NOTE ON SUBFOSSIL TEETH OF EQUUS ZEBRA L. FROM ORANGE FREE STATE

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With 3 plates and 1 textfigure

Some time ago Dr. L. D. Brongersma, curator of the Leiden Museum, entrusted me for examination some subfossil equine teeth, received from Mr. H. van Hoepen, who had found them between Glen and Mazelspoort, in Orange Free State. The teeth proved to belong all to one and the same individual, and to constitute the entire upper premolar-molar-series of the right side, almost undamaged. The importance of this find is evident, as most of the fossil or subfossil equine species from S. Africa are based on isolated teeth. An inner view of our specimen is given in pl. VI lower figure, the crown surfaces are represented in the upper figure of the same plate. It can be seen, that the P^4 is the longest tooth, its height is 72 mm.

The mesostyle is prominent, and especially marked off anteriorly. The parastyle is well defined in P^3 and P^4, less so in the molars, especially in M^1. Between these styles the ectoloph is almost straight in the premolars, and slightly concave in the molars. The posterior half of the ectoloph, however, is more concave in the premolars than in the molars, the latter having a less developed metastyle. The enamel pattern is comparatively simple, the pli protoloph [1]) and the pli hypostyle are hardly or not developed. A slight trace of a pli prefossette is found in P^4 only. A small pli postfossette is seen in the premolars, in the molars it is hardly indicated. The pli protoconule is present in all the teeth, though shorter in the molars than in the premolars. The groove between protocone and hypocone is sharply pointed towards the outer side, a pli caballin is absent. The protocones are remarkable for the very slight development of their anterior lobe; they increase in length from before backward.

First I compared the subfossil teeth with those of *Equus quagga*. Of this species I examined ten adult skulls; they belong to four subspecies,

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1) Nomenclature of Osborn (1918, pp. 5-7).

but I was unable to detect characters to distinguish between the teeth of the different races. In few cases only the age of a skull was recorded; the age of the other specimens was estimated by means of the data provided by veterinary works.

Equus quagga quagga Gmelin

1. Skeleton of male. Leiden Museum, cat. a. Cape, from M. Van Horstock, 15-6-1827. Age six years.
2. Skull of female, over sixteen years old. Amsterdam Museum, no. 522. From an animal that lived in the Amsterdam zoological garden from 9-5-1867 to 12-8-1883. Mounted skin figured in Proc. Zool. Soc. London, 1904 I, p. 430, fig. 86.

Equus quagga burchellii Gray

3. Skeleton of female. Leiden Museum, reg. no. 1513. From the Rotterdam zoological garden, 4-8-1926. Age twelve (?) years.
4. Skull of male. Amsterdam Museum, no. 529. Age seven years.
5. Skull of female. Amsterdam Museum. Age ten (?) years.

Equus quagga chapmanni Layard

6. Skeleton of female. Leiden Museum, cat. a. From the Rotterdam zoological garden, 20-8-1907. There is no trace of the left I^3 or of its alveolus. The left M_1 is displaced inwards. Age twelve years or more.
7. Skeleton of male, twenty years old. Leiden Museum, reg. no. 2284. From the Rotterdam zoological garden, 16-11-1934, born in the Amsterdam zoological garden in 1914. The left upper C is missing.
8. Skull of female, more than ten years old. Amsterdam Museum, from the Amsterdam zoological garden, 3-2-1940. Purchased from L. Ruhe, Alfeld, Germany, 26-6-1930. Between the upper central incisors there is a small malformed extra incisor (see fig. 1).

Equus quagga granti De Winton

9. Skeleton of male. Leiden Museum, reg. no. 2204. From the Rotterdam zoological garden, 7-12-1933. Showing "shear-bite", like in the skull figured by Colyer (1936, p. 630-633, figs. 852-854), on the left side. The wear of the incisors is normal. Age ten years.
10. Skull of male. Coll. Carp (Amsterdam Museum), from an animal shot at Margereni, in March 1939. Age four to five years.

It is a well known fact, that the degree of complexity of the enamel foldings in a horse tooth decreases with progressing wear, so that a strict comparison is only possible between specimens of about the same age. Of the height of the teeth in a complete skull only that of P^3 can be determined with some accuracy at the outside. In the skulls nos. 1, 4 and 9 of *Equus quagga,* with an estimated age of six, seven and ten years respec-

tively, the height of P^3 at the parastyle is about equal to that in our subfossil series, viz., ca. 60 mm. In specimen no. 10 (age four to five years) that height is more than 70 mm, whereas in older skulls the height of P^3 decreases, to about 20 mm in the twenty years old no. 7.

A careful comparison of our specimen with the ten upper tooth-series of *E. quagga* showed me, that the subfossil teeth differ from the recent in five important points, viz.,

1. the narrower parastyle, especially of P^3 and P^4,
2. the lesser concavity of the halves of the ectoloph,
3. the very slight development of the anterior prolongation of the protocone in all the teeth; consequently the groove between protoconule and protocone is less deep [1]),
4. the lesser depth of the groove between hypocone and hypostyle, and
5. the simpler foldings of the fossettes.

The characters 1-3 are not affected by age, and consequently have the greatest value; 4-5 hold only for the teeth in approximately the same stage of wear as our subfossil specimens; in the older ones the fossettes may present the simple type of, and the groove between hypocone and hypostyle may be even shallower than in the subfossil teeth.

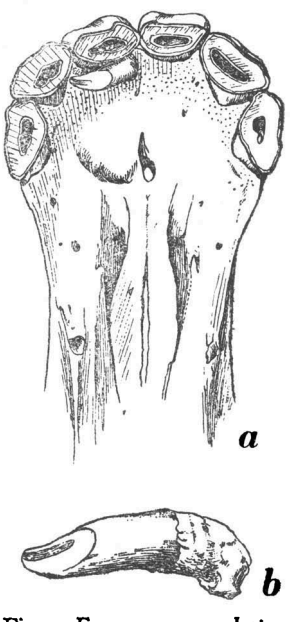


Fig. 1. *Equus quagga chapmanni* Layard, no. 8. a, anterior portion of upper jaw, showing the upper incisors with a supernumerary element in situ; b, the extra tooth. a, one half natural size; b, natural size.

The measurements of the latter fall within the limits of *E. quagga*, as is clear from table I. Only the length of P^2 (31 mm) is somewhat less than in my recent material (32½-38 mm), but Motohashi (1930, table 15, A.M. 27749) gives 30.2 mm as length of P^2 in one skull of *Equus quagga granti*. The protocones, in P^3 even slightly shorter than in any of the corresponding recent teeth, are comparatively short in our subfossil. Nevertheless, on the ground of size alone, it would be impossible to distinguish the subfossil teeth

1) In one skull of the quagga (no. 2) this character holds only for the posterior molars. The protocones of P^3-M^1 are not strictly elongated in the antero-posterior direction but are set obliquely, their posterior portion is directed backward and inward. Their anterior development is hardly or not greater than that in the corresponding subfossil teeth.

from the recent, and it is on the evidence of the structural characters that I am certain that the subfossil teeth are specifically distinct from *E. quagga*.

The second recent species that must receive consideration is the mountain zebra, *Equus zebra*. Fortunately I could examine one skull (Amsterdam Museum, from the Amsterdam zoological garden, 16-8-1903, age nine years) with the dentition in the same stage of wear as the subfossil teeth. Pl. VII represents the upper dentition of this zebra, Pl. VIII a typical quagga dention. It will be seen that the teeth of *Equus zebra* differ from those of *E. quagga* in exactly the same points as the subfossil teeth do. The differences between the teeth of *E. zebra* and the subfossil specimens consist only in the narrower mesostyles of P^2 and P^3, and the broader parastyle of P^4 in the former as compared to the latter. The variation in *E. quagga* shows these characters to be not reliable.

The teeth of *E. zebra* do not differ in size from those of *E. quagga*, as can be seen from table I.

In his review of the fossil Equidae of S. Africa, Haughton (1932, p. 424) refers the following four forms to *Equus quagga*:

1. *Equus platyconus* Van Hoepen (1930a, p. 4, fig. 3). Based on a P^4 dext., length 27, breadth 23 mm. The height is 77 mm, the tooth thus being slightly younger than the corresponding tooth in our series. The tooth is proportionally longer, but is at once distinguished from our form in the anterior development of the protocone, and the deeper posterior groove.

2. *"Kraterohippus" elongatus* Van Hoepen (1930a, p. 8, fig. 9). Founded on an incomplete upper tooth, 30 mm long and 24 mm broad, determined by Van Hoepen as a left P^2, but which must be of the right side. The outer surface, and the antero-internal angle are damaged, and reconstructed in the figure. Dreyer (1931, p. 29) remarks that for the striking resemblance to the P^3 of *Equus quagga quagga, Kraterohippus elongatus* must be very near to, or rather identical with, *E. quagga quagga*. The reconstruction of the metastyle, which is indicated as a rounded prominence in Van Hoepen's figure, is certainly incorrect. The parastyle is remarkably small, which would point to the tooth being a P^2, but the tooth is not elongated in front of this style. As even its serial position is uncertain, I prefer to leave the question of its specific identity with *E. quagga* open for the present.

3. *Equus lylei* Dreyer (1931, p. 30, pl. VI figs. 6, 7, pl. VII fig. 8), based on upper P (not figured) and M, and a lower series P_4-M_3. The upper molars differ from our subfossil specimens in the same points as those of *E. quagga* do, viz., the more concave halves of the ectoloph, the anterior

TABLE I

Measurements of upper teeth of *Equus quagga* Gmelin and *E. zebra* L. (mm)

	Equus quagga Gmelin										*E. zebra* L.	
No. of specimen	10	1	4	9	8	5	3	6	2	7	subfossil	A.M.
Age (in years)	4-5	6	7	10	10+	10(?)	12(?)	12+	16+	20	O.F.S	9
P^2 antero-posterior	35	33	35	34	38	32½	32½	37	—	33½	31	31
transverse	24	23	24	22	23	25	21	22	24	24	23	24
ant. post. protocone	7	7½	ca. 8	6½	8	6½	7	8	8	8	6½	7
P^3 antero-posterior	25½	26	26	24	26	23	22	26	—	27	24	24
transverse	25	24½	27	22½	26½	28	24½	25½	—	29	24½	25
ant. post. protocone	9	8	10	9	12½	10½	8	8½	8½	14	7½	8½
P^4 antero-posterior	25½	25	25	23	24	23	23½	25	23½	25	23	23½
transverse	25	25	26½	23	27	27	24	26½	29	29	24	25
ant. post. protocone	10	9½	10	10	12½	12	9	11	9	14	9	9
M^1 antero-posterior	23	23½	21	21	22	20	19	21	20½	20½	22	23
transverse	23	23	24½	22	24	25	23	24	25	26½	23	24½
ant. post. protocone	10	10	11	9	11	11	8½	11	9	11½	9½	9½
M^2 antero-posterior	23½	22½	21½	20½	23	21	19	22½	22	22	22	22½
transverse	22	22	24	22	23½	24	22½	24	24	25½	22½	23
ant. post. protocone	12	9½	11	10½	12	12½	9	12	10	14½	10½	10½
M^3 antero-posterior	21	—	22½	23	24	22½	24	28	26	23½	22	23
transverse	17	19½	21½	19½	22	22	20½	20	24	22	19½	21
ant. post. protocone	13	—	11	12	14	13	13	14	14	15	11	10

development of the protocone, the deeper posterior indent, and the more complicated enamel pattern of the fossettes.

4. *"Kolpohippus" plicatus* Van Hoepen (1930a, p. 9, fig. 10). Based on a right P_2-M_1, distinctly larger than in *E. quagga*, and consequently than in our form, as shown by the following measurements (table II, inter parentheses the range of variation in ten specimens of *E. quagga*):

TABLE II

P_2	antero-posterior	38	(25-31)
	transverse	18	(12-13½)
P_3	antero-posterior	33	(22-27)
	transverse	20	(13-16)
P_4	antero-posterior	30	(23-27)
	transverse	16	(12-15½)
M_1	antero-posterior	27	(21-24)
	transverse	19	(11-14½)

From the measurements given by the different authors it is evident that the following species can be excluded from comparison because of their distinctly larger size: *Equus capensis* Broom (1909, p. 282; 1913, p. 437; *E. westphali* Dreyer (1931, p. 36); *E. simplex* Van Hoepen (1930a, p. 5)), *Equus harrisi* Broom (1928, p. 441; *Sterrohippus robustus* Van Hoepen (1930a, p. 6)), *Equus cawoodi* Broom (1928, p. 443; *E. helmei* Dreyer (1931, p. 30)), *Equus kuhni* Broom (1928, p. 444; *E. louwi* Van Hoepen (1930b, p. 19)), *Equus gigas* Van Hoepen (1930a, p. 2), and *Equus sandwithi* Haughton (1932, p. 419).

An interesting form, also larger than ours, is *Eurygnathohippus cornelianus* Van Hoepen (1930b, p. 23). It is founded on the symphysial portion of a lower jaw with four large procumbent incisors, almost in a straight line. It does not seem to be an anomalous condition; the small C are placed directly behind the outer incisors.

To the *Hipparion* group, typified by its isolated protocone, our subfossil teeth do not belong either. This group comprises *Stylohipparion steytleri* (Van Hoepen, 1930b, p. 21; 1932, p. 33), *Notohipparion namaquense* Haughton (1932, p. 421), and *Stylohipparion hipkini* Van Hoepen (1932, p. 31).

There remains only one species, viz., *Equus simplicissimus* Van Hoepen (1930a, p. 6, fig. 7). The type is a P^4 dext., length 25, breadth 24 mm. The height is 74 mm, consequently the tooth is in the same stage of wear as the corresponding in our series. In this species our form finds its closest fossil relative. The tooth figured by Van Hoepen agrees with our specimen in the simplicity of the enamel pattern, and in the small depth of the

posterior groove. The protocone has the same length as that in our P^4, and is only very slightly more elongated anteriorly. The outer end of the groove between protocone and hypocone is blunt and rounded, instead of sharply pointed as in our form. The concavity of the anterior half of the ectoloph is more marked in Van Hoepen's specimen, and the parastyle is broader. In his second paper Van Hoepen (1930b, p. 21, figs. 12-13) refers to *E. simplicissimus* a right M^2, which in my opinion is indistinguishable from *E. quagga*. It differs from the corresponding tooth in our series in the strong development of the anterior prolongation of the protocone, in the more concave anterior half of the ectoloph, and in the broader parastyle. The enamel foldings of the fossettes are as simple as those in our specimen, which is younger (height of our M^2 70 mm, against 59 for Van Hoepen's).

As early as 1907 Fraas (1907, p. 237, pl. VIII fig. 2) recorded *Equus* cf. *zebra* from Barkly West. The teeth, however, are much too large to belong to the recent species, they are supposed by Broom (1909, p. 282) to belong to his species *Equus capensis*. The teeth described and figured in the present paper thus give the first evidence of the existence of *Equus zebra* L. in prehistoric South Africa.

LITERATURE

BROOM, R., 1909. On Evidence of a Large Horse recently extinct in South Africa. Ann. South Afr. Mus., vol. 7, pp. 281-282.

——, 1913. Note on Equus capensis Broom. Bull. Am. Mus. Nat. Hist., vol. 32, pp. 437-439, 1 fig.

——, 1928. On some New Mammals from the Diamond Gravels of the Kimberley District. Ann. South Afr. Mus., vol. 22, pp. 439-444, 3 figs.

COLYER, F., 1936. Variations and diseases of the teeth of animals. London, VIII + 750 pp., 1007 figs.

DREYER, T. F., 1931. Equidae, in: T. F. Dreyer and A. Lyle, New fossil Mammals and Man from South Africa. Bloemfontein, pp. 21-37, pls. V-VII (explanation on p. 59), 2 figs.

FRAAS, E., 1907. Pleistocäne Fauna aus den Diamantseifen von Südafrika. Zeitschr. deut. geol. Ges., vol. 59, pp. 232-243, pl. VIII, 2 figs.

HAUGHTON, S. H., 1932. The Fossil Equidae of South Africa. Ann. South Afr. Mus., vol. 28, pp. 407-427, 6 figs.

HOEPEN, E. C. N. VAN, 1930a. Vrijstaatse fossiele perde. Paleontologiese Navorsing v. d. Nasionale Mus. Bloemfontein, vol. 2, part 1, pp. 1-11, 10 figs.

——, 1930b. Fossiele perde van Cornelia, O.V.S. Id., vol. 2, part 2, pp. 13-24, 22 figs.

——, 1932. Die stamlijn van die sebras. Id., vol. 2, part 3, pp. 25-37, 23 figs.

MOTOHASHI, H., 1930. Craniometrical studies on skulls of wild asses from West Mongolia. Mem. Tottori Agr. Coll., vol. 1, no. 1, pp. 1-62, 5 pls., 6 figs., 16 tables.

OSBORN, H. F., 1918. Equidae of the Oligocene, Miocene, and Pliocene of North America. Iconographic Type Revision. Mem. Am. Mus. Nat. Hist., n. s., vol. 2, pp. 1-330 including 54 pls., 173 figs.

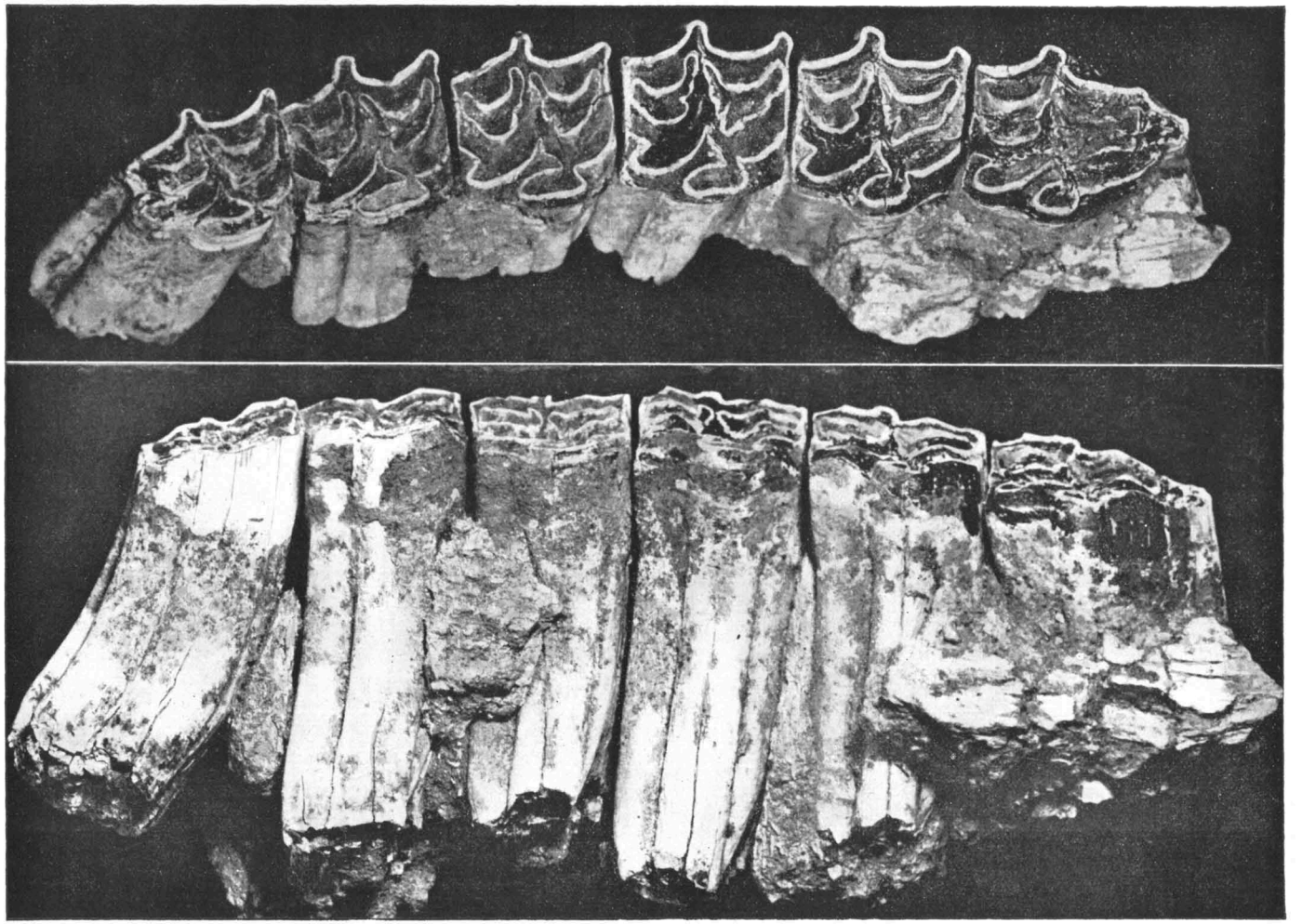
EXPLANATION OF THE PLATES

Pl. VI. *Equus zebra* L. Subfossil right P^2-M^3 from Orange Free State. Upper figure, crown view; lower figure, inner view.

Pl. VII. *Equus zebra* L. Amsterdam Museum. Upper dentition, crown view.

Pl. VIII. *Equus quagga burchellii* Gray. Amsterdam Museum, no. 529. Upper dentition, crown view.

All figures natural size.



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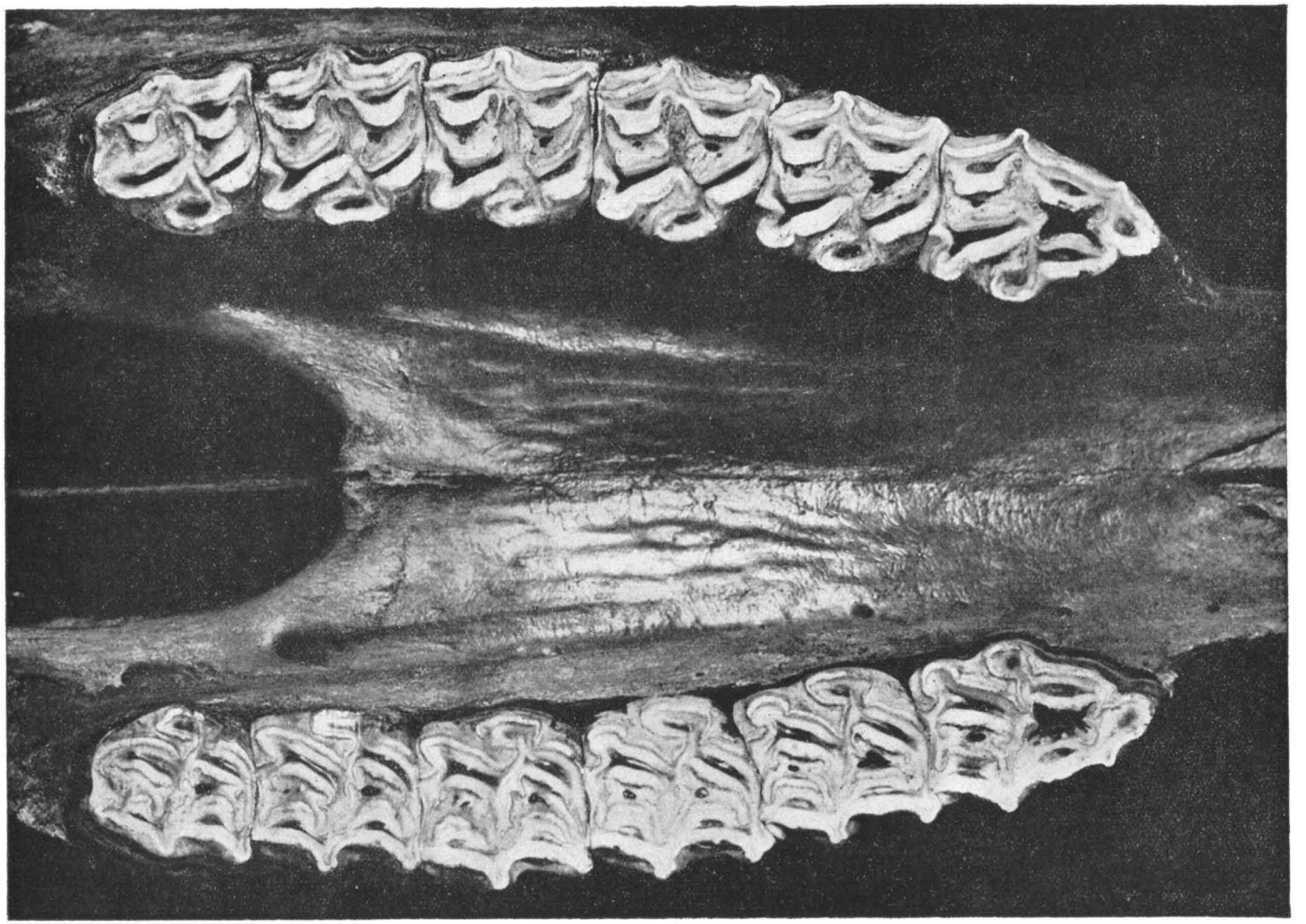

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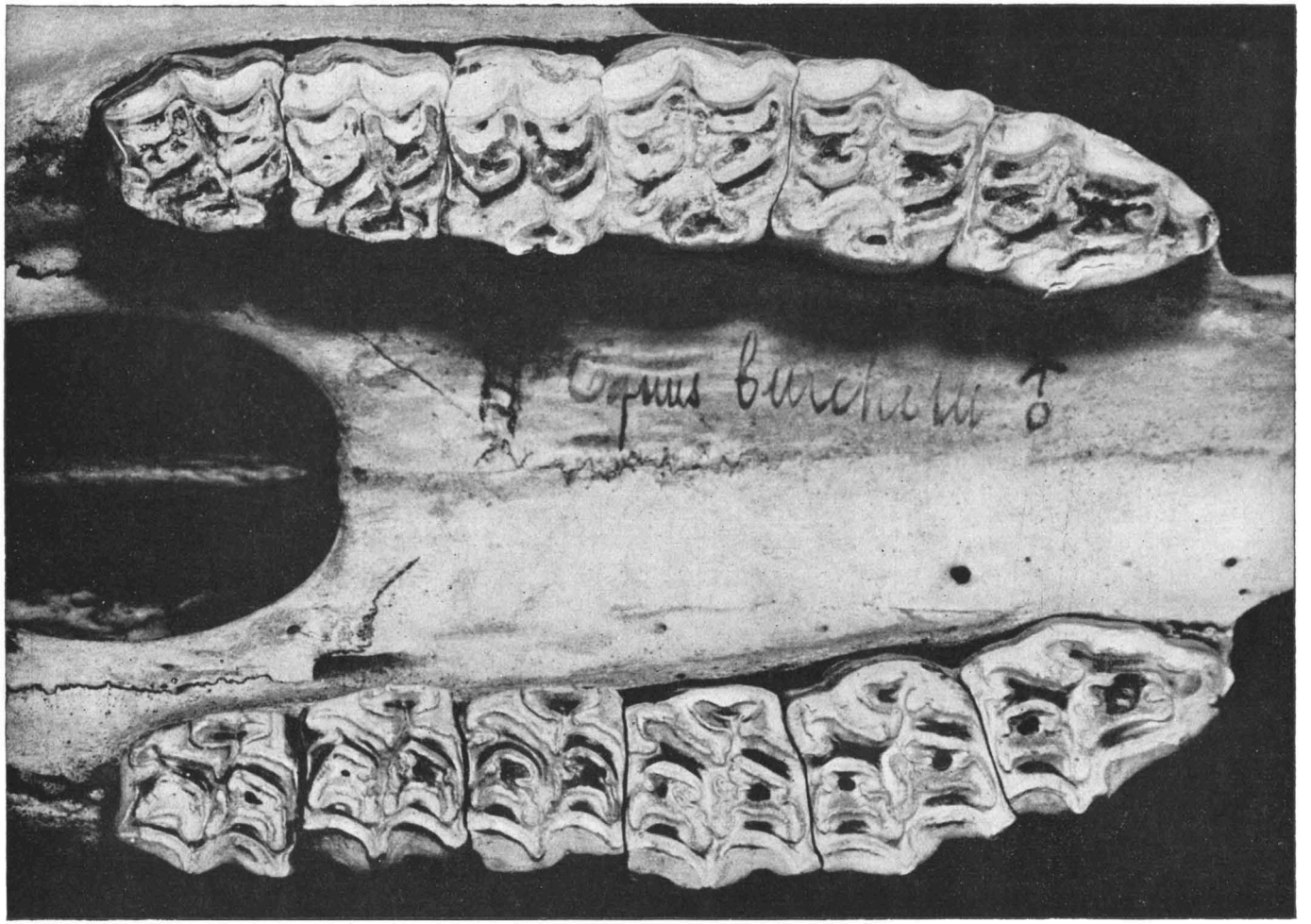

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