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THE CONFIGURATION OF THE LACRIMAL ORIFICES IN PECORANS AND TRAGULIDS (ARTIODACTYLA, MAMMALIA) AND ITS SIGNIFICANCE FOR THE DISTINCTION BETWEEN BOVIDAE AND CERVIDAE

J. J. M. LEINDERS* & E. HEINTZ**

* *Instituut voor Aardwetenschappen, Budapestlaan 4, postbus 80.021, 3508 TA Utrecht, The Netherlands*

** *Muséum Nationale d'Histoire Naturelle, 8 rue de Buffon, 75005 Paris, France*

ABSTRACT

The number and position of the orifices to the lacrimal duct in the lacrimal bone of ruminants is evaluated. It is concluded that the Bovidae, except the Bovini and Tragelaphini, have maintained the original one-orifice-inside-the-orbit configuration, whereas the two-orifices-on-the-rim-of-the-orbit morphology of the Cervidae was achieved before the M. Miocene in the evolution of this family. The classification of the Antilocapridae is discussed and it is concluded that the configuration of the lacrimal orifices corroborates with the suggested (Leinders, 1979) transfer of the Antilocapridae Gray, 1866 from the Bovoidea Simpson, 1931 to the Cervoidea Simpson, 1931.

INTRODUCTION

In general there is no difficulty in separating recent Cervidae and Bovidae by the character of their frontal appendages: cervids being typified by the bony, deciduous outgrowths from cylindrical processes of the frontals, bovids by the persistent horn sheaths covering bony cores on the frontals. However, the existence of pecorans in which the frontal appendages are wanting, such as the chinese waterdeer *(Hydropotes inermis)* and the muskdeer *(Moschus moschiferus),* and of pecorans with anomalous frontal structures such as the pronghorn *(Antilocapra americana),* made many zoologists search for other distinctive features of the Cervidae and the Bovidae (Flower, 1875; van Kampen, 1975; O'Gara and Matson, 1975). Brooke (1878, p. 885) listed 12 characters which distinguish the Cervidae from the Bovidae, but he stated: "none of the above characters can be taken singly as distinctive of a Cervine from a Bovine animal".

The distinction between fossil bovids and cervids is even more delicate due to the great diversity, the paucity of material and the restricted information on the anatomy and habitat of fossil pecorans when compared with the recent ones. Heintz (1970) described the differences in dentition and post-cranial skeleton between the Villafranchian Bovidae and Cervidae of western Europe. Some of the listed differences have a general applicability, especially that in the morphology of the gully at the anterior side of the metatarsus (Heintz, 1963; Leinders, 1979).

One of the features to distinguish between bovids and cervids mentioned by Flower (1875) and Brooke (1878) is the number and position of the orifices to the lacrimal duct in the lacrimal bone: cervids having two orifices situated on the rim of the orbit (Plate I, fig. 3), whereas bovids and tragulids have only one, inside the orbit (Plate II, fig. 2 and Plate I, fig. 1). Both authors emphasized the value of this character, although they reported several exceptions: *Tragelaphus* and *Antilocapra* have two orifices as in cervids, whereas in *Moschus* the same configuration is found as that generally present in bovids and tragulids.

The lacrimal ducts (ductus naso-lacrimalis) connect the orbita with the nasal cavity for the draining of the surplus of lacrimal fluid from the eyes to the nostrils.

The purpose of this paper is to evaluate the number and position of the lacrimal orifices for the distinction between Bovidae and Cervidae.

MATERIAL

The material studied is stored in: Muséum Nationale d'Histoire Naturelle, Paris; Institut Royal de Sciences Naturelles, Bruxelles; Rijksmuseum van Natuurlijke Historie, Leiden; Zoologisch Museum Universiteit van Amsterdam; Taxonomisch Instituut Rijksuniversiteit Utrecht; Instituut voor Aardwetenschappen Rijksuniversiteit Utrecht.

N = number of skulls examined.

Morphology of the lacrimal orifices in recent tragulids and pecorans.

Tragulidae Milne Edwards, 1864

	N		N
Tragulus sp.	3	*Tragulus napu*	2
Tragulus javanicus	3	*Hyemoschus aquaticus*	1
Tragulus meminna	1		

All tragulids examined have one elongated orifice just inside the rim of the orbit (Plate I, fig. 1).

Moschidae Gray, 1821

	N
Moschus moschiferus	5

In *Moschus* one elongated orifice is present just inside the orbit, which resembles that of tragulids. At the medial border of the orifice there is a small protuberance, however, which gives the impression that the single orifice in *Moschus* is either the result of fusion of two separated orifices or that the orifice in *Moschus* corresponds to an early (initial) stage of transformation from one into two, which is the normal configuration in cervids (Plate I, fig. 2).

Cervidae Gray, 1821

	N		N
Alces alces	4	*Hyelaphus kuhlii*	2
Axis axis	1	*Hyelaphus porcinus*	7
Blastoceros campestris	1	*Mazama americana*	9
Capreolus capreolus	89	*Mazama gouazoubira*	1
Cervus elaphus	3	*Muntiacus* sp.	1
Cervus rusa	1	*Muntiacus muntjak*	11
Cervus nippon	2	*Muntiacus reverii*	1
Dama dama	12	*Odocoileus virginianus*	2
Elaphodus cephalophus	2	*Rangifer tarandus*	14
Elaphurus davidianus	3	*Rucervus eldi*	1
Hydropotes inermis	3		

In cervids the lacrimal duct opens into two orificies, one above the other, on the rim of the orbit. Although the position of the orifices is slightly variable (from slightly on the internal side of the rim to slightly on the external side of the rim), the lower orifice has a more anterior position than the upper one (Plate I, fig. 3). In two of the skulls of *Muntiacus muntjak* both orifices are situated just inside the orbit. One of the skulls of *Hyelaphus porcinus* (Mus. d'Hist. Nat. Paris no. 1952-141) shows a very small upper orifice, which configuration is considered anomalous. Two anomalous specimens were found in the series of 89 skulls of *Capreolus* stored in the Taxonomical Institute in Utrecht. The right orbit of skull no. 11 has only one orifice on its rim, whereas the left orbit shows the normal cervid two. A similar phenomenon was observed on skull no. 77 of which the left orbit has only one orifice and the right is normal.

Antilocapridae Gray, 1866

	N
Antilocapra americana	6

The lacrimal duct of the single recent species of the antilocaprids opens into two orifices. They differ from those in the cervids by the position of the upper orifice, which is situated inside the rim of the orbit. The lower orifice is placed, as in cervids, more anteriorly, near the margin of the rim.

O'Gara and Matson (1975) reported that *Antilocapra* has only one orifice as the Bovidae, but this is neither confirmed by the literature (Flower, 1875; Frechkop, 1955) nor by our observations. For further discussion see the chapter on the classification.

Giraffidae Gray, 1821

	N
Okapia johnstoni	2
Giraffa camelopardalis	8

The *Okapia* skulls show one very small orifice inside the orbit. Of the eight skulls of *Giraffa* five have no lacrimal orifice at all, the other three an orifice similar to that of *Okapia.*

Bovidae Gray, 1821

	N		N
Alcelaphus major	1	*Madoqua saltana*	1
Antidorcas marsupialis	5	*Naemorhedus* sp.	1
Antilope cervicapra	1	*Naemorhedus goral*	1
Ammotragus lervia	4	*Neotragus pygmeus*	2
Budorcas taxicolor	1	*Nesotragus* sp.	1
Capra aegarus	1	*Oreamnos americanus*	2
Capra caucasica	1	*Ourebia ourebia*	41
Capra falconeri	1	*Oreotragus oreotragus*	7
Capra hircus	9	*Oryx* sp.	5
Capra siberica	1	*Oryx tao*	1
Capricornis sumatrensis	3	*Oryx beisa*	2
Cephalophus sp.	2	*Ovibos moschatus*	2
Cephalophus dorsalis	3	*Ovis aries*	9
Cephalophus ituriens	1	*Ovis musimon*	1
Cephalophus maxwelli	2	*Pantholops hodgson*	1
Connochaetes gnu	4	*Pelea capreolus*	3
Damaliscus albifrons	4	*Procapra gutturosa*	1
Damaliscus korrigum	2	*Pseudois nayaur*	3
Gazella dorcas	2	*Raphicerus campestris*	9
Gazella rufifrons	1	*Raphicerus melanotis*	1
Gazella soemmeringii	7	*Raphicerus sharpei*	11
Gazella dama	1	*Redunca redunca*	3
Gazella granti	10	*Rupicapra rupicapra*	4
Gazella thomsoni	1	*Saiga tartarica*	6
Gazella subgutturosa	4	*Sylvicapra grimmia*	2
Hemitragus sp.	1		
Hippotragus equinus	35	Boselaphini Simpson, 1945	
Hippotragus niger	8	*Boselaphus tragocamelus*	13
Kobus kob	1	*Tetracerus quadricornis*	2
Tragelaphini Sokolov, 1953			
Boocerus eurycerus	1	Bovini Simpson, 1945	
Taurotragus sp.	1	*Anoa* sp.	2
Taurotragus oryx	1	*Anoa depressicornis*	26
Tragelaphus sp.	1	*Bison bonasus*	1
Tragelaphus gratus	1	*Bison bison*	1
Tragelaphus imberbis	1	*Bos banteng*	3
Tragelaphus scriptus	17	*Bos indicus*	1
Tragelaphus spekii	2	*Bos gaurus*	1
Tragelaphus strepciceros	4	*Bos taurus*	7
Litocranius walleri	3	*Bubalus bubalus*	5
Madoqua sp.	3	*Syncerus caffer*	1

In most bovids one circular orifice to the lacrimal duct is found, situated inside the orbit (Plate II, fig. 2). In the tribes Bovini and Tragelaphini the morphology of the orifices is not according to this general rule, however. There is considerable variation, especially in the Tragelaphini. On the 17 examined skulls of *Tragelaphus scriptus* we observed the following configurations:

Two orifices on the rim separated by a very thin bone bar.

Two orifices on the rim about 7 mm. from each other.

Two orifices on the rim with the upper more anteriorly than the lower one.

One orifice on the rim.

One orifice inside the orbit.

Two orifices inside the orbit.

Two orifices inside the orbit; a large and a small one.

Two orifices inside the left orbit, one orifice inside the right orbit of the same skull.

Similar variation is found in the skulls of the other Tragelaphini.

On the skulls of the Bovini the following configurations have been observed:

Two orifices on the rim (*Bison bison, Bison bonasus,* one specimen of *Bos banteng*).

Two orifices inside the orbit (one skull of *Bubalus bubalus*).

One orifice on the rim of the orbit (*Bos indicus,* two skulls of *Bos taurus*).

One orifice inside the orbit (all other skulls).

REMARKS ON THE CLASSIFICATION OF PECORANS AND TRAGULIDS

According to Flower (1875, p. 186) the presence of one lacrimal orifice inside the orbit is the original configuration in artiodactyls, present in early forms like *Caenotherium* and *Xiphodon.* It is generally accepted that bovids and cervids have a traguloid ancestry. Tragulids and bovids (except the Bovini and Tragelaphini) still have one orifice inside the orbit, whereas the two-orifices-on-the-rim configuration in cervids may be interpreted as a new development during the early evolution of this family.

Ginsburg and Heintz (1966) proposed a new family (Dremotheriidae) for the paleogene antlerless cervoids, which they considered ancestral to the Cervidae and Giraffidae. According to Simpson (1945) *Prodremotherium* is a traguloid. However, Jehenne (1977) showed that *Prodremothe-*

rium is very close to *Dremotherium* and might be considered the ancestor of the latter genus. *Dremotherium* has the original one-orifice-inside-the-orbit configuration (Sigogneau, 1968).

The oldest Cervidae of which we have information on the lacrimal orifices is *Heteroprox* from the Aragonian (M. Miocene) of Steinheim (Germany). Although its antlers show no well developed pedicle, they already might have been deciduous (Ginsburg & Crouzel, 1976). *Heteroprox* has two orifices on the rim of the orbit (Heizmann, pers. comm.), indicating that this character is present in the Cervidae at least from M. Miocene onward.

It is generally accepted that *Moschus* and *Hydropotes,* although not closely related to each other, are the most primitive genera among the recent cervoids. In both genera antlers are wanting, which is compensated by large sabre-like upper canines. These two genera show certain resemblances with *Dremotherium* (Sigogneau, 1968).

Moschus shows a mixture of bovid and cervid characteristics (Flower, 1875; Sigogneau, 1968), and according to Thenius (1969) this genus may be a remnant of a pre-pecoran stage of the ruminant phylogeny, which justifies its classification in a separate family. The single lacrimal orifice inside the orbit of *Moschus* separates the musk-deer from the Cervidae and corroborates with this suggestion. However, the metatarsus of *Moschus* shows a closed gully at its anterior side (Flerov, 1930 Plate VII) just as it does in the cervids. Heintz (1963) and Leinders (1979) Emphasized the value of the morphology of the gully at the anterior side of the metatarsus as a distinctive character between Bovidae and Cervidae. In bovids the gully is open over the full length of the metatarsus, whereas in cervids it closes above the distal end of the shaft. In *Moschus* these two familial characteristics are contradictary (cervid-type metatarsus and bovid-type lacrimal orifices). As mentioned earlier in this chapter, the lacrimal duct of cervids opens into two orifices on the rim of the orbit since the Middle Miocene. Also the difference in morphology of the gully on the metatarsus between bovids and cervids was already present at that itme (Heintz, 1963). This indicates that *Moschus* ancestral line branched off from the Cervidae before the Middle Miocene. One may also conclude that the closed gully on the metatarsus was achieved earlier in the cervid evolution than the two lacrimal orifices on the rim of the orbit.

Hydropotes, on the other hand, incontestably belongs to the Cervidae (Garrod, 1877; Forbes, 1882), which is in agreement with the two orifices on the rim of their orbit (Plate I, fig. 3).

The Antilocapridae are generally considered to be related to the Bovidae which finds its expression in the classification of both families in one superfamily: the Bovoidea. Thenius (1969) and Leinders (1979), however, suggested that the antilocaprids are an offshoot from early american cervoids and for this reason Leinders (1979) proposed to shift the Antilocapridae from the Bovoidea to the Cervoidea. The presence in the pronghorn *(Antilocapra americana)* of two orifices to the lacrimal duct, although positioned more internally than in cervids (Plate II, fig. 1), supports the idea of a cervoid ancestry of the Antilocapridae.

On the other hand, O'Gara & Matson (1975) concluded from the similarity in the horn-forming process that *Antilocapra* is very close to the Bovidae and they proposed to lower the rank of the pronghorn and its fossil relatives from the separate familiy (Antilocapridae) to a subfamily (Antilocaprinae) of the Bovidae. The authors remarked: "Histologically horn formation resembled that of skin" and "the horn-forming process in pronghorns involves formation of a keratin similar to that of nails and claws". Combining these statements with the fact that horn formation is common in mammals, one might wonder if horn formation is a significant character for classification.

In addition to the similarity in horn formation, O'Gara and Matson (1975 : 840) listed about twenty features in which the antilocaprids resemble the Bovidae. However, most of these are also found in cervids (e.g. cannon bone, loss of upper incisors) or, they are variable in bovids and/or cervids (e.g. orbits large to medium, contact between lacrimal and nasal bones). Other similarities listed are: a) presence of a gall-bladder, b) one orifice to the lacrimal duct, c) presence of unbranched bony cores covered with keratin, d) hypsodont dentition.

Ad a) the presence of a gall-bladder in the pronghorn indeed makes it approach the bovids. But the presence of a gall-bladder in *Moschus* (Flower, 1875) may indicate that in primitive cervoids this bladder was still present and its occurence in *Antilocapra* can be explained as the retention of an original character. Flower (1875) reports also that the presence of a gall-bladder "seems to be a somewhat variable character even within the same species".

Ad b) according to O'Gara & Matson Antilocapra has only one lacrimal orifice inside the orbit as in bovids. According to our observations and the literature (Flower, 1875; Frechkop, 1955) the pronghorn has two orifices to the lacrimal duct. Frechkop (1955 : 616), however, reports that sometimes the two lacrimal orifices are fused into one, which could explain the contradicting observations.

Ad c) the horns of *Antilocapra* differ from those of the bovids by the forked form and by the annual shedding of the horny cover. These differences were the main reasons to place the pronghorn in a separate family. O'Gara & Matson pointed out that exfoliation of the horn covers also occurs in many bovids and from this they concluded that the shedding in *Antilocapra* is no reason for separating the pronghorn from the Bovidae. One can dispute wheter these differences are significant for classification on family level or not, but the shedding in bovids differs largely from that in *Antilocapra.* In the pronghorn the shedding occurs annually (in November) and is related to the rut. It takes about ten months to grow a new horn-cover (O'Gara & Matson, 1975: fig. 3). This parallels very much the growth and casting of antlers in cervids and probably has the same function in relation to the rut. On the other hand the reported exfoliation of the horn-covers in bovids is irregular and incidental and seems to be related to the growth and/or renewing of the horn-covers.

Ad d) The hypsodont dentition of the antilocaprids is frequently used as an argument to include this family in the Bovoidea (Frechkop, 1955; O'Gara & Matson, 1975). As can be concluded from the fossil record, hypsodonty is an adaptive attainment in mammals, which occurs together with brachydonty in many unrelated families, such as the Gliridae, Muridae, Cricetidae, Equidae, Suidae and Camelidae. Differences in hypsodonty may be usuable for genus or species classification within phylogenetic lineages, but certainly not on the level of families or superfamilies.

According to Frechkop (1955) the penis of *Antilocapra* resembles that of cervids by the absence of a processus urethrae and Cowper's gland (Glandulae bulbourethrales).

The Tagelaphini and the Bovini are the only pecorans with a variable configuration of the orifices to the lacrimal duct. This similarity fits in with the opinion (e.g. Thenius, 1969) that these two tribes are closely related. The third and most primitive tribe of the bovinae, the Boselaphini, have maintained the original one-orifice-inside-the-orbit configuration.

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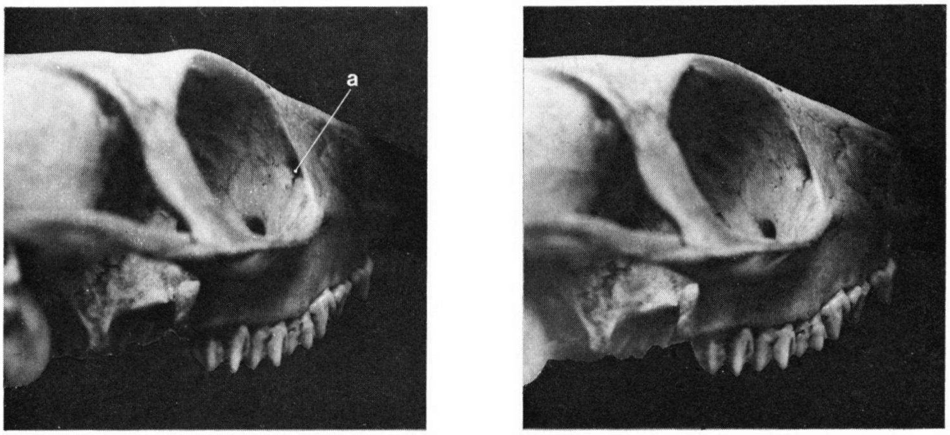
Institute of Taxonomic Zoology (Zoological Museum), University of Amsterdam,
P.O. Box 20125, 1000 HC Amsterdam, the Netherlands

Plate 1



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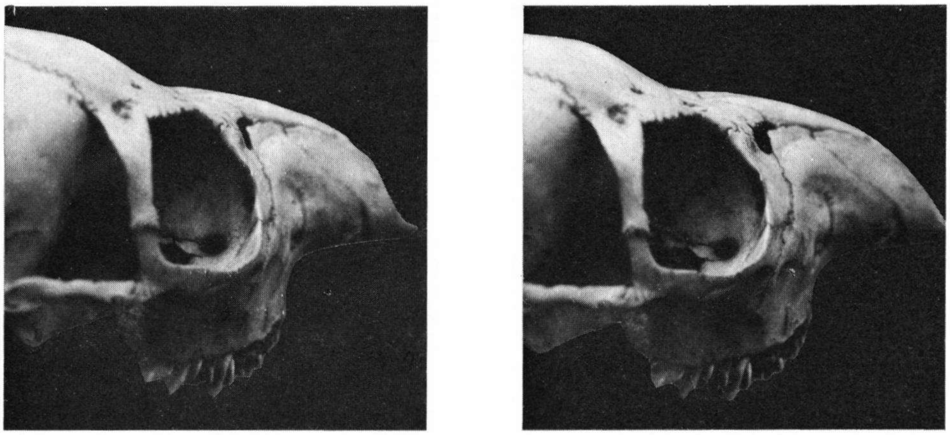

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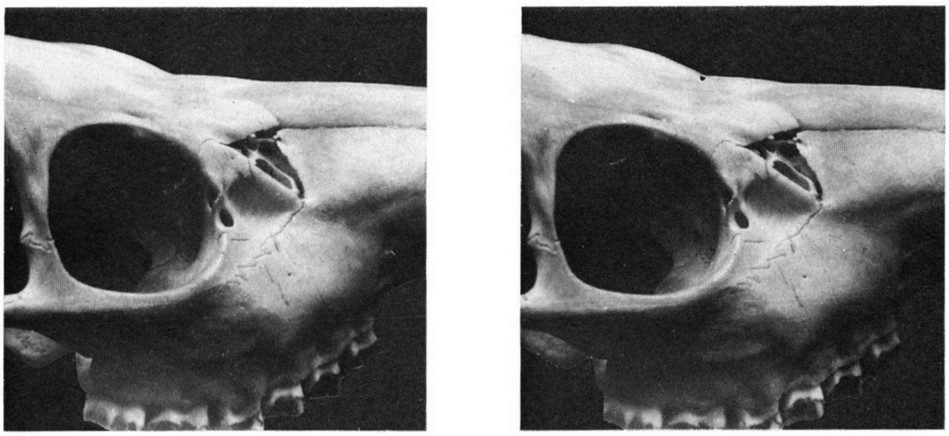
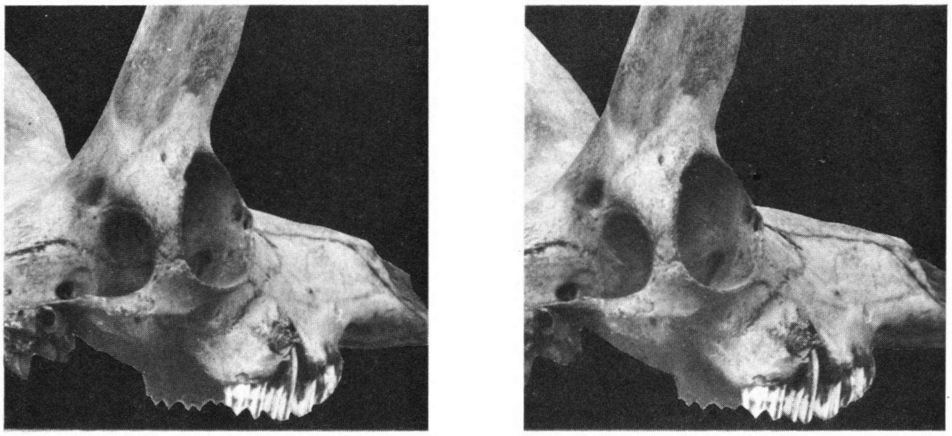


3 3cm 3

Fig. 1. *Tragulus napu* R.M.N.H. Leiden. a = lacrimal orifice. Fig. 2. *Moschus moschiferus* R.M.N.H. Leiden. Fig. 3. *Hydropotes inermis* no. 15789 R.M.N.H. Leiden.

Plate 2



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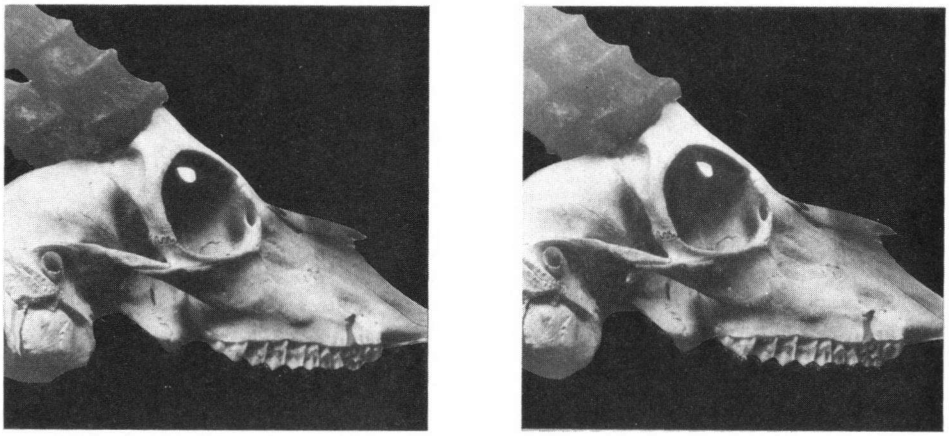

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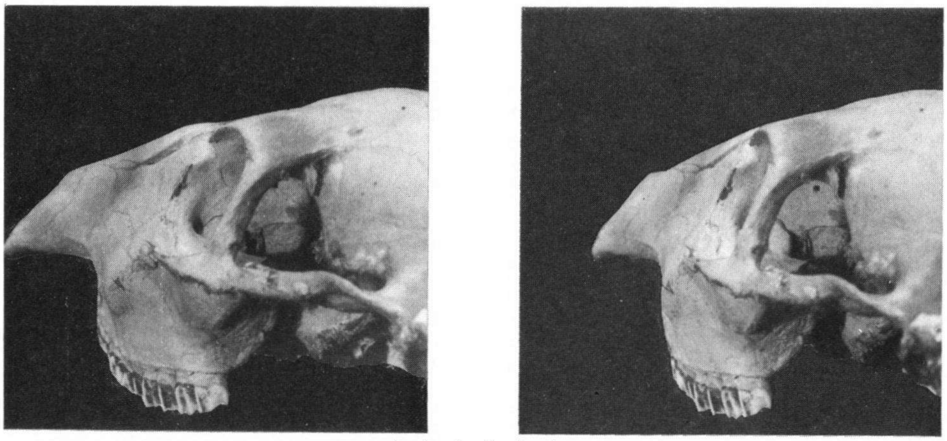

3 3

Fig. 1. *Antilocapra americana* no. 290 Z.M.A. Amsterdam. Fig. 2. *Gazella rufifrons* no. 1953-230 M.N.H.N. Paris. Fig. 3. *Tragelaphus spekii* no. 1951-273 M.N.H.N. Paris.