. Besides the holotype there is some more material from Veltheim. It is assumed that this is material of the same species, although in all small samples such assumptions are hazardous.

Table 2 Measurements (in mm) of the upper dentition of *Pseudoeotragus seegrabensis*.

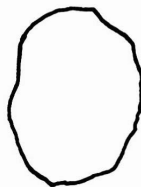
no.	p ² DAP h	DTa	DTp	p ³ DAP h	DTa	DTp	p ⁴ DAP h	DT	M ¹ DAP h	DTa	DTp	M ² DAP h	DTa	DTp	M ³ DAP h	DTa	DTp
3678	8,8	5,9	—	10,2	6,9	7,9	8,2	10,1	10,2	12,3	11,9	12,3	14,3	13,2	13,2	13,8	12,5
sin	9,3	5,8	—	10,2	6,7	+7,6	—	—	+10,0	12,2	12,0	12,1	14,2	13,6	12,6	13,1	12,0
3679				>8,9	6,1	8,3	8,5	10,3	10,5	12,7	12,1	—	12,9	11,3			
3680	9,8	6,2	7,2	9,6	6,5	8,3	+8	—	11,2	11,4	11,8	12,2	14,2	12,9	12,9	13,8	11,0
3701	10,3	5,7	7,2	9,7	6,3	8,4	7,9	10,2	9,6	11,1	11,6	12,4	14,4	12,5	12,6	13,1	10,3
3702				9,2		9,5	8,7	10,1									
				8,4			8,1										
3704												12,5	14,0	12,4	12,4	13,0	11,0
3706	9,3	5,6	7,0	8,6		8,6	7,7	9,6									
3707				9,0	6,4	9,0	7,7	10,1	11,5	11,7	12,2	13,7	14,0	12,5	12,5	13,1	+10,2
3709	9,1	5,8	6,9	9,4	6,6	8,1	7,9	9,8	10,2	11,3	11,8						
3743				9,4	6,4	8,9											
								>7,4	10,3								
								8,2	10,2								
								8,1	10,2								
									11,4	11,7	11,7						
									11,0	11,1	10,5						
									10,6	11,7	12,2						
									11,7	11,9	12,1						
									>>8,4								
												12,9	11,5	11,2			
												13,4	13,9	13,0			
												12,1	13,7	12,8			
												11,5	13,2	12,4			
												11,8	14,7	13,3			
												11,8	13,6	13,1			
															12,3	13,0	10,2
															+10,5	—	10,5
															+12,4	13,1	9,9
															13,3	13,9	11,1
															12,8	13,1	9,9
56.882															12,4	13,1	12,2
															>9,4		
															12,2	13,4	12,6
															12,1	12,6	11,8
															10,6		

For a comparison of dimensions of the cheek teeth the reader is referred to figure 2 & 3 and for a comparison of hypsodonty to table 3. If values are mentioned for a species this value is followed by the value for *P. seegrabensis* between square brackets: [...].

Eotragus sansaniensis

Pseudoeotragus differs from *Eotragus* in its skull structure. In *Eotragus* the horn cores are placed more internally. The mean distance between their bases is 28.8 mm (n = 19), the values varying between 23.9 and 33.4 mm [36.6 mm]. The horn pits are not placed at the edge of the orbit, but about 1 cm in from the edge. In *Eotragus* the width of the skull measured at the posterior part of the orbits is about 8 cm [approx. 7.5 cm]. The horn pits are not inclined so much backwards; the mean angle between the frontals and the anterior edge of the horn core is 37.5° (measurements rounded off at 2.5°), the extreme angles are 27.5° and 47.5° [25°]. The horn pits of *Eotragus* do not flare out or flare out only a little. The brain case of *Eotragus* is much more elongate. Sa 1034 is a part of a skull of a female *Eotragus*, the occipitals seem to have been broken off at the suture between the parietals and the occipitals. The distance between the posterior end of the zygomatic process of the frontal and the posteromedial end of the parietal, measured as a projection on the median plane, is 62 mm. If the complete length of the parietals in *P. seegrabensis* is preserved, the aforementioned distance is approx. 37 mm. The greatest width of the brain case in Sa 1058 is 50 mm. This is 62 mm or more in *Pseudoeotragus seegrabensis*. Even if these measurements are not very accurate they give the right impression: it can be seen that the brain case of *Eotragus* is much more cylindrical and elongate.

The horn pits of *Eotragus* have roughly the same diameter at the base as those of *Pseudoeotragus*, but are much shorter. Of 76 horn pits from Sansan the greatest preserved length was 86.5 mm [>80.8 mm and >9.5 cm]; lengths between 50 and 70 mm are more frequent. The specimens with a length comparable to that of the *P. seegrabensis* horn cores have a section that is much larger than the section of the *Pseudoeotragus seegrabensis* horn cores. The *Eotragus* horn cores tend to be a little wider and may have a triangular section. The surface structure is much more rugose.



Textfigure 1. Section of right horn core no. 3744. The section is taken near the base. Right is the external side and up is the anterior side.

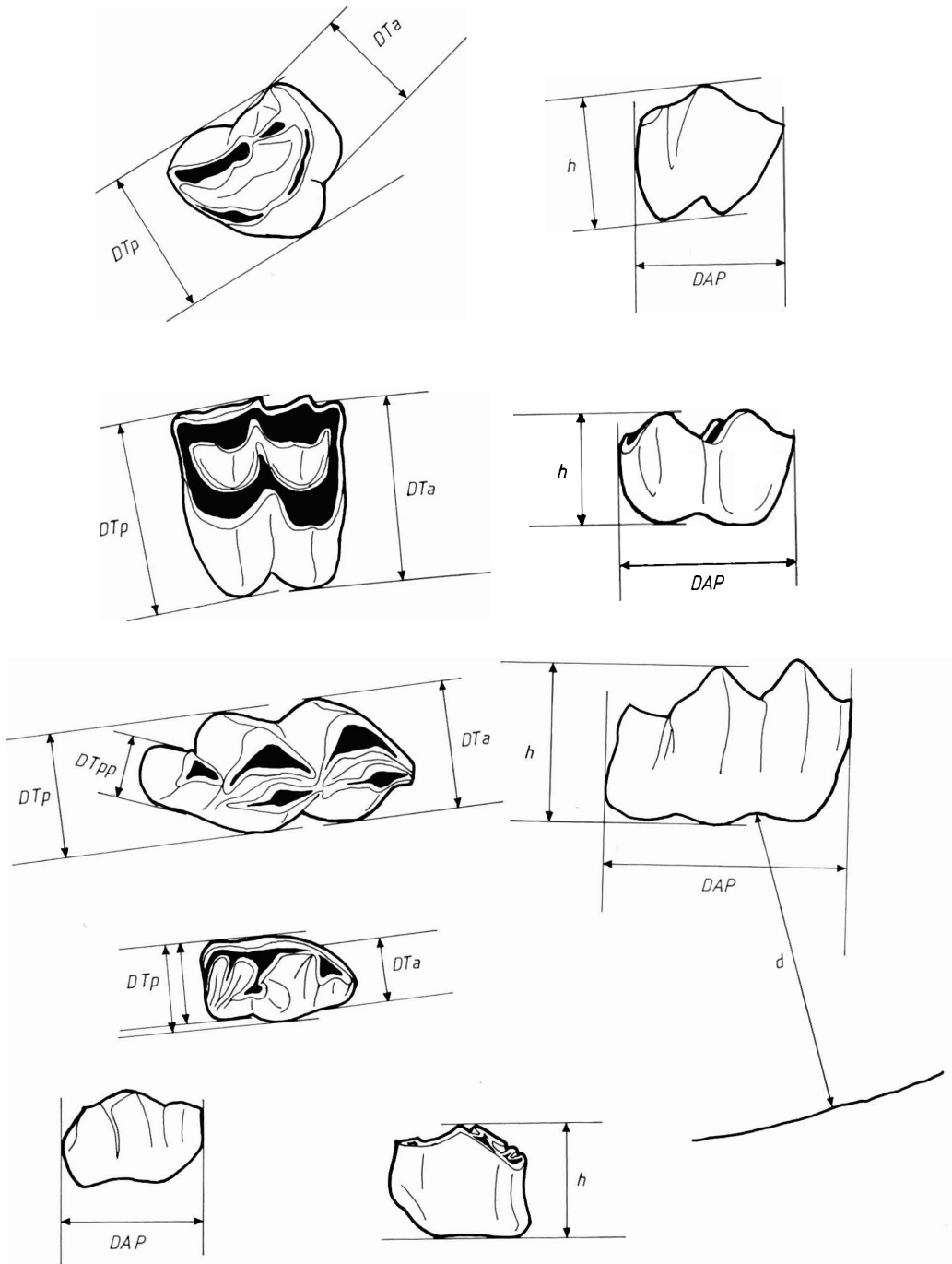


Fig. 1. The way the measurements have been taken.

d = depth of the mandible

DAP = antero-posterior diameter

DTa = transverse diameter of the anterior lobe

DTp = transverse diameter of the posterior lobe

DTpp = transverse diameter of the talonid in M_3

h = crown-height

(All measurements in mm.)

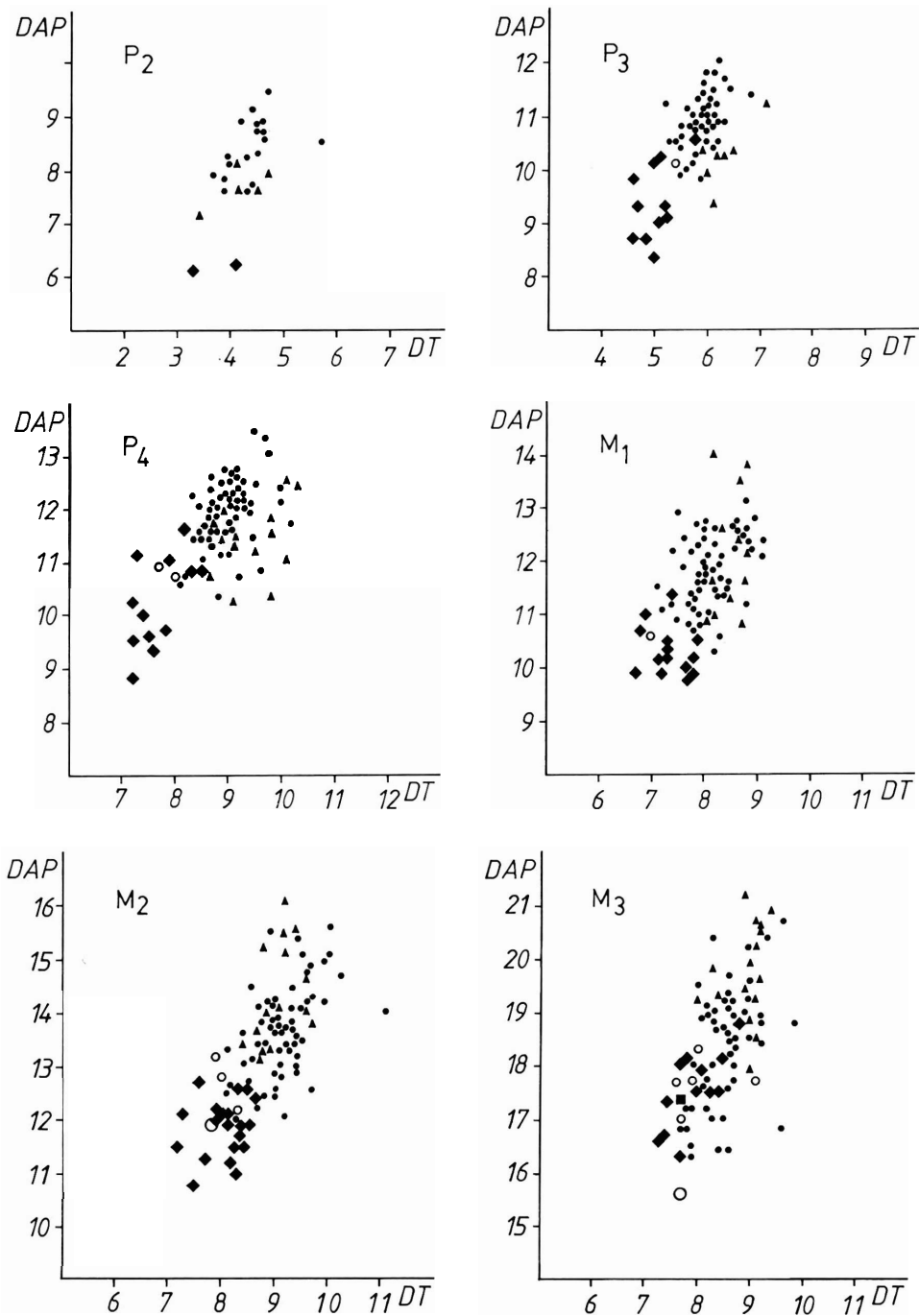


Fig. 2. Scatter diagrams of the lower cheek-teeth.

- ◆ 1 *Pseudoeotragus seegrabensis* from Seegraben
 - 2 *Eotragus sansaniensis* from Sansan
 - 3 *Eotragus aff. sansaniensis* from Seegraben
 - 4 *Eotragus artenensis* from Artenay
 - 5 '*Antilope*' *crinata* from Veltheim
 - ▲ 6 *Caprotragoides stehlini* from Arroyo del Val and Manchones
- DT is the greatest DT (DTa or DTp).

In the graphs it can be seen that *P. seegrabensis* and *E. sansaniensis* differ slightly in size. There is little size overlap in the premolars, but there is considerable size overlap in the last lower molar. The means of the lengths of the lower cheek teeth of the Seegraben population are smaller than those of the Sansan population, but the difference decreases from P₂ to M₃. The premolars of

Table 3 Hypsodonty of bovids. DT is greatest width, h is height of the entoconid. Measurements in mm. The crown-height of Eotragus from Sansan is taken from photographs.

		DAP	DT	h	h/DAP	h/DT
M₁						
<u>Pseudoeotragus seegrabensis</u>						
Seegraben	3742	10.7	6.6	8.3	0.8	1.3
<u>Caprotragoides</u>						
Arroyo del Val VI	AR VI 148	13.6	8.5	12.0	0.9	1.4
<u>Eotragus</u>						
Sansan	SA 1042	12.7	7.8	8.1	0.6	1.0
	SA 1054	12.0	8.5	9.1	0.8	1.1
M₂						
<u>Pseudoeotragus seegrabensis</u>						
Seegraben	3715	12.1	8.0	>9.2	>0.8	>1.2
	3716	12.7	7.6	>9.2	>0.7	>1.2
	3726	12.4	8.7	>9.3	>0.8	>1.1
	3742	12.1	7.8	>9.2	>0.8	>1.2
<u>Caprotragoides</u>						
Arroyo del Val IV	AR IV 298	15.1	9.2	14.1	0.9	1.5
Manchones I	MA I 5067	16.0	9.3	14.6	0.9	1.6
	MA I 5129	16.2	+9.0	13.8	0.9	+1.5
	MA I 5129	14.6	8.4	13.5	0.9	1.6
M₃						
<u>Pseudoeotragus seegrabensis</u>						
Seegraben	3715	17.0	7.7	>11.1	>0.7	>1.4
	3740	17.5	8.4	>10.1	>0.6	>1.2
	3742	--	7.9	>11.3	--	>1.4
	3742	--	7.8	>11.1	--	>1.4
<u>Caprotragoides</u>						
Arroyo del Val IV	AR IV 298	19.1	9.1	14.2	0.7	1.6
	AR IV 300	19.8	9.0	14.4	0.7	1.6
Paracuellos III	PA 1240	19.2	8.8	13.0	0.7	1.5
<u>Eotragus</u>						
Sansan	SA 1110	16.3	7.9	9.4	0.6	1.2
<u>Antilope cristata</u>						
Veltheim	468	16.7	--	9.4	0.6	--
M₂						
<u>Pseudoeotragus seegrabensis</u>						
Seegraben	56.882	12.4	13.1	>9.4	>0.8	>0.7
	56.882	12.1	12.6	10.6	0.9	0.8
	3743	13.4	13.9	>9.8	>0.7	>0.7
<u>Eotragus</u>						
Sansan	Sa 1083	13.4	14.5	+9.3	+0.7	+0.6
	Sa 1075	14.7	15.0	9.8	0.7	0.7
<u>Caprotragoides</u>						
Manchones I	MA I 5086	16.2	15.1	15.9	1.0	1.1
	MA I 5087	16.4	14.5	15.3	0.9	1.1
	MA I 5088	16.1	15.5	>14.1	>0.9	>0.9
	MA I 5097	14.6	--	11.5	0.8	--
Arroyo del Val III	AR III --	16.4	14.9	>12.9	>0.8	>0.9
Arroyo del Val VI	AR VI 158	15.2	15.1	>12.9	>0.8	>0.9
	AR VI 165	15.8	15.5	>15.1	>1.0	>1.0
	AR VI 167	15.2	14.2	>14.1	>0.9	>1.0
	AR VI 170	15.0	14.2	>14.0	>0.9	>1.0

Table 4 Distribution of some of the earliest European Bovids.

MN	<u>Pseudoeotragus seegrabensis</u>	<u>Eotragus</u>	<u>"Antilope" cristata</u>	<u>Caprotragoides</u>	<u>Miotragocerus sp.</u>
6		Arroyo del Val Manchones Sansan		Arroyo del Val Manchones Paracuellos	
5	Seegraben Labitschberg	Gßriach Seegraben	Veltheim?		Puente Vallecas
4b	Tarazona	Tarazona	Veltheim?		Valdemoros
4a		Artenay Córcoles Buñol	Veltheim?		

P. seegrabensis have a little more than 80% of the width of the premolars of *E. sansaniensis*, but in the molars this is about 90%. The P₄ is wider in *P. seegrabensis* than in *E. sansaniensis*.

The *E. sansaniensis* P₃ has a posterior stylid that may be much shorter and may be directed more distally. The *E. sansaniensis* P₄ may have the same morphology, although other types occur in the large Sansan sample. The Sansan molars are less hypsodont and have parastylids with a smaller dip; often they do not protrude much lingually, but more mesially. In most *Eotragus* molars the

Table 5 Measurements in mm of the dentition of Antilope cristata from Veltheim. DAP = antero-posterior diameter, DTa = transverse diameter of the anterior lobe, DTp = transverse diameter of the posterior lobe, in M₃ DTpp = transverse diameter of the talonid.

no.		P ₂	P ₃	P ₄	M ₁	M ₂	M ₃
63, sin.	DAP					11.3	
	DTa					--	
	DTp					--	
63, dext	DAP	9.9					
	DT	--					
no. 63, dext(?)	after Biedermann:						
	DAP	8	8	9	9	11	13
	DT	6	7	9	9	11	10
no.		P ₂	P ₃	P ₄	M ₁	M ₂	M ₃
467	DAP						17.3
	DTa						7.7
	DTP						7.2
	DTpp						3.8
468	DAP						16.7
	DTa						--
	DTp						--
	DTpp						--
469	DAP		9.0	+9.4	+9.6		
	DTa		--	--	--		
	DTp		--	--	--		

postmetacristid is not directly fused with the pre-entocristid: there is a small ridge connecting the metastylid with the pre-entocristid. The premetacristid and the preprotocristid are usually fused only in their lower parts. In nearly all *Eotragus* M_3 there is a talonid fossa, closed by a crest at the place of the entoconulid. In *E. sansaniensis* the P^3 tends to have a more posteriorly situated lingual cone. Anteriorly the tooth may also be wide, so it looks bi-lobed. The *Eotragus* P^4 does not have the rib of the labial cone parallel to the anterior style. The *E. sansaniensis* upper molars are less hypsodont and do not have the rib of the paracone parallel to the parastylid and if the precrista of the metaconule is fused with the postparacrista this occurs very low down (near the base of the crown).

Eotragus aff. *sansaniensis* and *E. artenensis*

Both *Eotragus* have cheekteeth that are less hypsodont than the cheek teeth of *P. seegrabensis*. The lower cheekteeth have flatter lingual walls in *P. seegrabensis*. The P^3 and P^4 of *E. artenensis* are larger and the M_3 smaller than in *P. seegrabensis*. Also *E. aff. sansaniensis* and, as we have seen already, *E. sansaniensis* have relatively large premolars. This seems to be a typical difference between genus *Eotragus* and the species *P. seegrabensis*. Horncores of *Eotragus* from Buñol and Córcoles (Moyà Solà 1983, Alferez et al. 1981) and from Seegraben resemble those of *E. sansaniensis* in morphology: they are shorter than those of *P. seegrabensis*

Antilope cristata

The holotype of *Antilope cristata* is a fragmentary skull with a right horn pit, parts of the frontals and parietals and a crushed palate; one tooth row is still covered by sediment the other one has been damaged since Biedermann made his description of *A. cristata*. The skull has been compressed laterally during diagenesis. It is not quite clear to me to what extent, but probably not very much since the matrix is sandstone. The M^3 is fairly worn; the animal must have been adult. The skull is wider at the place of the orbits than at the brain case, although this may be an artefact of the lateral compression. The width of the frontals between the horn pits is about 25.4 mm [36.6 mm]. The frontals are convex upwards in transverse section. This may be due also to lateral compression although the degree of convexity suggests that this is not all due to compression. The angle between the anterior side of the horn pit and the anteroposterior axis of the frontalia is about 40° [25°]. It is possible that the horn pit was placed more internally and not at the edge of the orbit. The general appearance of the skull must have been more like that of *Eotragus*: wide at the orbits and with a long and narrow cylindrical brain case, whereas the *Pseudoeotragus* skull has a relatively short and wide convex brain case.

The horn pits of *Antilope cristata* seem to be much more laterally compressed. This cannot be measured since neither specimen has been forced completely

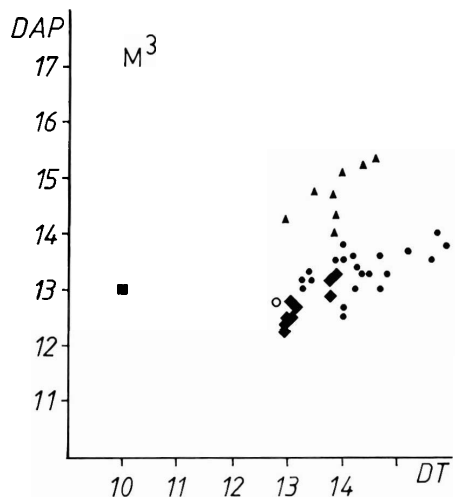
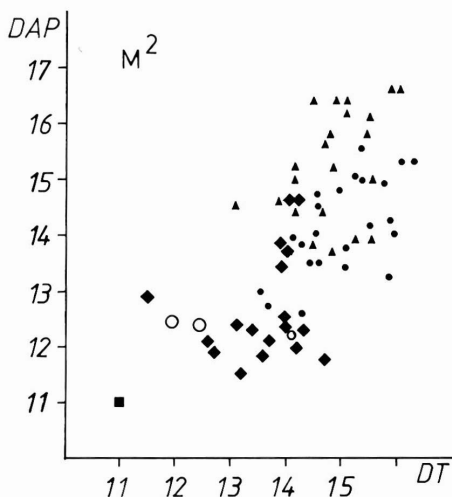
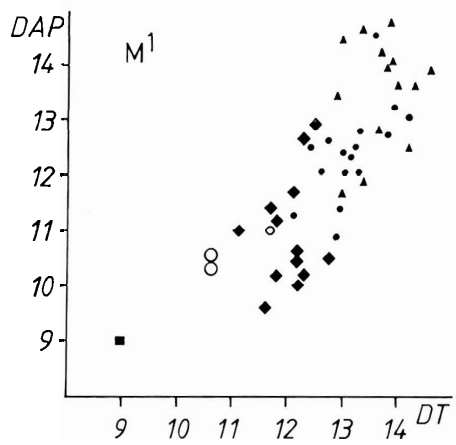
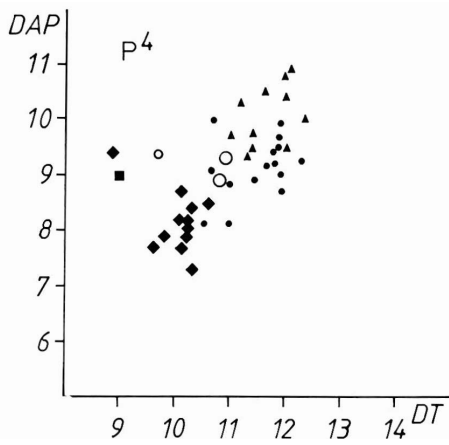
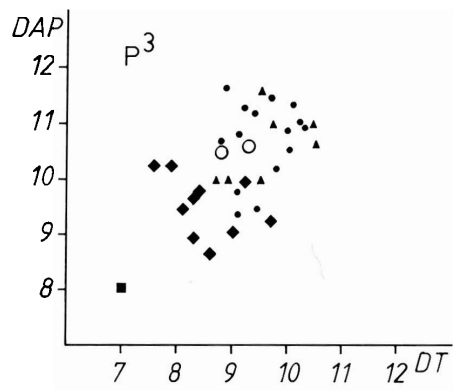
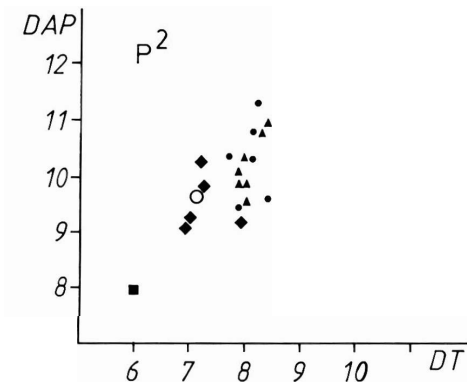


Fig. 3. Scatter diagrams of the upper cheek-teeth.
 Symbols as in figure 2.

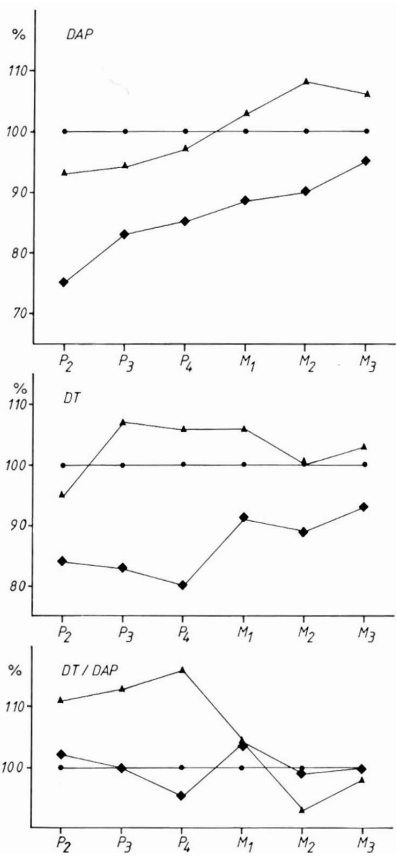
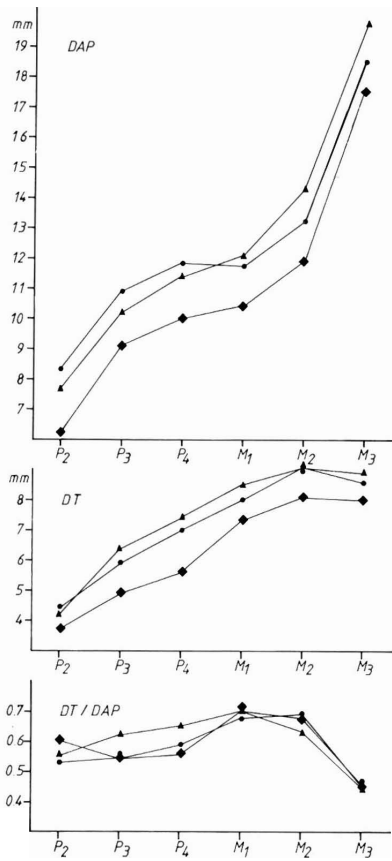


Fig. 4. Mean DAP and mean greatest DT of the lower cheek-teeth of the populations of *Eotragus* from Sansan and *Pseudoeotragus* from Seigraben and the combined material of *Caprotragoides* from Arroyo del Val and Manchones. Symbols as in figure 2. Fig. 4a and 4c in mm, fig. 4b, 4d and 4e in %; *Eotragus* is 100%.

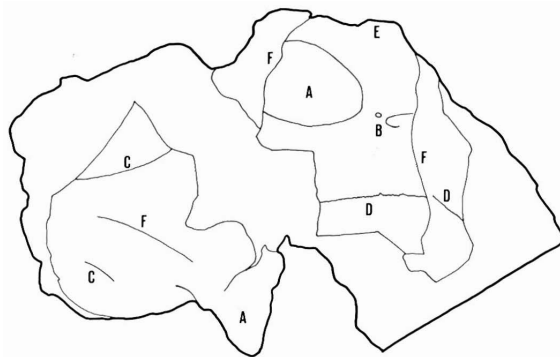


Fig. 5. Dorsal side of no. 3678.

A horn pit
B supraorbital foramen
C temporal line

D suture
E edge of the orbit
F fracture

from the sediment. The horn pit that belongs to the skull is very compressed at its distal end. This is also the case in 59.605, but this horn pit is not very compressed at the base.

The greater compression is probably not due to diagenetic compression since the bone of a horncore is much more compact than the skull itself. The DAP at the base is inferior. The pedicle seems to be higher. It is possible that the horn pit from Locle figured by Thenius 1952 (fig. 6) is *A. cristata* or *Pseudoeotragus*.

The measurements of the upper teeth of *A. cristata* are taken from Biedermann (op. cit.). All teeth are considerably smaller, save the P⁴. The M³ seems to be very narrow. Of the lower teeth only the length could be measured except in the case of one M₃. The lower teeth are short, but never shorter than the shortest teeth of *P. seegrabensis*. The *A. cristata* M₃ is less hypsodont. Its metastylid can be traced to near the base of the crown.

Caprotragoides stehlini

Caprotragoides stehlini has its horn pits at the edge of the orbit; they are very thick so they are only about 1.5 cm apart; this is much less than in *Pseudoeotragus seegrabensis*. The horn cores of *Caprotragoides stehlini* are curved backwards and their dimensions are larger.

There is nearly no size overlap between the smaller *P. seegrabensis* and the larger *C. stehlini*. The lower premolars of *Caprotragoides* are relatively wider. In *C. stehlini* the medial valley of the P₃ is frequently closed by fusion of the oblique cristid with the posterolingual conid. Nearer to the base of the tooth the oblique cristid and the posterolingual conid always fuse. The *C. stehlini* P₄ has a well-developed anterolingual conid that reaches the lingual side of the tooth over nearly its whole height. The valley between this conid and the anterior stylid disappears with only slight wear. The same is true for the posterior valley. The *Caprotragoides* molars are more hypsodont. The M₃ of *Caprotragoides* has the talonidal structure of *P. seegrabensis*; it never has a talonidal fossa. The *Caprotragoides* P² are more hypsodont and do not have well-developed anterior styles. The *Caprotragoides* P³ is much more hypsodont, this can also be seen clearly on the lingual side. The lingual wall is much more circular and smooth; lingually there is no real cone. The rib of the lingual cone of the *Caprotragoides* P⁴ is often less developed. In the upper molars of *Caprotragoides* the precrista of the metaconule is fused to the postparacrista; this always occurs at a high level. Its molars are more hypsodont and are often narrower. This is very clear in the M³.

Miotragocerus sp.

The hornpits of *Miotragocerus* sp. generally have a triangular section. This results from the postero-internal keel, which is typical for Boselaphini, and the sharper anterior keel. There is, however, some variation in the shape of this section. The P₃ and P₄ are longer than in *P. seegrabensis*, but have an equal or inferior width and the M₃ is larger (Moyà Solà, 1983)

DISCUSSION

The skull structure of *Pseudoeotragus seegrabensis* differs greatly from that of *Eotragus sansaniensis*: the zone of the parietals is much shorter and wider, the skull of *P. seegrabensis* is narrower at the place of the eyes, the horn pits are placed more externally, are inclined much more backwards and flare out. The skull differs in the same way from the skull of *Antilope cristata*. Moreover the horn cores are relatively long and narrow compared to *Eotragus*. The dentition is more hypsodont in *P. seegrabensis*. Most of the differences can be interpreted as primitive characters in *Eotragus* and *A. cristata*. The number of differences indicates that *Pseudoeotragus seegrabensis* is not closely related to the *Eotragus artenensis - sansaniensis* line.

Protoryx, *Pachytragus*, *Oioceros*, *Prostrepsiceros* and *Gazella sp.* have been reported from about the same levels in Turkey (Berg, 1975) as well as *Turocerus* and *Hypsodontus* (Köhler, 1988). These genera differ in having different horn cores; they are curved, spiralled and/or with keels.

Since *Pseudoeotragus seegrabensis* is still a primitive animal it is difficult to relate it to a more recent taxon.

In Styria *P. seegrabensis* is also found in Labitschberg. A horn pit from Tarazona (Ebro Basin) has been described as *Eotragus* (Astibia, 1985 & 1987). It has the same shape as the *P. seegrabensis* horn pits from Seegraben. Tarazona is placed in MN 4 and Seegraben in MN 5.

Shortening of the premolar row is a progressive feature in most Bovidae. This seems to be achieved in two ways: reduction of the size of the premolars or reduction of only the DAP of the premolars. The premolars of *Pseudoeotragus* are smaller than those of *Eotragus*. The premolars of *Caprotragoides* are shortened. Increase in the size of M 3 relative to the other molars seems to be another progressive feature. If compared to *Eotragus*, *Caprotragoides* and *Pseudoeotragus* are equally progressive in this character.

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APPENDIX

The bovid material from Seegraben to which reference is made, but which is not *Pseudoeotragus seegrabensis* is the following:

Eotragus aff. sansaniensis

- 3703 a left P⁴ (figured by Hofmann & Zdarsky, 1904, plate XVI, fig. 4)
- 3708 right M¹-M³ belonging together
- 3710 a left M₃
- 3713 a left P₄ (figured by Hofmann & Zdarsky, 1904, plate XVI, fig. 15-17)
- 3717 a left mandibula with M₁-M₃ (figured by Hofmann & Zdarsky, 1904, plate XV, fig. 18)
- 3718 a left mandibula with D₃-M₁
- 3728 a left mandibula with P₄-M₃
- 3729 a right mandibula with M₂-M₃
- 3742 2 right M₃, 1 right M₁
- 3743 2 M^x and several fragments
- 3745 5 fragments of horn cores one of which has been figured by Zdarsky, 1909 (plate VIII, fig. 14 & 15) and by Thenius, 1952 (fig. 5)

? *Eotragus aff. sansaniensis*

- 2024 right M₃
- 3711 a left P₃ (figured by Hofmann & Zdarsky, 1904, plate XVI, fig. 18-20)
- 3724 a left mandibula with P₂-M₃ (figured by Zdarsky, 1909, plate VIII, fig. 12)
- 3742 left M₁-M₂

Bovidae indet.

- 3683 proximal part of a metatarsus
- 3686 right astragalus
- 3689 distal part of a left tibia (figured by Hofmann & Zdarsky, 1904, plate XVI, fig. 24-25)
- 3690 6 distal ends of humeri one of which is figured by Zdarsky, 1909, plate VIII, fig. 16
- 3698 4 first phalanges of the central toes
- 3730 right I₁ (figured by Hofmann & Zdarsky, 1904, plate XVI, fig. 8-9)
- 3763 pisiform
- 3764 left calcaneum
- 3765 left calcaneum