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American Museum of Natural History.

New Series, Vol. I, Part III.

III.—CRANIOMETRY OF THE EQUIDÆ.

By HENRY FAIRFIELD OSBORN.

June, 1912.

(*Continued from 3rd page of Cover.*)

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New Series, Volume I, Part III.

CRANIOMETRY OF THE EQUIDÆ.

MEMOIRS

OF THE

AMERICAN MUSEUM OF NATURAL HISTORY.

PART III.—CRANIOMETRY OF THE EQUIDÆ.

BY HENRY FAIRFIELD OSBORN.

CONTENTS.

INTRODUCTION.

A promising as well as most difficult problem in modern mammalogy is the phylogeny of the Equidæ. Skull measurements and proportions represent one of many systems of cross-tests of affiliation and phyletic relationship which may be applied.

In 1902 the author pointed out the manifold effects of dolichocephaly and brachycephaly in the mammals.[1] Among the horses, as among the Oligocene titanotheres (see Figs. 1, 2), progressive brachycephaly or dolichocephaly sharply distinguishes certain phyla. Ewart

[1] 'Dolichocephaly and Brachycephaly in the Lower Mammals.' Bull. Amer. Mus. Nat. Hist., Vol. XVI, Art. VII, Feb. 3, 1902, pp. 77–89.

especially has pointed out the importance of the bending down of the face upon the cranium in the horses, a transformation to which Osborn has applied the term *cytocephaly*.[1] It is also very important to distinguish (see Fig. 2) between proöpic dolichocephaly (Osborn), in which the face is elongated, and opisthopic dolichocephaly (Osborn), in which the cranium is elongated. A line drawn through the postorbital process divides the face from the cranium.

The chief changes of skull proportion in Ungulates thus come under the following heads:

Brachycephaly, general broadening of the skull as whole.

Dolichocephaly, general lengthening of the skull as a whole.

Proöpic dolichocephaly, elongation of the facial region.

Opisthopic dolichocephaly, elongation of the cranial region.

Cytocephaly, upward or downward flexure of the facial upon the basicranial axis.

The *index* is a far better method of expressing these transformations than any system of absolute measurements. Earlier students of the skull of the horse, like Franck (1875) relied principally on percentages. It is obvious that among domesticated as among wild horses variations in size due to age, sex, favorable or unfavorable environment, vitiate any system of absolute measurements.

Non-blending or pure inheritance indices in the Skull of the Horse, Ass, Mule.

1. Cephalic Index:	$\frac{\text{Width of skull} \times 100}{\text{Basilar length}}$	Ass	46.9–49.9
		Mule	40.8–43.6
		Horse	40.4–44.1
2. Diastema Index:	$\frac{\text{Diastema} \times 100}{\text{Basilar length of skull}}$	Ass	15.6–17.6
		Mule	18.6–21.9
		Horse	18.2–23.0
3. Cranio-facial Index:	$\frac{\text{Length of cranium} \times 100}{\text{Length of face}}$	Ass	56.3–61.0
		Mule	48.9–51.8
		Horse	5.3–49.9
4. Orbital Index:	$\frac{\text{Vertical diameter of orbit} \times 100}{\text{Horizontal diameter}}$	Ass	96.0–104.2
		Mule	78.7– 99.1
		Horse	84.2– 93.5
5. Molar Index:	$\frac{\text{Transverse diameter of } M^2 \times 100}{\text{Total length of entire molar series}}$	Ass	15.2–16.0
		Mule	14.2–14.9
		Horse	13.9–15.7
6. Occiput-vertex angle Index:	Angle between vertex of skull and line connecting most posterior points of occipital crest with condyles	Ass	52.5–60.0
	i. e., nearly all horse skulls will stand when set up on end, some mule skulls (one out of four), no ass skulls	Mule	61.0–66.5
		Horse	64.0–76.5
Vomer Index:	$\frac{\text{Distance from palate to posterior end of vomer} \times 100}{\text{Distance from vomer to foramen magnum}}$	Ass	93.8–111.7
		Mule	95.5–110.3
		Horse	72.8– 86.5

The indices, or proportions between various parts, are less influenced by environmental modification but are largely influenced by age; thus the facio-cranial index alters rapidly as the horse attains maturity.

[1] 'The Continuous Origin of Certain Unit Characters as Observed by a Palæontologist.' Amer. Naturalist, Vol. XLVI, April, May, 1912, pp. 185–206, 249–278.

It also appears that the angle between the face and the cranium alters greatly during growth. That the index deserves more general use among mammalogists as of strong specific value is shown in the above table of comparison of the principal indices in the skulls of the ass ♂, of the horse ♂, and of the mule, taken from a recent paper by Osborn.[1]

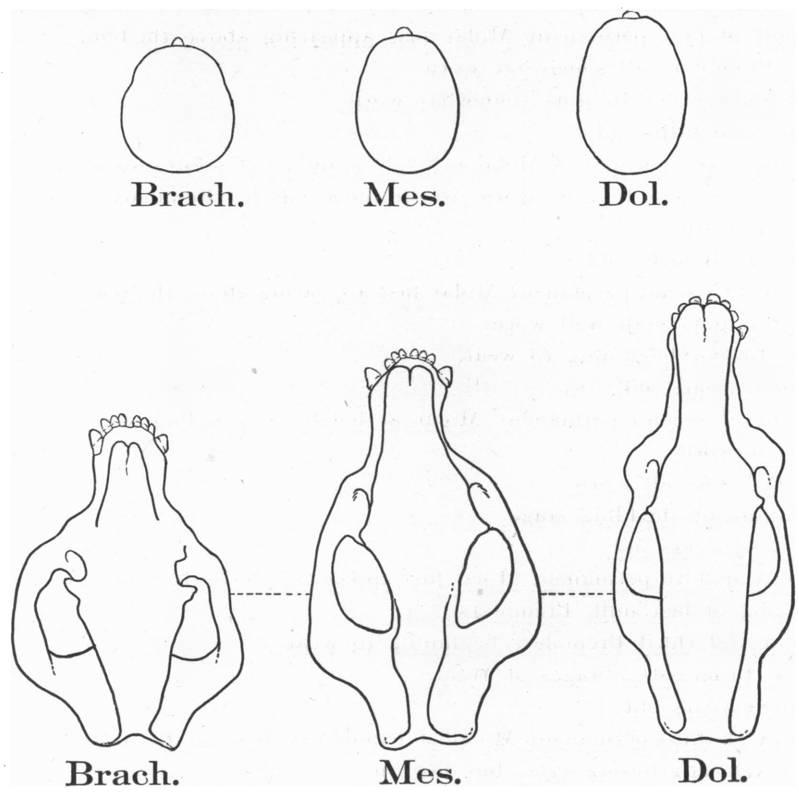

Fig. 1. Brachycephaly, mesaticephaly, dolichocephaly.
Upper: as observed in the human cranium.
Lower: as observed in the skull (*i. e.*, cranium and face) of the titanotheres.

The age of the animal measured is extremely important in its effect on all systems of measurement of both the skull and the teeth. The indices of brachycephaly and dolichocephaly, and the bending of the face on the cranium, or cytocephaly, as above noted all change with age. This last statement is demonstrated at the close of this paper. It is, therefore, extremely desirable to establish among the Equidæ a series of growth stages.

The accompanying table, prepared under the writer's direction by Messrs. S. H. Chubb and J. W. Gidley, from the very large series of preparations by Mr. Chubb in the American Museum, is an attempt to establish a series of eleven age stages, based upon the all-important succession and wear of the teeth.

[1] Amer. Naturalist, May, 1912, pp. 272, 273.

Age Stages of the Horse.

Milk Teeth and beginning of Permanent Teeth.

Stage I.— A few days old.
Milk series fully formed but unworn.

Stage II.— About 10 months old.
Summit of first permanent Molar just appearing above the bone.
Milk Premolars all somewhat worn.
First and second Incisors somewhat worn.

Stage III.— 12 or 13 months old.
Summit of first permanent Molar at height of milk series, but unworn.
First and second Incisors worn; third Incisor at height of others, but unworn.

Stage IV.— About 18 months old.
Summit of second permanent Molar just appearing above the bone.
Milk Premolars all well worn.
Third Incisor beginning to wear.

Stage V.— About 2 years old.
Summit of second permanent Molar at height of grinding series, but unworn.
Milk Incisors all worn.
Beginning of shedding stage.

Stage VI.— About $3\frac{1}{2}$ years old.
Summit of third permanent Molar just appearing above the bone.
Shedding of last milk Premolars.
Second and third Premolars beginning to wear.

Permanent Teeth only, in Progressive Stages of Wear.

Stage VII.— About 4 years old.
Summit of third permanent Molar and fourth permanent Premolar at height of grinding series, but unworn.
First permanent Incisor worn.

[Stages I–VII:] YOUNG OR IMMATURE HORSE WITH MILK AND PERMANENT TEETH (Adolescent stages)

Stage VIII.— About 5 years old.
Permanent teeth all in use.
Fourth Premolar and third Molar but little worn.
First and second Incisors worn; third beginning to wear.

Stage IX.— Between 15 and 20 years old.
All the teeth well worn.
Upper Incisors have the external dental cavities ('cups') greatly reduced.
Lower Incisors, external dental cavities (cups) have disappeared.

[Stages VIII–IX:] ADULT OR MATURE HORSE WITH EFFECTIVE PERMANENT TEETH (Mature stages)

Stage X.— Between 25 and 30 years.
Second Premolar worn to near fangs.
Tooth pattern of grinding teeth more or less obliterated.
Incisors worn down short, their angle of meeting acute, and external dental cavities ('cups') entirely worn away.

Stage XI.— Between 30 and 40 years.
Premolars and first Molar worn to near fangs.
Tooth pattern of grinding teeth more obliterated.
Incisors worn down very short and their angle of meeting very acute.

[Stages X–XI:] OLD HORSE WITH TEETH BECOMING LESS EFFECTIVE (Senescent stages)

I. CRANIOMETRIC SYSTEMS, 1875–1912.

The present preliminary review of previous cranio-metric systems of the Equidæ is chiefly based upon the notes of the writer's research assistant, Mrs. Johanna K. Mosenthal. It is historical, critical, and constructive. The diagrams are the work of Mr. Erwin S. Christman.

The systems reviewed are the following:

Franck,	1875	Salensky,	1902
Branco,	1883	Ewart,	1907
Nehring,	1884	Bradley,	1907
Tscherski,	1892	Osborn,	1912

The system of measurements introduced by each of these authors is clearly set forth by means of a uniform set of diagrams and explanatory keys prepared under the writer's direction by Mr. Erwin S. Christman. In each table the common usage of a certain measurement by other authors is indicated by round brackets ( ). There is also inserted, in square brackets [ ], the usage and terminology proposed by Osborn in the present paper.

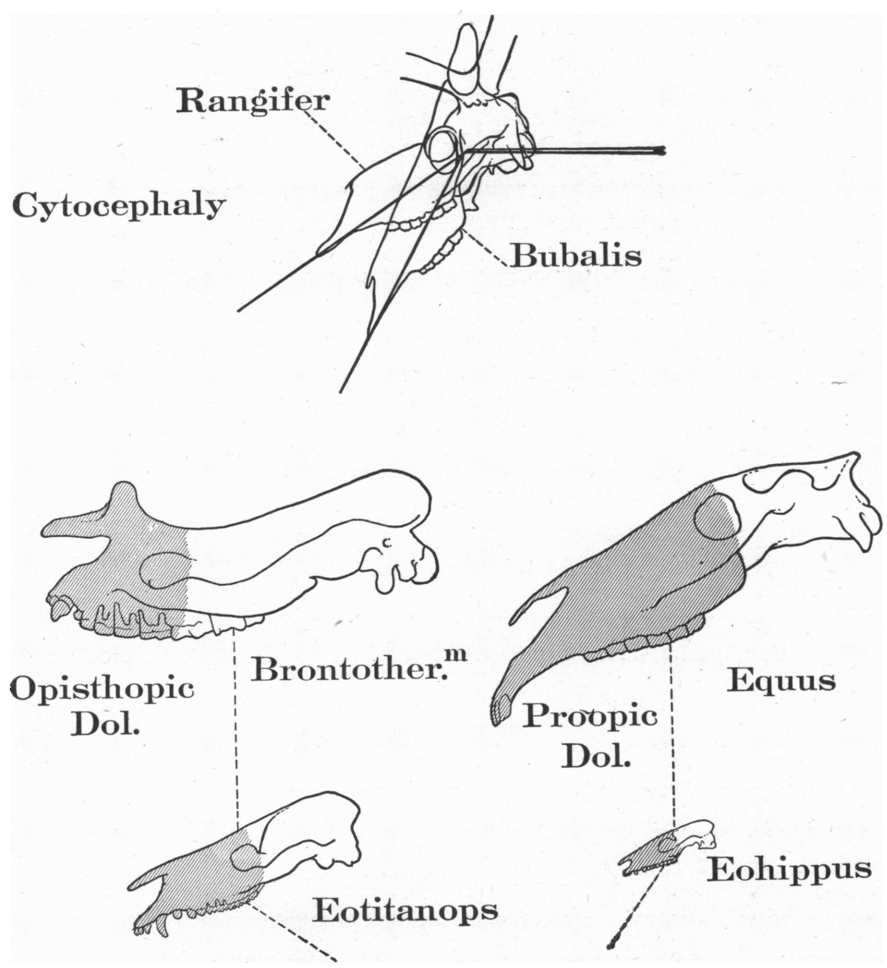

Fig. 2. Dolichocephaly and Cytocephaly in the Ungulates.
Upper: *Rangifer*, with slight facio-cranial deflection.
Bubalis, with strong facio-cranial deflection.
Middle: Opisthopic dolichocephaly in *Brontotherium;* proöpic dolichocephaly in *Equus;*
Lower: Mesaticephalic ancestors of *Brontotherium* (*Eotitanops*) and of *Equus* (*Eohippus*).

The Osborn terminology thus indicated [ ] includes: (1) the adoption from other authors of what appear to be the most natural and really significant measurements, (2) the adoption of the terminology which has been most generally used rather than the introduction of a new terminology, (3) some new measurements of the skull and teeth which appear to be especially applicable to extinct as well as to recent horses.

It is noteworthy that all previous craniometric systems have been based on recent horses; it is also noteworthy (p. 96) that some of the measurements and indices which are applicable to recent horses are not generally applicable to extinct horses, owing to accidents of preservation.

Sources of Craniometric Error. There are two grand sources of error in measurements of the cranium and teeth in existing domestic horses: first, polyphyly, or the mixture of ancestral stocks, or breeds; second, cœnogenesis, or progressive changes due to age.

The 'breed mixture' is a factor almost impossible to avoid because, as shown especially by the researches of Ewart, most of our common horses of the present day contain the blood of four or five wild and remotely ancestral stocks. To this so-called blood mixture, representing actually the persistence of certain distinctive 'unit characters,' are probably due many of the so-called *variations* in the skulls of horses. The only standard existing horse is the Przewalsky.

Franck's System, 1875.[1]

(Text Fig. 3, page 70.)

Materials. The materials used in the pioneer treatise of Franck were clearly insufficient, and although most of his "points of distinction between different existing and prehistoric breeds of horses" are borne out by his measurements, the differences are too slight to carry much weight because they are based on so small a number of individuals, namely:

5 Noric horses (2 not typical, according to Tscherski).
4 Arab horses (2 not typical, according to Tscherski).
3 Feldmochinger (1 not typical, according to Tscherski).
2 Neolithic horses (from Pile-dwellings).
2 Greek ponies.

All of the twenty-five measurements of Franck are computed in terms of percentage to the basilar length (see B, Fig. 3, iii).

No measurement is given to determine the relative facial and cranial length or facio-cranial index, although one of the main differences between various races of horses lies in the proöpic dolichocephaly.

Of the eight or nine points of comparison between the skull of the horse and of the ass given by Franck, Tscherski, and Salensky, we find only those afforded by Franck's 'vomer index' valuable. However, most of the important measurements taken by later authors are to be found in Franck excepting the facio-cranial above noted.

Franck's Noric Horse is equivalent to the 'Nordic' horse of other authors, the 'Forest Horse' of Ewart, the occidental, or western, horse, as distinguished from the oriental, or eastern, horse.

[1] 'Ein Beitrage zur Rassenkunde unserer Pferde,' Landwirthschaftliche Jahrbücher, 1875, Vol. IV.

Franck's Craniometry of Oriental and Occidental Horses.[1]

Note:—Measurements in percents, computed with basilar length taken as 100.

Measurements	Noric	Arab
1. Length from foramen magnum to point between I, I	100 (57.4)	100 (50.8)
2. From foramen magnum to posterior end of palatal suture	46.6	47.2
3. From foramen magnum to beginning of vomer	25.2	27.6
4. From posterior end of palatal suture to point between I, I	53.5	53.1
5. From posterior end of palatal suture to beginning of vomer	22.0	20.5
6. Width between maxillary crests at their origin	32.3	30.9
7. Width between canines	11.0	9.6
8. Greatest width of skull	39.3	40.1
9. Greatest width between orbital processes	40.8	41.7
10. Greatest distance between pterygoid processes of palatal bones	14.0	13.8
11. Length of molar row of upper jaw, not including P^1	33.5	33.8
12. Greatest distance between M^3, M^3	23.1	23.2
13. Distance between P^2, P^2, anterior end	14.4	13.5
14. Straight line from middle of transverse process of occipital bone to point between I, I	108.8	108.5
15. From middle of transverse process of occipital bone to tip of nasal bones (with tape measure)	98.8	97.3
16. From middle of transverse process of occipital bone to tip of nasal bones (straight line)	97.0	95.8
17. From middle of occipital bone to point between orbits	35.7	36.5
18. From middle of occipital crest to end of nasal process of frontal bone	49.3	51.9
19. Median length of nasal bones	50.7	46.5
20. Straight line between tip of nasal bones and I, I	22.6	22.2
21. Greatest breadth of cerebral portion of skull, above zygomatic processes of temporal bones	19.2	21.5
22. Smallest breadth of skull capsule on small pterygoid foramina	10.7	11.2
23. Greatest width on parietal bump	16.6	18.2
24. Width between supraorbital foramina	29.4	30.1
25. Width between infraorbital foramina	18.1	16.3

Noric is average of 5 individuals.
Arab is average of 4 individuals.

[1] Taken from Franck's table in 'Ein Beitrag zur Rassenkunde unserer Pferde,' Landwirthschaftliche Jahrbücher, Vol. IV, 1875.

Franck's conclusions. All modern horses are derived from two original races, 'oriental' and 'occidental,' which are respectively exemplified by the following types:

Oriental.	*Occidental.*
Type: Arab.	Type: Noric.
" Persian.	" Pinzgauer.
" Greek.	" Flanders.
" Russian.	" Old Norman.
" Hungarian.	" Palfrey of knights.
" Feldmochinger.	" Ardennes.
" Neolithic horse (one).	" Luxemburg.
" Ponies of Greece, China, Persia, etc.	

The testimony of philology goes to show that the Aryans possessed horses while they were still in Asia and that the horse migrated into Europe with them. The Arab horse is a branch of the 'oriental stock' that has been improved by breeding and that has spread over all countries. The occidental, or western, or 'Noric' horse may be identical with or descended from the *E. robustus* Pomel of the Swiss Dwellings. The earliest mention of this animal is in the account by Rogers of the horses of Dacia and Panonia.

The chief distinctions between these two great races are the following:

Oriental.	*Occidental.*
Brachycephalic.	Dolichocephalic.
Profile straight or concave.	Facial proportion developed at the expense of cranial.
Of small size and swift motion.	Profile rounded or sheep-like.
More closely related to the ass.	Size large, movements heavy and slow.

Branco's System, 1883.[1]

(Text Fig. 4, page 72.)

Materials. Branco's object is to show the relation of *Equus andium* of the Upper Pliocene or Lower Pleistocene of South America to other Equidæ. The materials on which he based his thirty-two measurements of modern horses are insufficient. They consist of the following:

1 zebra.
4 asses (2 very aged).
3 Arab horses, the same individuals used by Franck
Greek ponies, individuals used by Franck.
Shetland ponies.
4 Pinzgaur horses.
5 fœtal and young stages, ranging from 1 month to 2½ years.

Methods. Of Branco's thirty-two measurements twenty are represented in the accompanying table. It will be observed that he does not introduce the facio-cranial index. While his measurements and indices are important in proving his points, they are of little general value as data by which we may distinguish the various breeds of horses, or distinguish the horses, asses, and zebras. Many of the measurements are so difficult to take with precision that there is great room for error, which is increased by the fact that the measurements are mostly in small numerals. Measurement No. 5, *i. e.*, the length of the maxillary behind m^3, has little value because age probably has as much to do with this measurement as species or breed.

[1] 'Uber eine Fossile Säugethier Fauna von Punin bei Riobamba in Ecuador,' Paläont. Abhandl. Dames u. Kayser, Vol. I, No. 22, 4to., Berlin, 1883.

From the fœtal and young stages studied Branco constructs some interesting tables showing progressive changes, but since the breeds of the five individuals selected are not indicated, we cannot be certain that the differences are not due to breed as well as to age, since breed-variation in horses is so great.

In short, Branco's system stands apart from all the rest; he takes a different series of measurements, and there are no references to his memoir in the other later authors.

His conclusions as to the affinities of *E. andium* are: (1) that it is nearer to *E. caballus* than *E. asinus* or *E. burchelli;* (2) that the trend of development in all South American Equidæ is more or less away from that of *E. caballus* and the Diluvial forms of the Old World.

Nehring's System of 1884.[1]

(Text Fig. 5, page 74.)

Materials. Pleistocene horses of northern Europe.

Methods. Nehring's system of measurement is one of the foundations of modern craniometry; his measurements are less numerous, more simple, and more to the point than those of his predecessors; they bring out the essential and racial rather than the detailed characters. They especially form a basis for the systems of Tscherski and Salensky.

Nehring's system of indices is, however, faulty and misleading because he departs from the method used by anthropologists. Instead of dividing the lesser measurement by the greater, as in computing the cephalic index of the human skull wherein anthropologists divide the greatest width by the greatest length, Nehring reverses this system and divides the greatest length by the greatest width. For example,

$$\text{Nehring's Index I} = \frac{\text{basilar length} \times 100}{\text{frontal width}}$$

$$\text{Index II} = \frac{\text{length of vertex} \times 100}{\text{frontal width}}$$

$$\text{Index III} = \frac{\text{anterior segment of ocular line} \times 100}{\text{posterior segment of ocular line}}$$

The obvious disadvantage of Nehring's system of indices is that the broad-skulled forms (brachycephaly) give the lowest figures while the narrow-skulled forms (dolichocephaly) give the highest figures, these indices being just the reverse of those obtained in the human skull. Unfortunately Nehring's Index I, or Frontal Index, is used by Tscherski and Salensky.

Similarly the 'Preorbital' and 'Postorbital' indices and Index III, the 'Ocular Index,' are not satisfactory as representing the proportions of the face and of the cranium or of the eye, since no allowance is made for the width of the skull. These indices have been criticised by both Tscherski and Salensky although, owing doubtless to the weight of Nehring's authority, they are adopted by both these authors.

Tscherski's System, 1892.[2]

(Text Fig. 6, page 76.)

The object of this very exhaustive monograph is to show the relation of the Post-Pliocene horses of northern Asia to other fossil and recent Equidæ and determine ultimately the origin of the modern horses.

[1] 'Fossile Pferde aus deutschen Diluvial-Ablagerungen und ihre Beziehungen zu den lebenden Pferden. Ein Beitrag zur Geschichte des Hauspferdes,' Sonderabdr., Landwirthschaftl. Jahrbucher, 1884.

[2] 'Beschreibung der Sammlung posttertiärer Säugethiere,' Mém. Acad. Imp. d. Sci. St. Petersbourg, Sér. 7, Vol. XL, No. 1, 1892, pp. 1–511.

Materials. Measurements were taken of a very extensive series of Post-Pliocene horses. The measurements of the skull of *E. przewalskii* are based on a single young individual, yet they correspond quite closely to those given in Salensky's subsequent memoir and point to the same conclusions. Only two zebras and one Arab horse are measured, but the data on his own materials are supplemented from the work of other authors.

Post-Pliocene Eurasian horses, numerous specimens.
E. przewalskii, 1 skull, young.
E. ?burchelli, 2 skulls.
Arab horse, 1 skull.

Methods. Tscherski's system as a whole is based on those of Franck and Nehring, from whom he adopted many features. The measurements are most exhaustive and the tables on account of the very multiplicity of measurements and confused arrangement, do not bring out very clearly the essential distinctions between the races. The age of the horses measured is not indicated.

Nor can we adopt the facio-cranial index of Tscherski because he measures the face from the anterior border (9) of the orbit instead of measuring it from the posterior border, thus:

$$\text{Tscherski's facial index: } \frac{\text{Length of face to anterior border of orbit} \times 100}{\text{Basilar Length of Skull}}$$

(See Addendum, facing this page.)

Salensky's System of 1902.[1]

(Text Fig. 7, page 78.)

Salensky's fine memoir was called forth by the necessity of determining the phyletic relationships of the wild Asiatic horse *E. przewalskii.*

Materials. The materials are more extensive and important than those used by any previous author, including sixty-four skulls, representing the following species:

9 *E. przewalskii* (4 young, 5 adult)
15 Pleistocene horses from Russia and Siberia
6 Domesticated asses, *E. asinus*
11 Kiang's, *Equus kiang*
18 Onagers, *Equus onager*
1 Mountain zebra, *Equus zebra*
1 Grevy's zebra, *Equus grevyi*
1 Burchell's zebra, *Equus burchelli*
1 Chapman's zebra, *E. chapmani*
1 mule

Methods. Of the thirty-five measurements of Salensky twenty-four are important as represented in Fig. 7. Salensky's measurement system is chiefly based on that of Nehring. Salensky, however, gives absolute measurements only, which renders it difficult to draw inferences from his large tables. The following criticisms of his measurements may be made.

The length of face (30) to the inter-nasal suture is inadequate because the face should be measured back to the frontal lines (*F F*).

The author follows Nehring in adopting his Indices I, II, III, in which the greater measurement is divided by the lesser instead of the lesser by the greater. The five measurements given

[1] Salensky, W. 'Equus przewalskii Poljak.' Wissensch. Resultate, N. M. Przewalski nach Centrale-Asien Unternommenen Reisen auf Kosten einer von Seiner Kaiserlichen Hoheit dem Grossfürsten Thronfolger Nikolai Alexandrowitsch. Published by Kaiserlichen Akad. d. Wissenshaften. Zool. Theil. Bd. 1, Mammalia, Abth. 2 Ungulata, Lieferung 1. 76 pp. 4 pll. St. Petersburg, 1902.

'Prjevalsky's Horse,' Translation by Capt. M. Horace Hayes and O. Charnock Bradley, with an introduction by J. Cossar Ewart, 8vo., London, 1907.

ADDENDUM.

(*To follow line 16, p. 66.*)

The use of the basilar length of skull as a divisor is an advance upon Nehring, because the long-faced forms were given the highest figures and the short-faced forms the lowest figures, Thus the mode of reckoning may be adopted but not the mode of measurement of the face because the face should certainly include the orbit.

Tscherski's conclusions. Tscherski classifies the Equidæ into three great groups.

Eastern, or Oriental.	Western.
1. Broad-forehead type, *i. e.*, brachycephaly, typified by the Arab.	3. Narrow-forehead type, typified by the Forest Horse.
2. Medium-forehead type.	

The Post-Pliocene horses of Siberia belong to several races. They vary in size almost as much as the present races of domesticated horses in Europe. All have skulls of the median-forehead type, with a dentition, however, which resembles that of the long-headed occidental, or Noric Horses. Most of them have hoofs of medium or great breadth. The materials do not justify the assumption that among the Siberian fossil horses can be found forms which are identical with the Post-Pliocene horses of Europe. Thus the facts do not contradict the view of Madame Pavlow that these Siberian horses of medium-forehead type are of Eastern stock, arising from such Tertiary Indian horses as *E. namadicus* and *E. sivalensis*.

to determine the shape of the nasal bones do not bring out the essential differences between the horse and the ass very clearly.

Salensky's conclusions. There is no attempt to distinguish between the various original breeds of horses. Many important points of difference between the horses and the Asiatic and African asses are brought out incidentally. *E. przewalskii* is found to belong to a special and separate type which, however, is more closely allied to the domestic horse than to the ass.

Ewart's System, 1907.[1]

(Text Fig. 8, page 80.)

Ewart's system was called forth by the necessity of analyzing the skulls found in a Roman fort at Newstead. His epoch-making successive contributions in this and other papers to the study of recent and prehistoric horses have pointed the way to the clear distinction of the original stocks of horses. His system of measurements is clearly brought out in the important paper of 1907 above cited.

Materials. The twelve Newstead skulls are measured, although the conclusions reached in the system of the author are based upon examination of many other types.

Methods. The eight measurements given in the table bring out the chief differences in the general proportions of the Newstead skulls under observation in a most telling manner. They serve this purpose, but a more extensive system of measurements is needed to bring out the essential points of difference, for example, between the horses, asses, and zebras.

The frontal width measurement is that adopted by all previous authors and by Osborn. The cranium length (F'S) is also that adopted by Osborn. Ewart's frontal index (*i. e.*, $\frac{\text{frontal width} \times 100}{\text{facial length}}$ does not give as true a conception of the relations of the width and length of the skull as the 'cephalic index' of Osborn and other authors (*i. e.*, $\frac{\text{frontal width} \times 100}{\text{basilar length}}$).

Ewart has not put into his table any exact measurements of the facio-cranial angle, which constitutes one great point of difference between the three original stocks of horses which he distinguishes.

Con clusions. The Newstead skulls include "beside cross-bred animals" three very distinct types of horses which may be referred to three original stocks from which the modern domesticated horses sprang, namely, the Forest, the Steppe, and the Plateau. All three of these original stocks may well have existed in a pure and wild state at the end of the first century A. D. The descendants of these three stocks are now distributed as follows:

Forest variety. (Broad-headed.)	*Steppe variety.* (Long-headed.)	*Plateau variety.* (Medium-to narrow-headed.)
Northwest of Europe.	Spain.	Britain (native horses).
Norway.	Ireland.	Shetland and Faroe Isles.
Scotch highlands and islands.	Mexico.	Southern Mexico.
Iceland.	South America.	Jamaica.
Asia.	Austria.	Java.
Korea, etc.	(= Ridgeway's large-headed *E. caballus.*)	

The Arab belongs to the narrow-headed or Plateau Variety, the existing Arabs being mingled with Steppe and Forest blood. It is not necessary at this point to give Ewart's more recent phyletic conclusions since the object of the present communication is chiefly craniometric.

[1] 'On Skulls of Horses from the Roman Fort at Newstead, near Melrose, with Observations on the Origin of Domestic Horses.' Trans. Roy. Soc. Edinburgh, Vol. XLV, pt. 3, No. 20, 1907, pp. 555–587.

Contribution of Bradley, 1907.[1]

(Text Fig. 9, page 82.)

Bradley's contribution was based upon a comparison of the Przewalsky with the Forest type of Ewart as well as with the Celtic and Iceland ponies. In several respects it marks a departure from all previous systems of measurement, and this is regrettable because it prevents comparison with all other tables although serving the author's immediate purpose of bringing out several of the important differences between the types examined. The chief points brought out by Bradley's observations and measurements may be summarized as follows:

The actual width of the cranium of *E. przewalskii* is less than an examination of this animal during life would lead us to suppose. It has a long, narrow face in contrast with the short, broad face of the Iceland pony and the intermediate face of the Celtic pony. Thus the face of *E. przewalskii* forms a considerable portion of the total length of the skull. The orbit of *E. przewalskii* has an elongate form and is placed relatively far back in the head. The premaxillary width in *E. przwalskii* is relatively less than in either the Celtic or the Iceland ponies.

System of Cranial Measurement, Osborn, 1912.

(Text Fig. 10, page 84; Text Fig. 11, p. 86.)

The system here proposed is synthetic; (1) it retains so far as possible the measurement standards of Franck, Branco, Nehring, Tscherski, Salensky, Ewart, Bradley, in order that students may avail themselves of the absolute measurements given in the craniometric tables of these authors; (2) it contains nine measurements which are of especial value in distinguishing horses, asses, and zebras; (3) it contains measurements which will be of value in the comparison of fossil and recent animals and will be expressive even where proportions of the skull only are preserved.

The *absolute measurements* from which the indices are calculated are the following, made in each instance by calipers or orthogonal projection:

1. Vertex length	7. Cranial length
2. Basilar length	11. Occiput height
3. Frontal width	15. Diastema length
5. Facial length	16. Muzzle width

17. Dental length.

The *indices* are obtained by the combination of the above actual measurements as follows:

4. Cephalic index, ratio of width to length.
6. Facio-cephalic index, ratio of face to total length.
8. Cranio-cephalic index, ratio of length of cranium to basilar length.
12. Orbital index, ratio of the length to the height of the orbit.
13. Vomerine index, expressing posterior extension of vomer.
18. Dental index, ratio of superior grinding series to total length of skull.
19. Molar index, ratio of breadth of a single grinder to length of entire molar-premolar series.

In each instance the index is obtained by dividing the lesser diameter by the greater.

[1] 'Craniometrical Observations on the Skull of Equus prjevalskii and other Horses.' Proc. Roy. Soc. Edinburgh, Vol. XXVII, Pt. I (No. 8), 1907, pp. 46–50.

The *angles* believed to be most significant are the following:

9. Palatal angle, elevation of posterior border of palate.
10. Palato-cranial angle, approximately representing deflection of face on cranium.
11. Occiput-vertex angle, expressing the backward prolongation of the occiput above the condyles.
21. Facio-cranial angle, expressing more accurately than the palato-cranial the deflection of the face on the cranium.

The manner of taking these measurements, indices, and angles is very clearly shown in the accompanying key (p. 85) and in Figs. 10, 11.

(*Text continued on page 88.*)

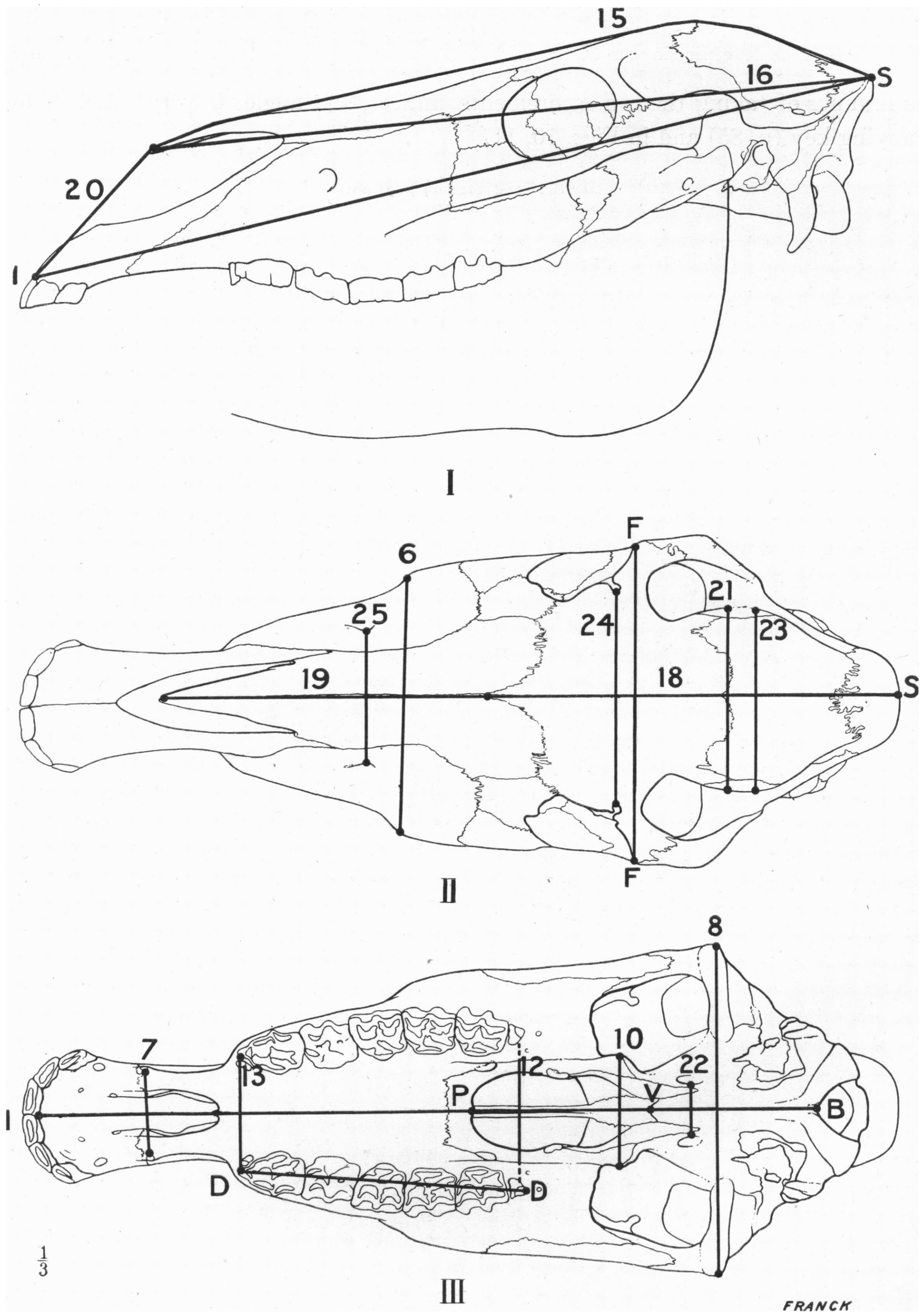

Fig. 3. Franck's system, 1875.

KEY TO FRANCK'S SYSTEM OF 1875.

1. *Length from foramen magnum to point between* I^1, [= BASILAR LENGTH, O.] (as measure also by Branco, Nehring, Tscherski, Salensky, Osborn). Fig. 3, III, B–I.
2. *From foramen magnum to posterior end of palatal suture* (as measured also by Tscherski). Fig. 3, III, B–P.
3. *From foramen magnum to beginning of vomer* (as measured also by Branco, Nehring, Tscherski, Salensky, Osborn). Fig. 3, III, B–V.
4. *From posterior end of palatal suture to point between* I^1, [= PALATAL LENGTH, O.] (as measured also by Tscherski, Bradley, and Osborn,— fossil Equidæ). Fig. 3, III, P–I.
5. *From posterior end of palatal suture to beginning of vomer* (as measured also by Branco, Nehring, Tscherski, Salensky, Osborn). Fig. 3, III, P–V.
6. *Width between maxillary crests at their origin* [= FACIAL-MAXILLARY WIDTH, O.] (as measured also by Nehring, Tscherski, approximately as measured by Salensky and Osborn,— fossil Equidæ). Fig. 3, II, 6.
7. *Width between canines* (as measured by Franck only). Fig. 3, III, 7.
8. *Greatest width of skull* (as measured also by Tscherski, Bradley, approximately as measured by Osborn,— fossil Equidæ). Fig. 3, III, 8 (between outer ends of joint surfaces for lower jaw).
9. *Greatest width between orbital processes* [= FRONTAL WIDTH, O.] (as measured also by Branco, Nehring, Tscherski, Salensky, Ewart, Bradley, Osborn). Fig. 3, II, F–F.
10. *Greatest distance between pterygoid processes of palatal bones* (as measured by Franck only). Fig. 3, III, 10.
11. *Length of molar row of upper jaw, not including* p^1 (as measured also by Nehring, Tscherski, Salensky, Osborn). Fig. 3, III, D–D.
    Nehring, Tscherski, Salensky: measure both along wearing surfaces and along alveoli.
12. *Greatest distance between* M^3, M^3 (as measured by Franck only). Fig. 3, III, 12.
13. *Distance between* P^2, P^2, *anterior end* [= PALATAL WIDTH (2), O.] (as measured also by Tscherski, Osborn,— fossil Equidæ). Fig. 3, III, 13.
14. *Straight line from middle of transverse process of occipital bone to point between I, I* [= VERTEX LENGTH O.] (as measured also by Nehring, Tscherski, Salensky, Ewart, Osborn). Fig. 3, I, S–I.
15. *From middle of transverse process of occipital bone to tip of nasal bones* (with tape measure) (as measured by Franck only). Fig. 3, I, 15.
16. *From middle of transverse process of occipital bone to tip of nasal bones* (straight line) (as measured by Franck only). Fig. 3, I, 16.
17. *From middle of occipital crest to point between orbits* (?).
    Ewart, Osborn, Bradley: cranial length is taken from middle of line connecting posterior borders of orbits to occipital crest.
18. *From middle of occipital crest to end of nasal process of frontal bones* (as measured also by Tscherski, Salensky). Fig. 3, II, 18.
19. *Median length of nasal bones* (as measured also by Tscherski, Salensky). Fig. 3, II, 19.
20. *Straight line between tip of nasal bones and* I^1, (as measured by Franck only). Fig. 3, I, 20.
21. *Greatest breadth of cerebral portion of skull, above zygomatic processes of temporal bones* (as measured also by Tscherski, Salensky, Ewart). Fig. 3, II, 21.
22. *Smallest breadth of skull capsule on small pterygoid foramina* (as measured by Franck only). Fig. 3, III, 22.
    Branco: measures width of cranium at bases of styloid processes of petrosum.
    Tscherski: measures greatest width of head behind orbits at mastoid processes.
23. *Greatest width on parietal bump* (as measured also by Tscherski, Salensky, Ewart). Fig. 3, II, 23.
24. *Width between supraorbital foramina* (as measured by Franck only). Fig. 3, II, 24.
    Tscherski: measures width of forehead between points taken in middle of length of upper orbital edge.
25. *Width between infraorbital foramina* (as measured by Franck only). Fig. 3, II, 25.

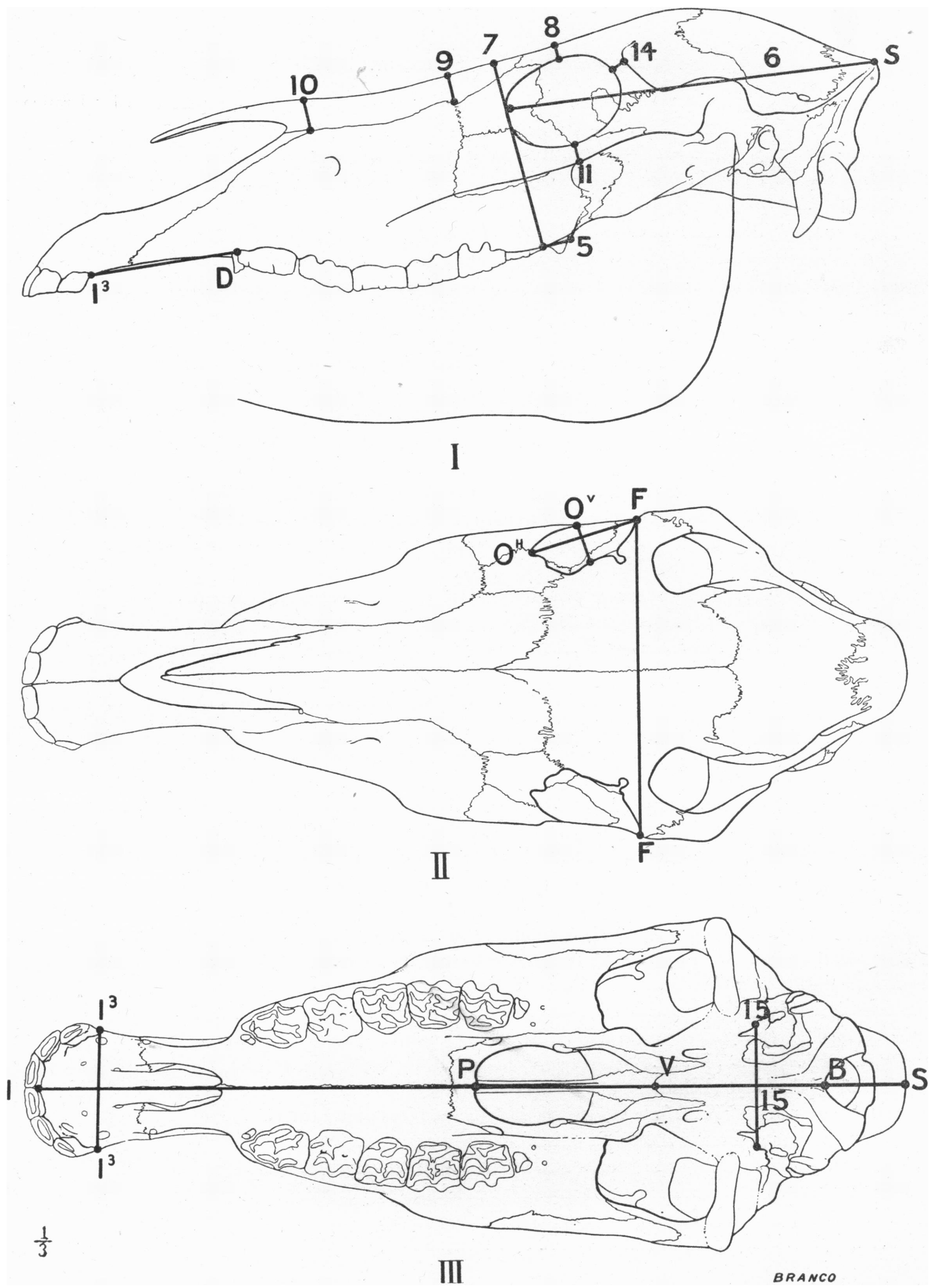

Fig. 4. Branco's system (principal measurements), 1883.

Key to Branco's System of 1883.

1. *Lower edge of foramen magnum to alveolar border of premaxillaries, between I^1, I^1.* [= Basilar length, O.] (as measured also by Franck, Nehring, Tscherski, Salensky, Osborn). Fig. 4, III, B–I.
2. *Lower edge of foramen magnum to middle of posterior end of vomer* (as measured also by Franck, Nehring, Tscherski, Salensky, Osborn). Fig. 4, III, B–V.
3. *Middle of posterior end of vomer to middle of posterior border of palate* (as measured also by Franck, Nehring, Tscherski, Salensky, Osborn). Fig. 4, III, V–P.
4. *Diastema from anterior end of P^2 to posterior end of I^3* [= Diastema length, O.] (as measured also by Nehring, Tscherski, Salensky, Osborn). Fig. 4, I, D–I^3.
5. *Length of maxillary behind M^3* (as measured by Branco only). Fig. 4, I, 5.
6. *Horizontal line from posterior point of occipital crest to point in a vertical line with most anterior part of anterior orbital edge* (as measured by Branco only). Fig. 4, I, 6.
7. *Vertical line from alveolar border of maxillaries, immediately behind M^3, to plane of upper profile line of skull* [= Depth of skull (2) (as measured also by Tscherski, Salensky, Osborn,— fossil Equidæ). Fig. 4, I, 7.
8. *Vertical line from highest point of upper orbital edge to plane of upper profile line of skull* (as measured by Branco only). Fig. 4, I, 8.
9. *Vertical line from plane of internasal suture to upper angle of suture of lachrymal and maxillary* (as measured by Branco only). Fig. 4, I, 9.
10. *Vertical line from plane of internasal suture to upper point of suture of premaxillary and maxillary* (as measured by Branco only).
11. *Vertical distance from lower edge of zygomatic arch to upper* (as measured by Branco only), at median point of lower orbital edge. Fig. 4, I, 11.
12. *Lower edge of foramen magnum to highest point of occipital crest* (as measured also by Nehring, Tscherski, Salensky). Fig. 4, III, B–S.
13. *Vertical diameter of orbit; horizontal diameter of orbit* (as measured also by Tscherski, Salensky, Ewart, Bradley, Osborn). Fig. 4, II, Ov Oh.
14. *Width of posterior border of orbit* (as measured also by Tscherski at its narrowest point). Fig. 4, I, 14.
15. *Width of cranium* (as measured by Branco only, at bases of styloid processes of petrosum). Fig. 4, III, 15.
    Franck: measures smallest breadth of skull capsule on pterygoid foramina.
    Tscherski: measures greatest width of head behind orbits at mastoid processes.
16. *Width of premaxillaries at outer posterior borders of I^3, I^3* [= Muzzle width, O.] (as measured also by Franck, Nehring, Tscherski, Salensky, Bradley, Osborn). Fig. 4, III, I^3–I^3.
17. *Distance between most prominent points of orbital processes of frontals* [= Frontal width, O.] (as measured also by Franck, Nehring, Tscherski, Salensky, Ewart, Bradley, Osborn). Fig. 4, II, F–F.
18. *Height of horizontal ramus of lower jaw at posterior border of M_3* [= Depth of jaw, O.] (as measured also by Osborn,— fossil Equidæ). Fig. 4, 5.
19. *Height of horizontal ramus of lower jaw between P_4 and M_1* [= Depth of jaw, O.] (as measured also by Tscherski and Osborn,— fossil Equidæ). Fig. 4, 6.
20. *Height of horizontal ramus of lower jaw between P_2 and P_3* (as measured by Branco only). Fig. 4, 7.

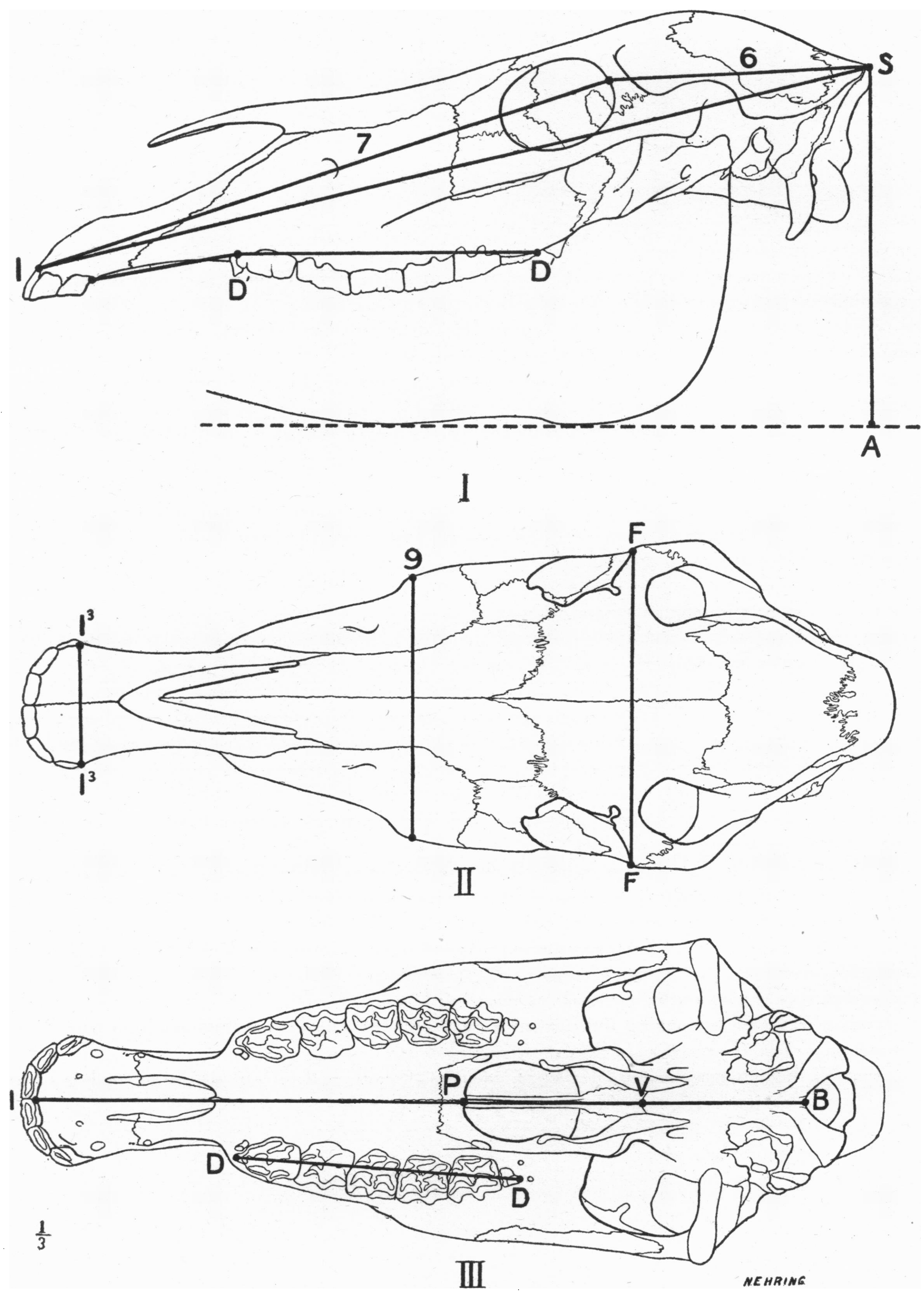

Fig. 5. Nehring's system (principal measurements), 1884.

Key to Nehring's Principal Measurements, 1884.

1. *Length of vertex* (as measured also by Franck, Tscherski, Salensky, Ewart, Osborn) from edge of occipital crest along external upper surface of skull to base of middle incisors. Fig. 5, I, S–I.
2. *Basilar length* (as measured also by Franck, Branco, Tscherski, Salensky, Osborn) along base of skull from lower border of foramen magnum to base of middle incisor teeth. Fig. 5, III, B–I.
3. *Frontal width* (as measured also by Franck, Branco, Tscherski, Salensky, Ewart, Bradley, Osborn) between posterior margins of orbital cavities. Fig. 5, II, F–F.
4. *Index I* [= Frontal index, O.] (as taken also by Branco, Tscherski, Salensky); basilar length (2) × 100 ÷ frontal width (3).
   Ewart: Frontal index is frontal width × 100 ÷ facial length.
5. *Index II* (as taken also by Tscherski, Salensky); length of vertex (1) × 100 ÷ frontal width (3).
6. *Posterior segment of ocular line* (as measured also by Tscherski, Salensky) from middle of occipital crest to most external point on posterior border of orbital cavity. Fig. 5, I, 6.
7. *Anterior segment of ocular line* (as measured also by Tscherski, Salensky) from most external point on posterior border of orbital cavity to base of middle incisors. Fig. 5, I, 7.
8. *Index III — Ocular Index* (as taken also by Tscherski, Salensky); anterior segment of ocular line (7) × 100 ÷ posterior segment of ocular line (6).
9. *Facial width* [= Facial-maxillary width, O.] (as measured also by Franck, Tscherski; approximately as measured by Salensky, Bradley, Osborn,— fossil Equidæ) between zygomatic ridges of superior maxillary bones. Fig. 5, II, 9.
10. *Width of muzzle* (as measured also by Franck, Branco, Tscherski, Salensky, Osborn) at posterior alveolar borders of I^3, I^3. Fig. 5, II, I^3–I^3.
11. *Franck's vomer index* (as measured also by Franck, Branco, Tscherski, Salensky, Osborn); distance from posterior border of palate to middle of posterior edge of vomer (P V) × 100 ÷ distance from same point on vomer to anterior border of foramen magnum (V B). Fig. 5, III.
12. *Height of skull at occipital crest* [= Occiput height, O.] (as measured also by Branco, Tscherski, Salensky, Osborn); length of perpendicular from middle of occipital crest to base of mandible. Fig. 5, I, S–A.
13. *Length of diastema, I^3–P^2* (as measured also by Branco, Tscherski, Salensky, Osborn). Fig. 5, I, I^3–D^1.
14. *Length of series of upper cheek-teeth,* along wearing surfaces (as measured also by Franck, Branco, Tscherski, Salensky, Osborn). Fig. 5, III, D–D.
   Along alveoli (as measured also by Tscherski, Salensky). Fig. 5, I, D^1–D^1.
15. *Length of mandible* (as measured also by Tscherski, Salensky, Osborn,— fossil Equidæ) from condyle to base of central incisors. Fig. 11, 1.
16. *Height of mandible* (as measured also by Tscherski, Salensky, Osborn,— fossil Equidæ) from condyle to base. Fig. 11, 2.

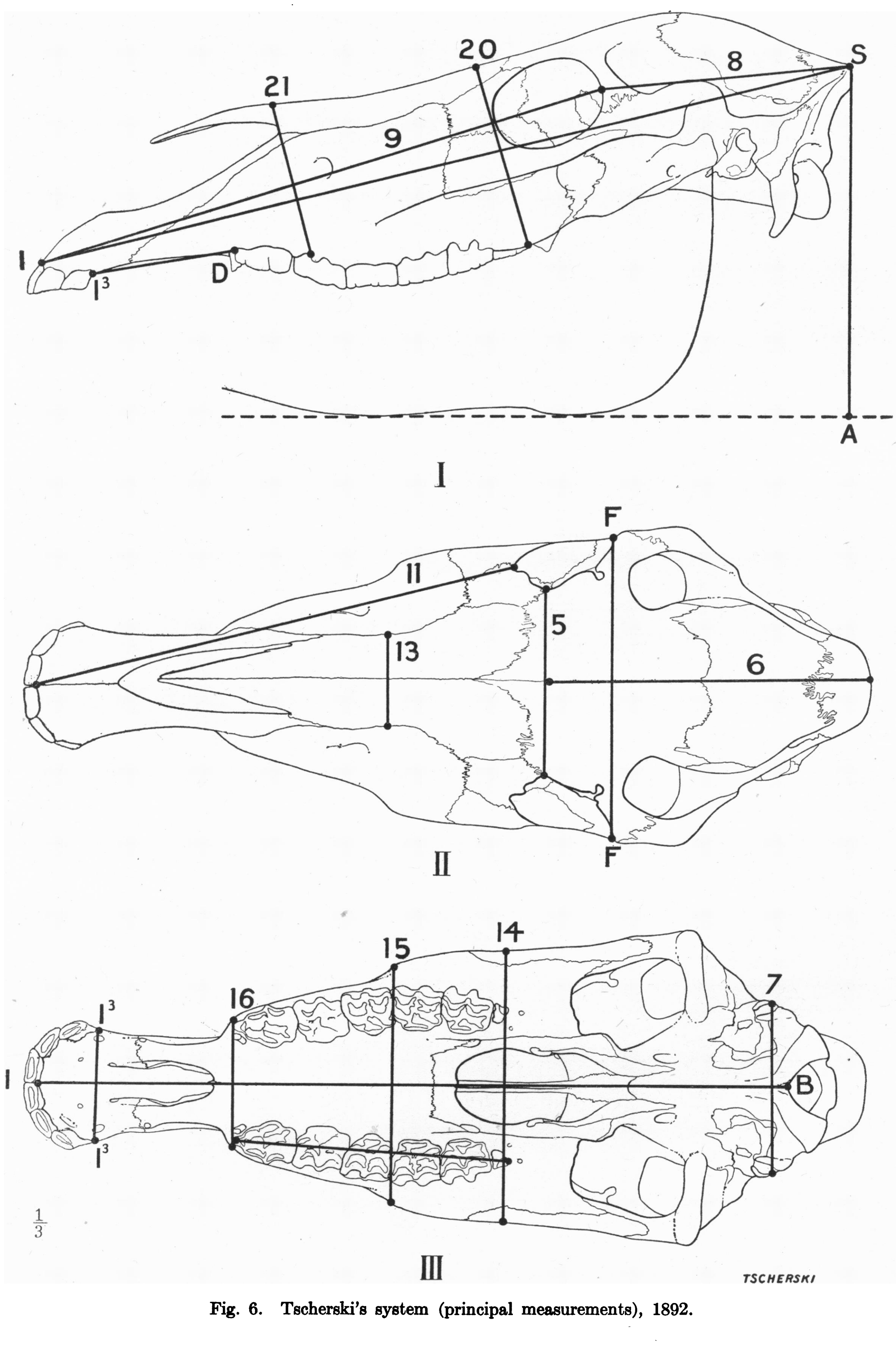

Fig. 6. Tscherski's system (principal measurements), 1892.

KEY TO TSCHERSKI'S PRINCIPAL MEASUREMENTS, 1892.

1. *Length of base* [= BASILAR LENGTH, Osborn] (as measured also by Franck, Branco, Nehring, Salensky, Osborn) from point between central incisors to lower edge of foramen magnum. Fig. 6, III, I–B.
2. *Cranial length (greatest length)* [= VERTEX LENGTH, Osborn] (as measured also by Franck, Nehring, Salensky, Ewart, Osborn) from point between central incisors to occipital crest). Fig. 6, I, I–S.
3. *Greatest breadth of forehead* [= FRONTAL WIDTH, Osborn] (as measured also by Franck, Branco, Nehring, Salensky, Ewart, Bradley, Osborn) at posterior borders of orbits. Fig. 6, II, F–F.
4. *Frontal index* (as measured also by Branco, Nehring, Salensky); length of base (1) × 100 ÷ greatest breadth of forehead (3).
   Ewart, Bradley: Frontal index is frontal width × 100 ÷ facial length.
   Nehring: Index II is length of vertex × 100 ÷ frontal width.
5. *Transverse convexity of forehead — Index* (as measured by Tscherski only), measuring between middle points of upper orbital edges, arc × 100 ÷ cord. Fig. 6, II, 5.
6. *Longitudinal convexity of forehead — Index* (as measured by Tscherski only), measuring from line connecting middle points of upper orbital edges to occipital crest, arc × 100 ÷ cord. Fig. 6, II, 6.
7. *Greatest breadth of head behind orbits* (as measured by Tscherski only) at mastoid processes. Fig. 6, III, 7.
   Franck: measures smallest breadth of skull capsule on pterygoid foramina.
   Branco: measures width of cranium at bases of styloid processes of petrosum.
8. *Posterior section of eye-line* (as measured also by Nehring, Salensky) from middle of occipital crest to most external point on posterior border of orbital cavity. Fig. 6, I, 8.
9. *Anterior section of eye-line* (as measured also by Nehring, Salensky) from point between central incisors to most external point on posterior border of orbital cavity. Fig. 6, I, 9.
10. *Eye index* (as measured also by Nehring, Salensky) anterior section of eye-line (9) × 100 ÷ posterior section of eye-line (8).
11. *Length of face* (as measured by Tscherski only), from point between central incisors to nearest point of anterior orbital edge. Fig. 6, II, 11.
    Salensky: Length of face is measured from middle incisors to posterior end of internasal suture.
    Ewart, Bradley, Osborn: Facial length is measured from median incisive border to middle of line connecting posterior borders of orbits.
12. *Facial index* (as measured by Tscherski only) length of face (11) × 100 ÷ length of base (1).
    Salensky: Index IV is length of vertex × 100 ÷ length of face (see 11, note, above).
    Ewart, Osborn: Facio-cranial index is facial length (see 11, note, above) × 100 ÷ cranial length.
13. *Convexity of nasals — Index* (as measured by Tscherski only) measuring smallest width of nasal bones behind infra-orbital foramina, arc × 100 ÷ cord. Fig. 6, II, 13.
14. *Breadth of snout at maxillary crests* [= FACIAL-MAXILLARY WIDTH, O.] (as measured also by Franck, Nehring; approximately as measured by Salensky, Bradley, Osborn,— fossil Equidæ). Fig. 6, III, 14.
15. *Breadth of snout at points between P^4 and M^1*. (as measured by Tscherski only). Fig. 6, III, 15.
16. *Breadth of snout at anterior ends of alveoli of P^2* [= PALATAL WIDTH (2), O.] (as measured also by Franck, Osborn,— fossil Equidæ). Fig. 6, III, 16.
17. *Breadth of snout at posterior ends of alveoli of I^3* [= MUZZLE WIDTH, Osborn] (as measured also by Franck, Branco, Nehring, Salensky, Osborn, Bradley). Fig. 6, III, 17.
18. *Length of diastema between I^3 and P^2* [= DIASTEMA LENGTH, Osborn] (as measured also by Branco, Nehring, Salensky, Osborn). Fig. 6, I, I^3–D.
19. *Length of dentition, P^2–M^3* along wearing surfaces (as measured also by Franck, Branco, Nehring, Salensky, Osborn); along alveoli (as measured also by Nehring, Salensky). Fig. 6, III, D–D.
20. *Perpendicular height of face at posterior alveolus of M^3* [= DEPTH OF SKULL (2), Osborn] (as measured also by Branco, Salensky, Osborn,— fossil Equidæ). Fig. 6, I, 20.
21. *Perpendicular height of face at posterior end of anterior nasal opening* (as measured by Tscherski only). Fig. 6, I, 21.
22. *Height of head* [= OCCIPUT HEIGHT, Osborn] (as measured also by Branco, Nehring, Salensky, Osborn), perpendicular from occipital crest to base of mandible. Fig. 6, I, S–A.
23. *Length of lower jaw* (as measured also by Nehring, Salensky, Osborn,— fossil Equidæ) from median incisive point to posterior, outer edge of head of condyle. Fig. 11, 1.
24. *Height of ascending ramus* (as measured also by Nehring, Salensky, Osborn,— Fossil Equidæ) from head of joint perpendicularly to plane of table. Fig. 11, 2.
25. *Width of incisive portion* [= WIDTH OF SYMPHYSIS (2), Osborn] (as measured also by Salensky, Osborn,— fossil Equidæ). Fig. 11, 3.
26. *Narrowest width* [= WIDTH OF SYMPHYSIS (1), Osborn] (as measured also by Osborn,— fossil Equidæ). Fig. 11, 4.
27. *Height of lower jaw in region of space between P_4 and M_1* [= DEPTH OF JAW, Osborn] (as measured also by Branco, Osborn,— fossil Equidæ). Fig. 11, 6.

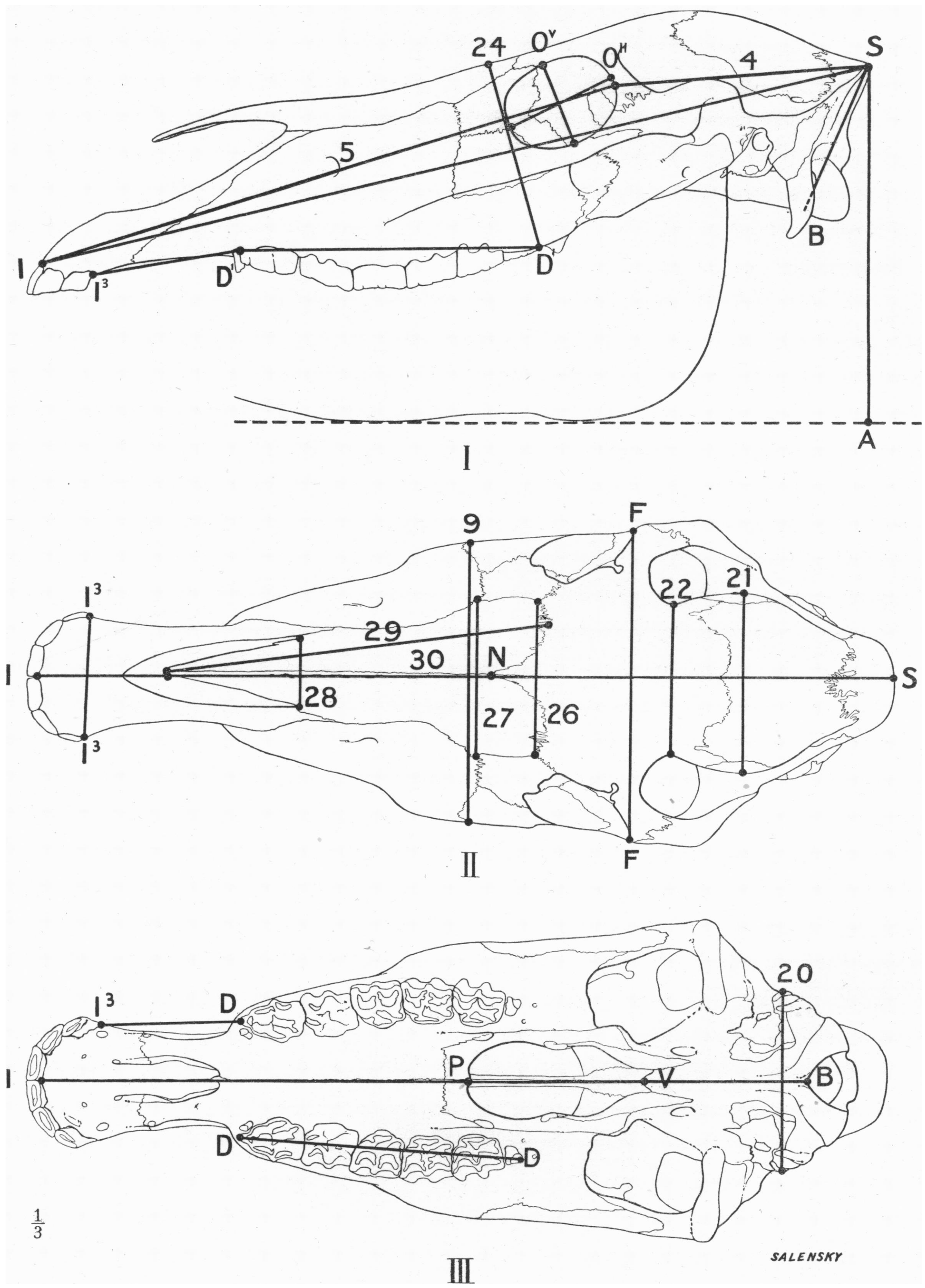

Fig. 7. Salensky's system (principal measurements), 1902.

SALENSKY'S PRINCIPAL MEASUREMENTS, 1902.

1. *Frontal width* (as measured also by Franck, Branco, Nehring, Tscherski, Ewart, Bradley, Osborn), between posterior margins of orbital cavities. Fig. 7, II, F–F.
2. *Basilar length* (as measured also by Franck, Branco, Nehring, Tscherski, Osborn) from base of middle incisors to lower border of foramen magnum. Fig. 7, III, I–B.
3. *Length of vertex* (as measured also by Franck, Nehring, Tscherski, Ewart, Osborn) from base of middle incisors to edge of occipital crest. Fig. 7, I, I–S.
4. *Posterior ocular line* (as measured also by Nehring, Tscherski) from occipital crest to most external point on posterior border of orbital cavity. Fig. 7, I, 4.
5. *Anterior ocular line* (as measured also by Nehring, Tscherski) from base of middle incisors to most external point on posterior border of orbital cavity. Fig. 7, I, 5.
6. *Index I* [= FRONTAL INDEX, Osborn] (as measured also by Branco, Nehring, Tscherski, Osborn) basilar length × 100 ÷ frontal width.
   Ewart: Frontal index is frontal width × 100 ÷ facial length.
7. *Index II* (as measured also by Nehring, Tscherski) length of vertex × 100 ÷ frontal width.
8. *Index III* (as measured also by Nehring, Tscherski) anterior ocular line (5) × 100 ÷ posterior ocular line (4).
9. *Facial width* [= FACIAL-MAXILLARY WIDTH, Osborn] (as measured also by Osborn,— fossil Equidæ, approximately as measured by Nehring, Tscherski at maxillary crests). Fig. 7, II, 9.
10. *Length of series of upper cheek teeth* along wearing surfaces (as measured also by Franck, Branco, Nehring, Tscherski, Osborn). Fig. 7, III, D–D.
    along alveoli (as measured also by Nehring, Tscherski). Fig. 7, I, D^1–D^1.
11. *Distance from margin of foramen magnum to vomer* (as measured also by Franck, Branco, Nehring, Tscherski, Osborn). Fig. 7, III, B–V.
12. *Distance from vomer to palatine bone* (as measured also by Franck, Branco, Nehring, Tscherski, Osborn). Fig. 7' III, V–P.
13. *Nasal width of upper jaw* [= MUZZLE WIDTH, Osborn] (as measured also by Franck, Branco, Nehring, Tscherski, Bradley, Osborn) at posterior alveoli of I^3. Fig. 7, II, I^3–I^3.
14. *Length of diastema, I^3–P^2* (as measured also by Branco, Nehring, Tscherski, Osborn). Fig. 7, I, I^3–D^1.
15. *Height of skull* [= OCCIPUT HEIGHT, O.] (as measured also by Branco, Nehring, Tscherski, Osborn) perpendicular from occipital crest to base of mandible. Fig. 7, I, S–A.
16. *Length of cranium* (as measured by Salensky only) from posterior end of internasal suture to occipital crest. Fig. 7, II, N–S.
    Ewart, Osborn: Cranial length is measured from middle of line connecting posterior borders of orbits, to occipital crest.
17. *Length of face* (as measured by Salensky only) from middle incisors to posterior end of internasal suture. Fig. 7, II, I–N.
    Tscherski: Length of face is measured from point between central incisors to nearest point on anterior orbital edge.
    Ewart, Bradley, Osborn: Facial length is measured from median incisive border to middle of line connecting posterior borders of orbits.
18. *Antero-posterior diameter of orbital cavity* (as measured also by Branco, Tscherski, Ewart, Osborn, approximately as measured by Bradley). Fig. 7, I, Oh.
19. *Vertical diameter of orbital cavity* (as measured also by Branco, Tscherski, Ewart, Osborn, approximately as measured by Bradley). Fig. 7, I, Ov.
20. *Width of cranium* (as measured by Salensky only) between superior margins of external auditory meati. Fig. 7, III, 20.
21. *Greatest width of cranium* (as measured by Franck, Tscherski, Ewart) above zygomatic processes of temporal bones. Fig. 7, II, 21.
22. *Least width of cranium* (as measured also by Tscherski) behind orbital cavities. Fig. 7, II, 22.
23. *Height of occipital bone* (as measured also by Branco, Nehring, Tscherski) from lower edge of foramen magnum to occipital crest. Fig. 7, I, S–B.
24. *Height of face* [= DEPTH OF SKULL (2), Osborn] (as measured also by Branco, Tscherski, Salensky, Osborn) from base of M^3 to middle of internasal suture. Fig. 7, I, 24.
25. *Index IV* (as measured by Salensky only) length of vertex (3) × 100 ÷ length of face (17).
    Tscherski: Facial index is length of face (see 17, note, above) × 100 divided by basilar length.
    Ewart, Osborn: Facio-cranial index is facial length (see 17 note above) × 100 ÷ cranial length, (see 16, note, above).
26. *Width of nasal bones in their posterior part* (as measured by Salensky only) at posterior and most external point on naso-lachrymal suture. Fig. 7, II, 26.
27. *Width of nasal bones in middle of their length* (as measured by Salensky only) at anterior and most external point on naso-lachrymal suture. Fig. 7, II, 27.

28. *Width of nasal bones in their anterior part* (as measured by Salensky only) at point of contact of intermaxillary and nasal bones. Fig. 7, II, 28.
29. *Length of nasal bones* (*oblique*) (as measured by Salensky only) at highest point of naso-frontal suture. Fig. 7, II, 29.
30. *Length of nasal bones* (*median*) (as measured also by Franck, Tscherski. Fig. 7, II, 30.
31. *Length of lower jaw* (as measured also by Nehring, Tscherski, Osborn,— fossil Equidæ) from condyle to base of central incisors. Fig. 11, 7.
32. *Height of lower jaw* (as measured also by Nehring, Tscherski, Osborn,— fossil Equidæ). Fig. 11, 2.
33. *Width of lower jaw* [= WIDTH OF SYMPHYSIS (2), Osborn] (as measured also by Tscherski, Osborn,— fossil Equidæ). Fig. 11, 3.
34. *Length of series of lower cheek teeth* along wearing surfaces (as measured also by Tscherski, Osborn,— fossil Equidæ); along bases (as measured also by Tscherski). Fig. 11, 8.
35. *Length of diastema, I_3–P_2* (as measured also by Tscherski, Osborn,— fossil Equidæ). Fig. 11, 9.

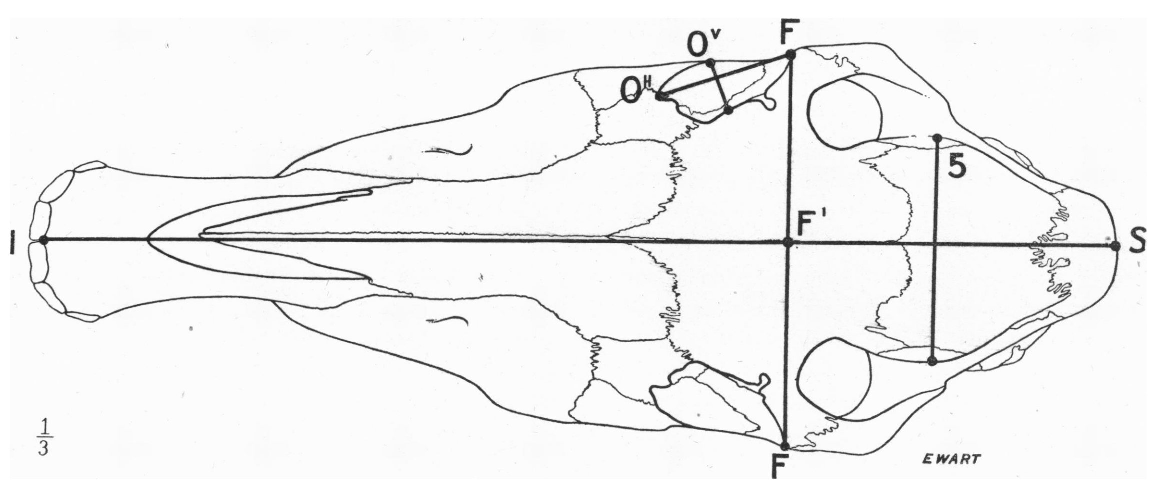

Fig. 8. Ewart's system, 1907.

Ewart's Principal Measurements, 1907.

1. *Total length* [= Vertex length, Osborn] (as measured also by Franck, Nehring, Tscherski, Salensky, Osborn) from occipital crest to alveolar point, i. e. to wedge-like piece which projects between upper central incisors. Fig. 8, I, S–I.
2. *Facial length* (as measured also by Bradley, Osborn) from central incisors to a line connecting posterior borders of orbits. Fig. 8, I, S–F′.
   Tscherski: Facial length is taken from point between central incisors to nearest point on anterior orbital edge.
   Salensky: Facial length is taken from central incisors to posterior end of internasal suture.
3. *Frontal width* (as measured also by Franck, Branco, Nehring, Tscherski, Salensky, Bradley, Osborn) between outer margins of orbits. Fig. 8, I, F–F.
4. *Cranium length* (as measured also by Osborn) from occipital crest to line connecting posterior borders of orbits. Fig. 8, I, S–F′.
   Salensky: Cranial length is taken from posterior end of internasal suture to occipital crest.
5. *Cranium width* (as measured also by Franck, Tscherski, Salensky) at widest part. Fig. 8, I, 5.
6. *Frontal index* (as measured also by Bradley) frontal width (3) × 100 ÷ facial length (2).
   Branco, Nehring, Tscherski, Salensky, Osborn: Frontal index is basilar length × 100 ÷ frontal width.
7. *Cephalic index* (as measured by Ewart only) cranium width (5) × 100 ÷ cranium length (4).
8. *Orbital index* (as measured also by Branco, Tscherski, Salensky, Osborn, approximately as measured by Bradley) vertical diameter of orbit × 100 ÷ horizontal diameter. Fig. 8, I, O^v–O^h.
9. *Angle of deflection of face (line)* [= Palato-cranial angle (line), Osborn] (as measured also by Osborn) distance from middle of posterior border of palate to a line connecting median incisive border and foramen magnum.
10. *Angle of deflection of face* [= approximately Palato-cranial angle, Osborn] (approximately as measured by Osborn) between line of palate and basicranial axis.

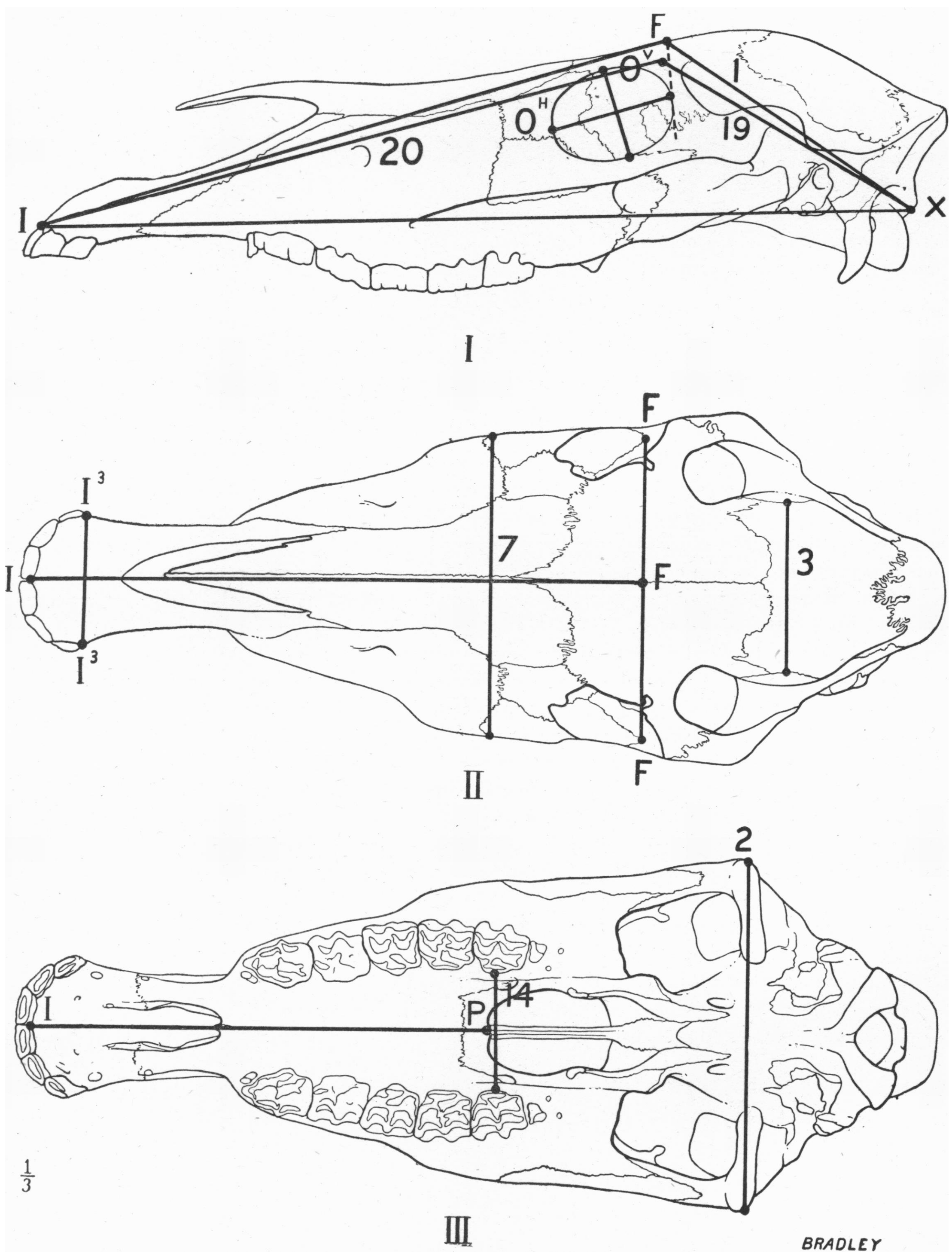

Fig. 9. Bradley's system, 1907.

Bradley's Principal Measurements, 1907.

1. *Cranium length* (as measured by Bradley only) from the opisthion to the interorbital point, *i. e.*, to the middle point of a transverse line on a level with the anterior border of the post-orbital process of the frontal bone. Fig. 9, I, X–F′.
2. *Condylar breadth of cranium* (as measured also by Franck, Tscherski, approximately as measured by Osborn,— fossil Equidæ) transverse diameter from the outermost part of the condyles on the squamous temporal bones. Fig. 9, III, 2.
3. *Maximum parietal breadth of cranium* (as measured by Bradley only) between points on the parieto-squamosal suture. Fig. 9, II, 3.
4. *Cephalic index A* (as measured by Bradley only): condylar breadth (2) × 100 ÷ cranium length (1).
5. *Cephalic index B* (as measured by Bradley only): maximum parietal breadth (3) × 100 ÷ cranium length (1).
6. *Facial length* (as measured also by Ewart, Osborn) from the alveolar point to the interorbital point, *i. e.*, to the middle point of a transverse line on a level with the anterior border of the postorbital process of the frontal bone. Fig. 9, I–II, I–F′.
7. *Facial breadth* (approximately as measured by Salensky, Osborn,— fossil Equidæ) between the most distant points on the sutures separating the malar and maxillary bones. Fig. 9, II, 7.
8. *Facial index* (as measured by Bradley only) facial breadth (7) × 100 ÷ facial length (6).
9. *Frontal breadth* (as measured also by Franck, Branco, Nehring, Tscherski, Salensky, Ewart, Osborn) maximum breadth of skull at posterior borders of orbits. Fig. 9, II, F–F.
10. *Frontal index* (as measured also by Ewart) frontal breadth (9) × 100 ÷ facial length (6).
11. *Cranio-facial length* (as measured by Bradley only) from the opisthion to the alveolar point. Fig. 9, II, I–X.
12. *Cranio-facial index* (as measured by Bradley only) length of face (6) × 100 ÷ cranio-facial length (11).
13. *Palate length* (as measured also by Franck, Tscherski, Osborn,— fossil Equidæ. Fig. 9, III, I–P.
14. *Palate width* (as measured also by Osborn,— fossil Equidæ). Fig. 9, III, 14.
15. *Palatine index* (as measured by Bradley only) palate width (14) × 100 ÷ palate length (13).
16. *Maximum diameter of orbit* (approximately as measured by Branco, Tscherski, Salensky, Ewart, Osborn). Fig. 9, I, Oh.
17. *Minimum diameter of orbit* (approximately as measured by Branco, Tscherski, Salensky, Ewart, Osborn). Fig. 9, I, Ov.
18. *Orbit index* (approximately as measured by Branco, Tscherski, Salensky, Ewart, Osborn) minimum diameter of orbit (17) × 100 ÷ maximum diameter (16).
19. *Distance from opisthion to supraorbital foramen* (as measured by Bradley only). Fig. 9, I, 19.
20. *Distance from supraorbital foramen to alveolar point* (as measured by Bradley only). Fig. 9, I, 20.
21. *Index* (as measured by Bradley only) distance from opisthion to supraorbital foramen (19) × 100 ÷ distance from supraorbital foramen to alveolar point (20).
22. *Maximum width of premaxilla* [= Muzzle width, Osborn] (as measured also by Franck, Branco, Nehring, Tscherski, Salensky, Ewart, Osborn) measured from the bases of the third incisor teeth. Fig. 9, II, I^3–I^3.
23. *Index* (as measured by Bradley only) facial length (6) × 100 ÷ width of premaxillæ (21).

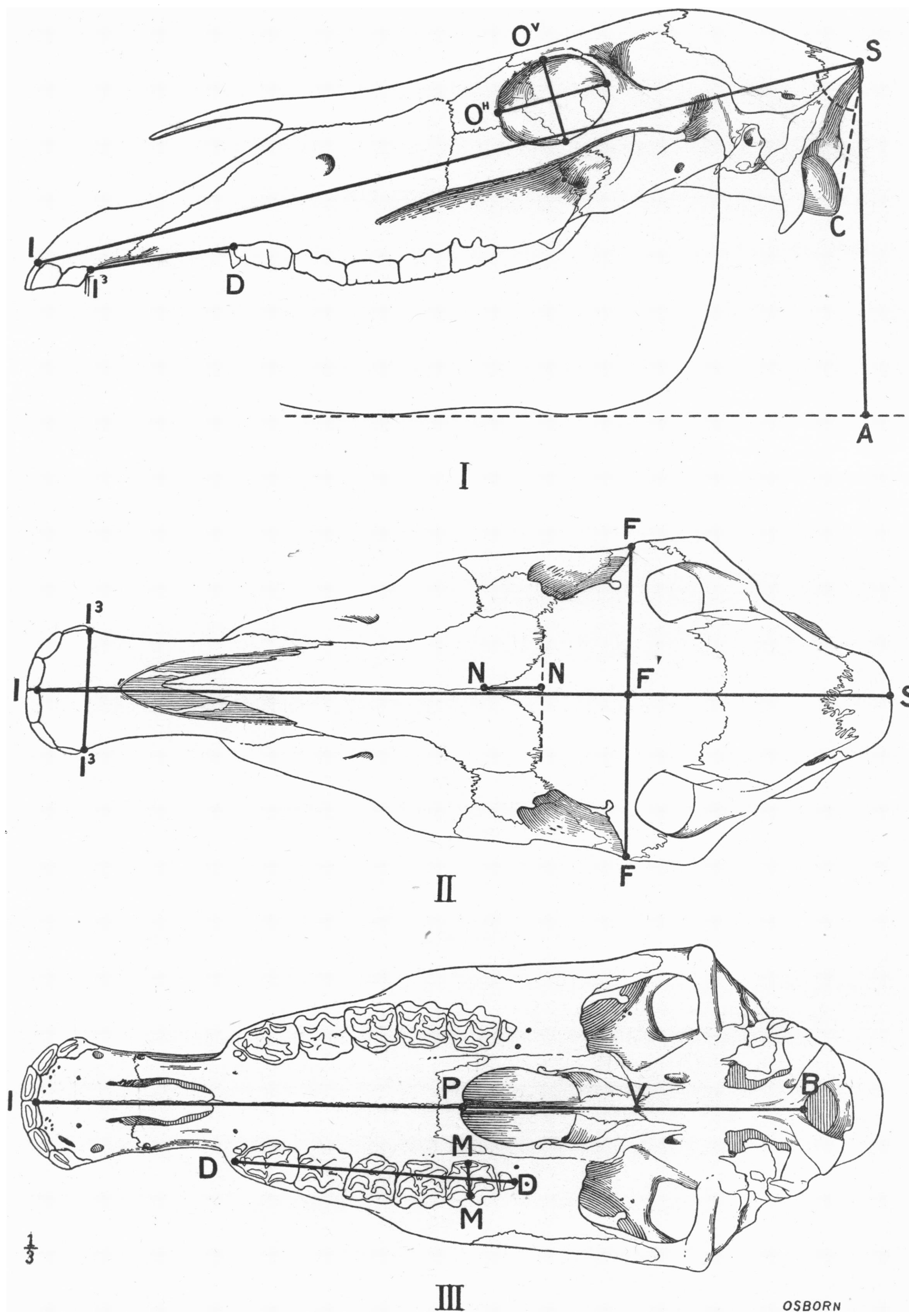

Fig. 10. Osborn's system, skull, 1912.

Key to Cranial Measurements, Osborn, 1912.

1. *Vertex length* (from median incisive border to middle of occipital crest). Fig. 10, I, I–S.
   As measured also by Franck, Nehring, Tscherski, Salensky, Ewart.
2. *Basilar length* (from median incisive border to anterior edge of foramen magnum). Fig. 10, III, I–B.
   As measured also by Franck, Branco, Nehring, Tscherski, Salensky.
3. *Frontal width* (at posterior borders of orbits). Fig. 10, II, F–F.
   As measured also by Franck, Branco, Nehring, Tscherski, Salensky, Ewart, Bradley.
4. * *Cephalic index* (frontal width × 100 ÷ basilar length).
   Ewart, Bradley: Frontal index is frontal width × 100 ÷ facial length. Nehring, Tscherski, Salensky: index II is length of vertex × 100 ÷ frontal width.
   As measured by Osborn only.
5. *Facial length* (from median incisive border to middle of line connecting posterior borders of orbits). Fig. 10, II, I–F′.
   Tscherski: facial length is measured from point between central incisors to nearest point on anterior orbital edge.
   Salensky: facial length is measured from incisors to posterior end of internasal suture.
   As measured also by Ewart and Bradley.
6. *Facio-cephalic Index* (facial length × 100 ÷ basilar length).
   Tscherski: facial index is length of face (see 5, note, above) × 100, divided by basilar length.
   Salensky: index IV is length of vertex × 100 ÷ length of face (see 5, note, above).
   As measured by Osborn only.
7. *Cranial length* (from middle of line connecting posterior borders of orbits to middle of occipital crest).
   Salensky: cranial length is measured from posterior end of internasal suture to occipital crest.
   As measured also by Ewart.
8. *Cranio-cephalic Index* (cranial length × 100 ÷ basilar length).
9. *Palatal angle,* line (vertical distance from middle of posterior border of palate to a line [dots] connecting median incisive border and foramen magnum). Fig. 16, P–P^2.
   As measured also by Ewart.
10. *Palato-cranial angle* (angle between basicranial line, taken outside, and basifacial line, *i. e.*, line passing through median incisive border and middle of posterior border of palate). Fig. 16, B–B^1, I–P^1.
    Lankester: a vertical longitudinal section of skull is made. Angle is taken between basicranial line, which follows cut surface of bones, and "palatine horizontal," which connects anterior border of premaxillaries and foramen magnum (see Fig. 16, lower, I–B).
    Ewart: angle is measured between line of palate and basicranial axis.
    As measured by Osborn only; approximately as measured by Lankester, Ewart, and others.
11. * *Occiput-vertex angle* (angle between vertex and line connecting most posterior points of occipital crest and condyles). Fig. 10, I, I S C.
    As measured by Osborn only.

(* Denotes importance in comparing horses with asses and zebras.)

12. * *Occiput height* (length of perpendicular from middle of occipital crest to base of mandible). Fig. 10, I, S–A.
As measured by Branco, Nehring, Tscherski, Salensky.
13. * *Orbital index* (vertical diameter of orbit × 100 ÷ horizontal diameter). Fig. 10, I, Ov, Oh.
As measured also by Branco, Tscherski, Salensky, Ewart, approximately as measured by Bradley.
14. * *Franck's vomer index* (distance from posterior border of palate to middle of posterior edge of vomer × 100 ÷ distance from same point on vomer to anterior edge of foramen magnum). Fig. 10, III, P–V, V–B.
As measured also by Franck, Branco, Nehring, Tscherski, Salensky.
15. * *Convexity of nasofrontal suture* (distance from posterior end of internasal suture to middle of line connecting two most posterior points of frontonasal suture). Fig. 10, II, N–N.
As measured by Osborn only.
16. * *Diastema length* I^3–P^2. Fig. 10, I, I^3–D.
As measured by Branco, Nehring, Tscherski, Salensky.
17. * *Muzzle width* (at posterior alveolar borders of I^3). Fig. 10, II, I^3–I^3.
As measured also by Franck, Branco, Nehring, Tscherski, Salensky, Bradley.
18. *Molar-premolar series total length (upper)* p^2–m^3 (length of wearing surface). Fig. 10, III, D–D.
Nehring, Tscherski, Salensky measure both wearing surface and length along alveoli.
As measured also by Franck, Branco, Nehring, Tscherski, Salensky.
19. * *Dental Index* (Molar-premolar series total length (upper) × 100 ÷ basilar length).
20. * *Molar Index* (transverse diameter of m^2 × 100 ÷ molar-premolar series total length). Fig. 10, III, M–M, D–D.
As taken by Osborn only.
21. *Facio-cranial angle* (from optic foramen to middle of incisive border as compared with basi-cranial line).

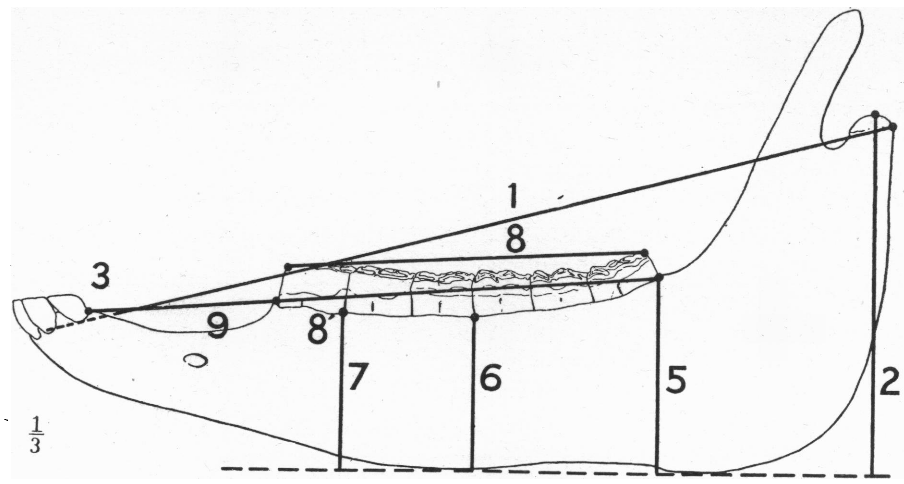

Fig. 11. Osborn's system, lower jaw, 1912.

System of Measurements of Lower Jaw, Osborn, 1912.

Branco.

(1) *Height of horizontal ramus at posterior border of M_3* [= DEPTH OF JAW, Osborn] (as measured also by Osborn,— fossil Equidæ). Fig. 11, 5.

(2) *Height of horizontal ramus between P_4 and M_1* [= DEPTH OF JAW, O.] (as measured also by Tscherski and Osborn,— fossil Equidæ). Fig. 11, 6.

(3) *Height of horizontal ramus between P_2 and P_3* (as measured by Branco only). Fig. 11, 7.

Nehring.

(4) *Length of mandible* (as measured also by Tscherski, Salensky, Osborn,— fossil Equidæ) from condyle to base of central incisors. Fig. 11, 1.

(5) *Height of mandible* (as measured also by Tscherski, Salensky, Osborn,— fossil Equidæ) from condyle to base. Fig. 11, 2.

Tscherski.

(6) *Length of mandible* (as measured also by Nehring, Selensky, Osborn,— fossil Equidæ) from median incisive point to posterior outer edge of head of condyle. Fig. 11, 1.

(7) *Height of ascending ramus* (as measured also by Nehring, Salensky, Osborn,— fossil Equidæ) from head of joint perpendicularly to plane of table. Fig. 11, 2.

(8) *Width of incisive portion* [= WIDTH OF SYMPHYSIS, (2) Osborn] (as measured also by Salensky, Osborn,— fossil Equidæ). Fig. 11, 3.

(9) *Narrowest width* [= WIDTH OF SYMPHYSIS (1), Osborn] (as measured also by Osborn,— fossil Equidæ).

(10) *Height in region of space between P_4 and M_1* [= DEPTH OF JAW (1), Osborn] (as measured also by Branco, Osborn,— fossil Equidæ). Fig. 11, 6.

Salensky.

(11) *Length of lower jaw* (as measured also by Nehring, Tscherski, Osborn,— fossil Equidæ) from condyle to base of central incisors. Fig. 11, 1.

(12) *Height of lower jaw* (as measured also by Nehring, Tscherski, Osborn,— fossil Equidæ) from condyle to base. Fig. 11, 2.

(13) *Width of lower jaw* [= WIDTH OF SYMPHYSIS (2), Osborn] (as measured also by Tscherski, Osborn,— fossil Equidæ) at posterior alveoli of I_3. Fig. 11, 3.

(14) *Length of series of lower cheek teeth* along wearing surfaces (as measured also by Tscherski, Osborn,— fossil Equidæ); along bases (as measured also by Tscherski). Fig. 11, 8.

(15) *Length of diastema, I_3–P_2* (as measured also by Tscherski, Osborn,— fossil Equidæ). Fig. 11, 9.

II. DISTINCTIONS BETWEEN HORSES, ASSES, AND ZEBRAS.

Attention may be called to some of the distinctions between the skulls of horses, asses, and zebras as observed by the following authors: Branco (1883), Dugés (1898), Salensky (1907); with annotations by S. H. Chubb and J. K. Mosenthal, whose observations are enclosed in square brackets [ ]:

Branco, 1883:

Orbital dimensions.

Horse, longitudinal diameter greater than vertical.

Ass, longitudinal and vertical diameters nearly alike; vertical may be greater than horizontal.

[Very prominent, brow projecting laterally.]

Distance from m^3 *to a vertical line from the anterior border of orbit.*

Horse, not so great as in

Ass.

[Increases greatly with age.]

Distance from i^3 *to* i^3.

Horse, greater relatively than in

Ass.

Proportion of transverse and anteroposterior dimensions of Molars and Premolars.

Horse, transverse relatively less than in

Ass.

Shape of mandible.

There are two types of mandibles: (1) the horizontal ramus has a straight lower border, (2) the horizontal ramus has an indentation (Gefässausschnitt) in a line with m_3, which makes the ramus less high at this point.

Horse, both types occur.

Ass, generally has the latter type.

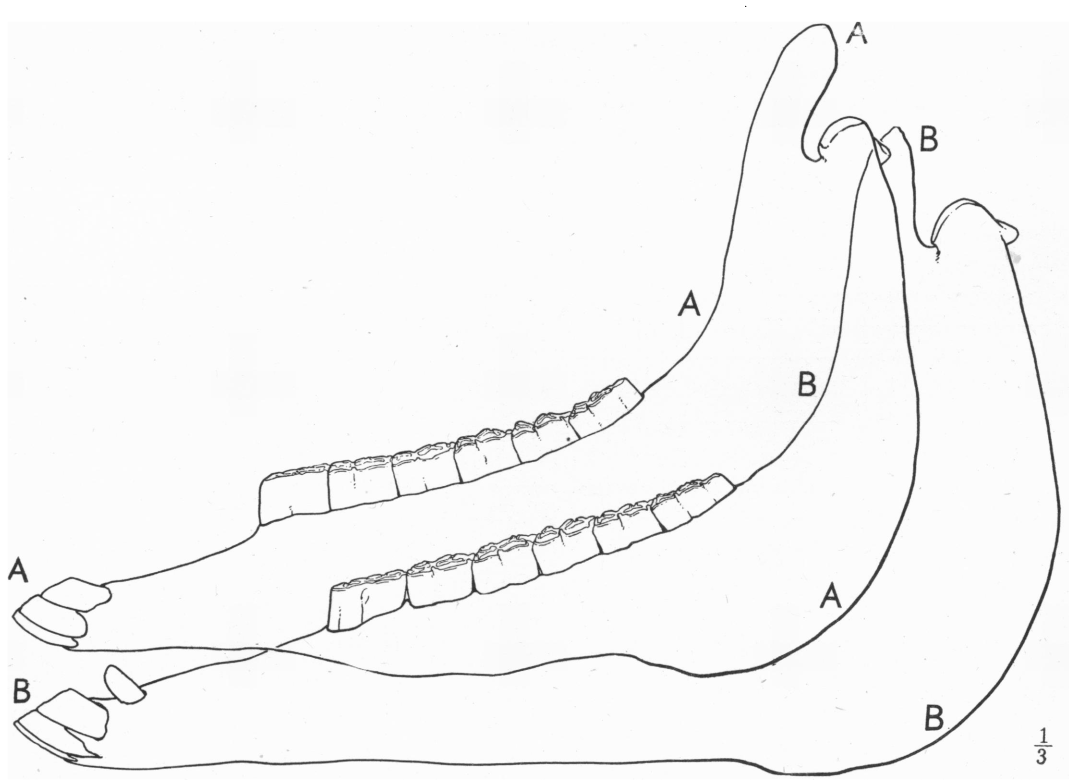

Fig. 12. Lower jaws of domestic ass (above) and horse (below), showing characteristic differences in lower border of horizontal rami (ass, Amer. Mus. spec. 15675; horse, Amer. Mus. spec. 16613).

Dugés, 1898:

Ass.
1. Well marked longitudinal convexity of forehead [valid].
2. Face short and high [valid].
3. Orbit subtriangular (its posterior border is straight) [see notes].
4. Vertical line, from occipital crest to plane of base of mandible, passes well behind condyles [see notes].
5. Occipital crest is prominent.
6. Line of Lesbre (through anterior end of maxillary crest and point just above external auditory opening) passes through occipital crest.
7. Upper molars lack the internal fold, 'pli caballin' of Lesbre.

Horse.
1. Forehead straight.
2. Face long and relatively narrow.
3. Orbit subcircular [see notes].
4. Vertical line (as above, No. 4) passes between condyles or touches them.
5. Occipital crest less prominent and continues curve of occiput.
6. Line of Lesbre (as above, No. 6) passes behind (below) occipital crest.
7. 'Pli caballin' very distinct.
   [Absence of 'pli caballin' extremely rare except in very old subjects.]

Note: drawings from Lesbre, 1892, Bull. Soc. Anthropol., Lyon, No. I. Cornevin, Lesbre, Piétrement, Gaudry, cited in Supplementary Note to Dugés article.

Salensky, 1907:

Franck's Index.

(1) distance from posterior edge of vomer to posterior edge of palate; (2) distance from posterior edge of vomer to foramen magnum.

(1) is greater in ass.

(2) is greater in horse.

[Not characteristic for Asiatic asses. Varies with species and within species of zebras.]

[Franck gives 9 characteristic differences between ass and horse skulls. Salensky and Tscherski consider them insufficient, with the exception of the above.]

Shape of nasals.

Horse, nasals narrow gradually anteriorly (wedge-shape).

Ass, nasals narrow rapidly anteriorly (club-shape).

Horse, naso-frontal sutures are two fairly high arches.

Ass, naso-frontal sutures are two almost straight lines.

Horse, posterior ends narrow anteriorly.

Ass, posterior ends increase in width anteriorly.

[Not characteristic for Asiatic asses.]

Naso-lachrymal suture.

Horse, a straight line, nearly parallel with long axis of skull.

Ass, lachrymal border concave.

[Not characteristic for Asiatic asses.]

Position of infraorbital foramen.

Horse, nearer naso-maxillary suture than in

Ass.

[By no means constant.]

Post-orbital process of frontal.

Horse, three-sided.

Ass, oval and compressed.

[In Kiang narrow.]

Height of skull at occiput, mandible included.

Horse, lower than in

Ass.

Length of diastema.

Horse, longer than in

Ass.

[Even shorter in Kiang.]

[Variable in Asiatic Asses.]

Shape of mandible.

Horse, inferior border smooth and straight.

Ass, inferior border curved and furnished with prominences; inferior border thicker than in horse; between horizontal and vertical rami a characteristic indentation.

[Very important.]

S. H. Chubb, 1911.

Mule:

Much closer to horse ♀ than to ass ♂.

Occipital crest horse-like, only slightly modified.

Nasal very close to horse though convexity in posterior third very slight. Well arched in central transverse section, though not quite so high as in horse.

Diastema very little shorter than in horse.

Lachrymal hardly differs from horse.

Kiang in very many points approaches horse rather than ass.

Horse:

Strong convexity in posterior third of nasals (profile aspect), not present, however, in Arabs.

Highly arched in central transverse section, coming low to meet maxillaries.

Ass:

Nasals, naso-premaxillary suture very short and high; premaxilla inserted well into nasal.

Kiang shows the opposite extreme. Suture is very low. Nasal process coming down to meet premaxilla, the horse being somewhat intermediate in this point.

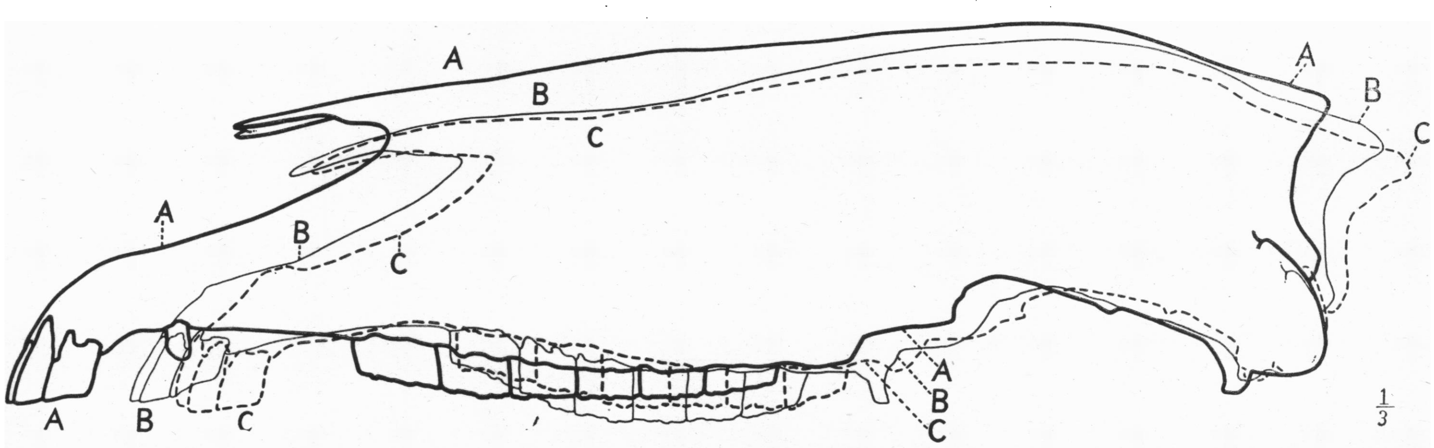

Fig. 13. Outlines of typical skulls of horse (heavy line), zebra (fine line), and domestic ass (dotted line), showing differences in occiput. The skulls are drawn so that the lines connecting the condyles and the median incisive border in each case coincide. The individuals represented are of approximately the same age (Horse, Amer. Mus. spec. 16613, Zebra, Amer. Mus. spec. 35153, Ass, Amer. Mus. spec. 15675).

Occiput Vertex Angle.

The outlines of the crania of the horse (A), the zebra (B), the ass (C) in Fig. 13 expresses the fairly constant differences in the proportions and profiles of these three types. It is especially designed to express the occiput-vertex angle, in which the horse is seen to be more perpendicular, the zebra intermediate, and the ass more retrocumbent.

This is set forth in the following measurements in a series of horses, asses, and zebras, in which it appears that the occiput vertex angle in the horse varies from 76.5° to 64°, while the ass varies from 60° to 52.5°. The averages are as follows:

Horse, average, not including *E. przewalskii*	= 70.33°
Zebra, average	= 61.35°
Ass, average	= 55.75°

Angle of Occiput and Vertex (Occiput-vertex Angle).

Horses:			
Pony (Texas, A. M. No. 166613)	Stage	8–5 years	76.5°
Horse (Indian Territory, A. M. No. 19173)	"	8–5 "	75.°
Horse (A. M. No. 16275)	"	9–15 "	74.5°

Horse (New Mexico, A. M. No. 15753)	Stage 9–1 years	73.°
Arab horse (Chubb No. 70)	" 8–8 "	70°
Horse (New York, A. M. No. 14131)	" 8–10 "	69°
Horse (Wyoming, A. M. No. 16279)	" 10–25 "	65.5°
Horse (New York, A. M. No. 14132)	" 9–15 "	65.5°
Horse (A. M. No. 15093)	" 9–15 "	64.°
E. przewalskii (hybrid, Chubb No. 71)	" 8–5 "	66.°
Horse, average, not including *E. przewalskii* = 70.33°		
Zebras:		
Burchell's Zebra (A. M. No. 35167)	Stage 8–5 years	65.5°
Burchell's Zebra (A. M. No. 35153)	" 9–15 "	63°
Burchell's Zebra (A. M. No. 14096)	" 3–1 "	62.5°
Burchell's Zebra (Chubb No. 47)	" 8–13 "	61°
Burchell's Zebra (Chubb No. 45)	" 6–4 "	61°
Burchell's Zebra (Chubb No. 46)	" 13 "	58.5°
Grevy's Zebra (Chubb No. 65)	" 5+–3 "	58°
Zebra average = 61.35°		
Asses:		
Mexican Burro (A. M. No. 13982)	Stage 5–2 years	60°
E. asinus from Soudan (A. M. No. 295)	" 4–1½ "	57°
E. asinus from Jamaica (A. M. No. 15675)	" 8–5 "	53.5°
E. asinus from Soudan? (A. M. No. 139)	" 11–over 30 years	52.5°
Ass average = 55.75°		

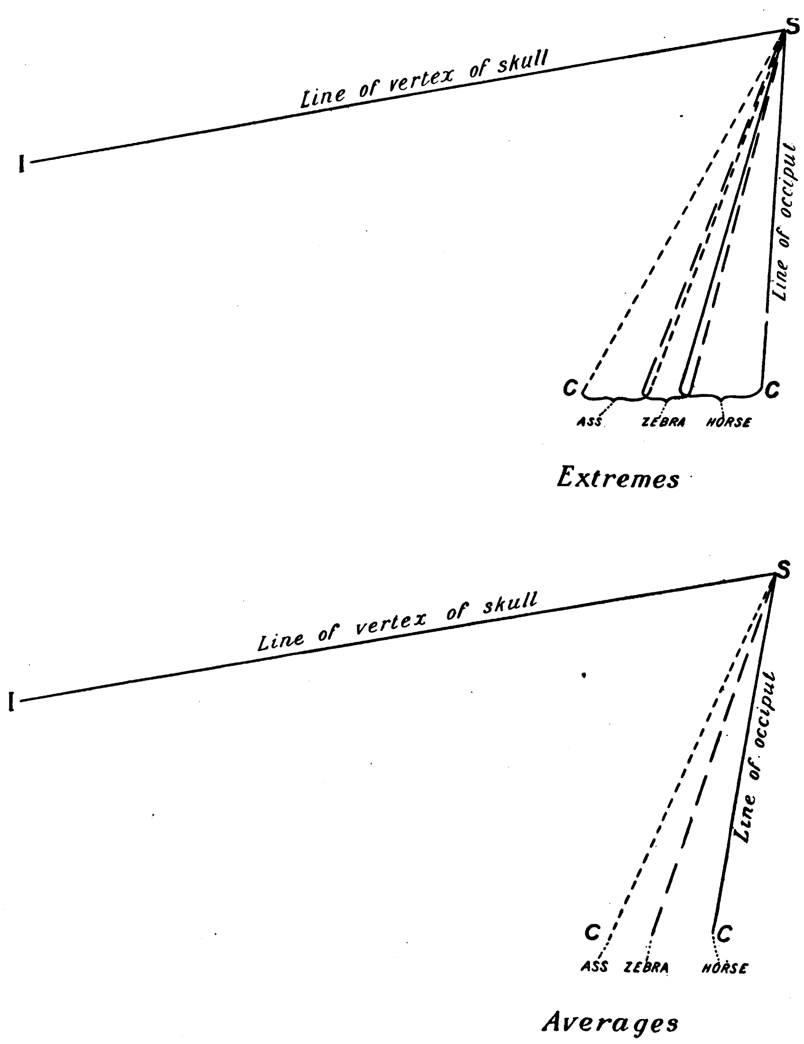

Fig. 14. Diagrams showing differences in occiput-vertex angle (see Osborn's system, No. 10) of skulls of horses, zebras and asses. Measurements were made on the skulls of ten horses of various breeds and ages, seven zebras (chiefly *E. burchelli*), and four domestic asses. The upper diagram indicates the largest and the smallest angle in each series of measurements. The lower represents the averages of all the measurements.

Naso-Frontal Sutures.

The accompanying diagrams exhibit the extreme variations in the forms of the naso-frontal suture in the horse (left) and in the ass (right). The middle figure represents the Grevy's zebra in which the fronto-nasal suture is seen to correspond closely with that of the ass although the elongate and narrow cranial proportions correspond with those of the horse.

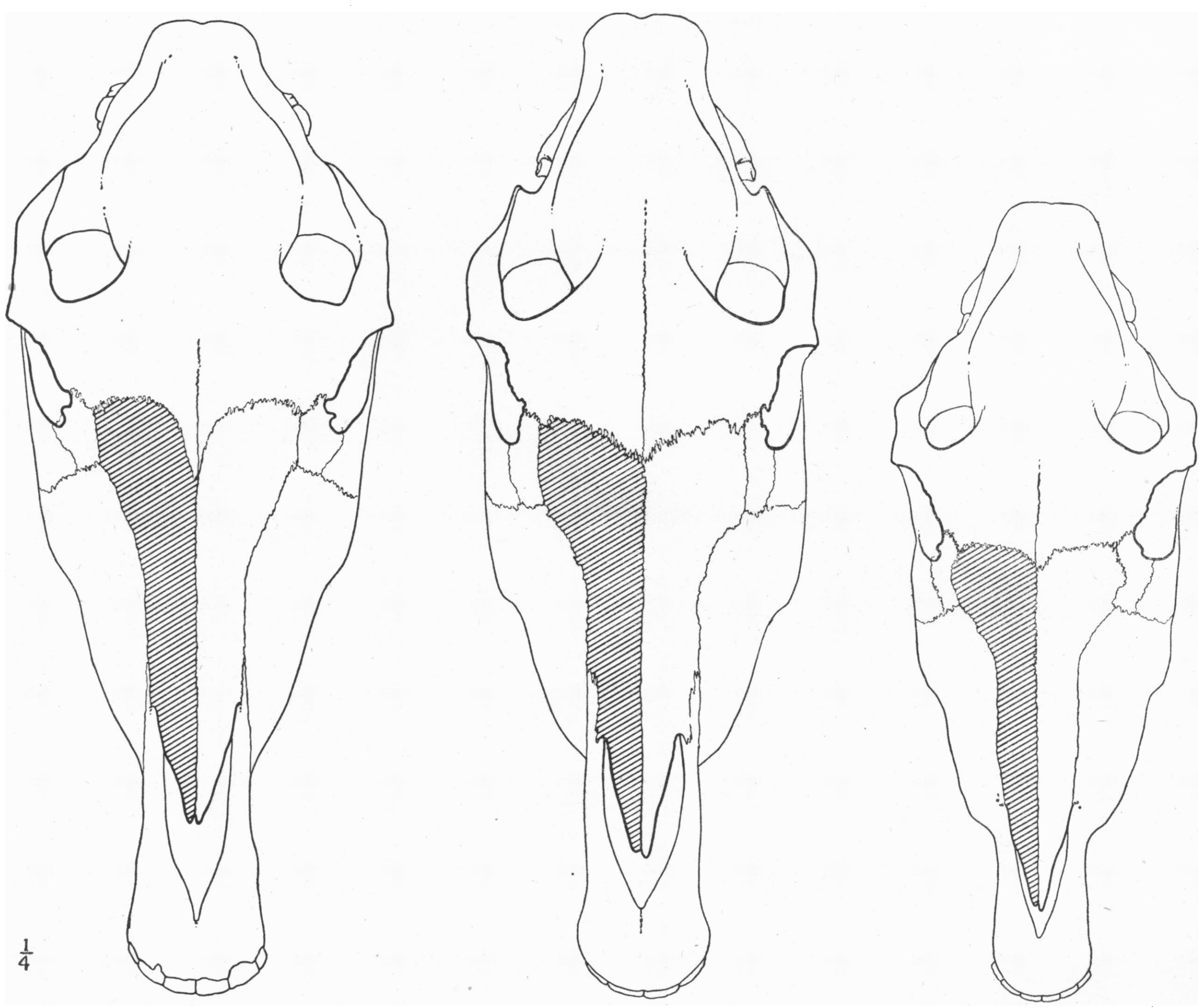

Fig. 15. Skulls of horse (left hand), domestic ass (right hand), and of zebra (center), showing characteristic differences in shape of nasal bones. Note unlikeness of fronto-nasal sutures and naso-lachrymal sutures in the two skulls (horse, Amer. Mus. spec. 16613; zebra, *E. grevyi*, Chubb No. 65; ass, Amer. Mus. spec. 13982).

III. CYTOCEPHALY, THE BENDING OF THE FACE ON THE CRANIUM.

Among the many authors who have more or less directly contributed to this subject are: Rütimeyer, 1882; Flower, 1891; Lankester, 1902; Ewart, 1907.

The whole literature and philosophy of this upward and downward deflection of the face on the cranium has not as yet been thoroughly reviewed by anyone. It appears that there is a general functional adaptation expressed in this deflection in which the following principles appear: (1) in young animals the palatal and cranial lines are more nearly in the same plane; (2) in certain animals the deflection increases rapidly with age; (3) a horizontal and upward deflection is generally characteristic of primitive browsing types; (4) the downward deflection of the face and palate is highly characteristic of certain grazing types.

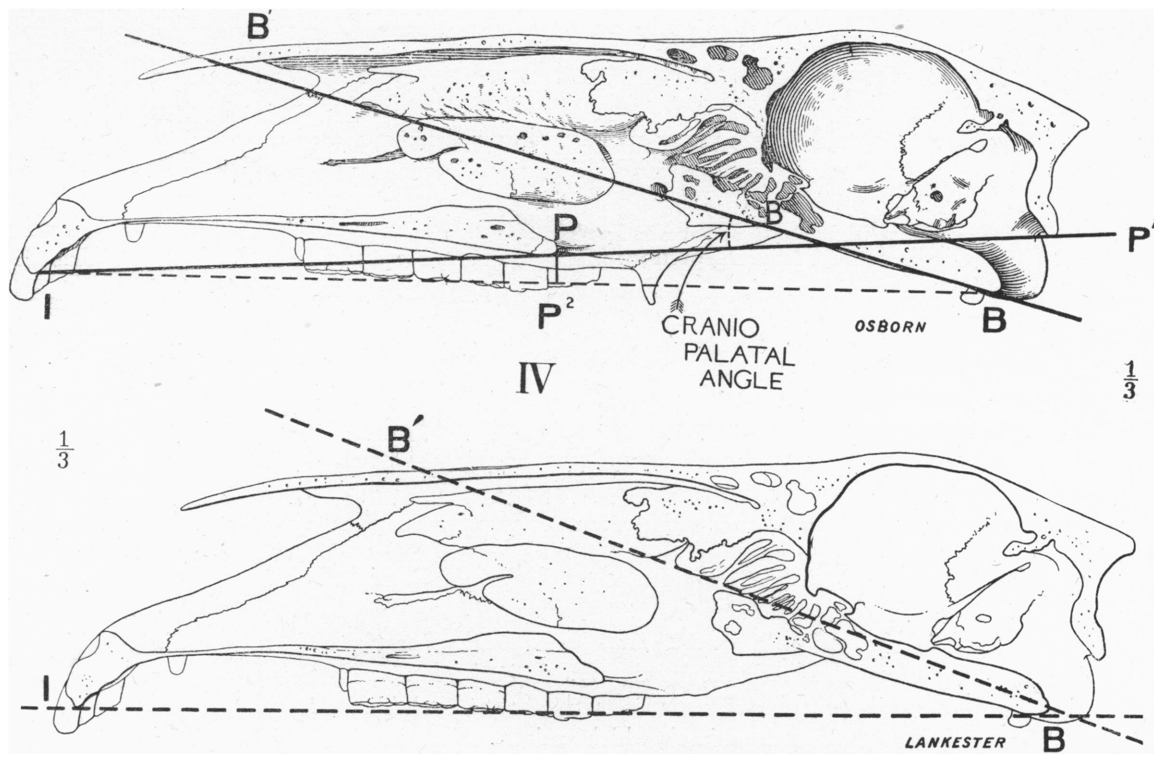

Fig. 16. Cytocephaly, modes of measuring cranio-palatal angle. Lower: Lankester's system. Upper: Osborn's system.

Rütimeyer (1882[1]) makes the following observations as to the deer (p. 12):

"The very much extended, almost cylindrical form of the skull is characteristic for Cervidæ. This is due chiefly to the uniformly horizontal axis of the skull, which rarely shows the deflection so conspicuous in most of the Cavicornia, either from their youth or appearing in the course of their later growth and development.

The straightness and cylindrical shape of the skull is most pronounced in the adult deer; but from the beginning the cranial portion of the skull is longer and flatter relatively than in the Cavicornia."

Lankester (1902) published a series of more extended observations suggested by his studies of *Okapia*.[2] In this paper are given figures of vertical longitudinal sections of skulls of giraffe, elk, waterbuck, domestic goat. For the facial plane a line is drawn connecting the anterior border of the premaxillaries and the foramen magnum. This line is called the 'palatine horizontal.'

His chief observations are as follows:

The skull of the Okapi, p. 285, is not only astonishingly long in the postorbital region, but it presents a great peculiarity in the fact that this region is in the same horizontal plane as the præorbital region. In fact, the basicranial axis and the basifacial axis of the Okapi's skull appear to lie nearly (not quite) in one plane. This is a primitive and unusual character. It is more or less retained by the genus Alces and others of the Cervidæ, where the planes of the two axes form a very open angle; but in the Bovidæ a much less obtuse angle is formed.....

The whole of the brain-case or postorbital region of the skull of the Bovidæ appears to be bent down as on a joint formed across the junction of the cranial and facial portions of the skull.

There is good ground, p. 286, for connecting the presence of the deflection of the cranial cavity, above noted, with the mechanical conditions arising from the use of horns having the position and direction of those found in the Bovidæ and the Giraffe. Even in the hornless females of certain Antelopes the deflection is maintained. The absence or small size of the deflection is almost certainly to be regarded within the group Pecora as a primitive character, and in the horizontality of the skull or tendency to coincidence of the basicranial and basifacial axis-planes the Okapi bears evidence of (1) being relatively primitive, (2) not having had horn-bearing forebears, (3) of being remote from the cavicorn stock.

[1] Rütimeyer, L. 'Studien zu der Geschichte der Hirschfamilie. I Schädelbau.' Verh. d. Naturforsch. Gesell. Basel, Bd. VII, pp. 3–61. Year on separate, 1882; on bound vol. of Verh. Nat. Ges., 1885.

[2] Lankester, E. Ray. 'On Okapia, a new Genus of Giraffidæ, from Central Africa.' Trans. Zool. Soc. London, Vol. XVI, Pt. VI, August, 1902.

Ewart (1907) first, to our knowledge, applied cytocephaly as a means of distinguishing various phyla of horses. His principal observations are as follows:

The extent to which the face is bent down on the cranium is made evident when outlines of photographs of side views of skulls are placed one above the other, and when the angle formed by the line of the palate with the basi-cranial axis is given.

The elk and sheep illustrate the two types of skull. The difference in these two forms is perhaps accounted for by the fact that the elk is a short-necked forest form adapted for feeding on shrubs and trees, *i. e.*, for holding the head in a nearly horizontal position, while the sheep is a denizen of the mountains, adapted for holding the head when feeding in a nearly vertical position.

There are excellent reasons for believing that a bent skull greatly facilitates feeding on very short herbage. In a sheep when feeding the grass is pressed by the sharp-edged lower front teeth against the hard pad attached to the upper jaw; and then the head is as a rule jerked rapidly forwards, with the result that the grass is severed partly by cutting and partly by tearing. In the Steppe variety of the horse the head instead of being invariably jerked forwards, is sometimes moved forwards, sometimes backwards, but more frequently from side to side.

If, as Lankester in his paper 'On Okapia' suggests, the deflection in Bovidæ and the Giraffe is connected with the use of horns, it should doubtless be regarded as due to the downward bending of the cranium on the face. If the deflection is connected with grazing, with feeding on short herbage close to the ground, it might be more accurate to regard it as due to the bending of the face on the cranium.

In the Forest variety the hard palate is nearly parallel with the basi-cranial axis, but even in such skulls the face is not in line with the cranium, for when a line is carried through the basi-cranial axis it emerges a considerable distance above the level of the incisors. In members of the Forest variety the face at birth is nearly as bent downwards as in adults of the Steppe variety. The reason may be that in animals which suck standing the necessary pressure on the mammary gland is more easily exerted on this account. Thus in the young giraffe the face is as much deflected as in fullgrown sheep and goats. But though the deflection may facilitate sucking it was probably originally acquired to facilitate grazing, which during the first year is very dfficult on account of the long legs and the short neck.

In the Steppe horse the face gradually unbends in the first year, so that the skull of a 15 months Prjevalsky resembles that of an adult Forest horse. During the second year the face begins to bend down again. Thus it repeats during its growth one of the most striking characters of its remote forest-haunting ancestors. Moreover, since the bending of the face has probably been effected very gradually (since forests and marshes were abandoned for a free life on open plains) it follows that the Steppe variety branched off from the common stem at a very remote period.

In *Neohipparion* of the Miocene, *Hipparion* of the Pliocene, and *E. scotti* of the Pleistocene, the face is strongly bent down on the cranium.

Cytocephaly in the Artiodactyla.

Extremes of Palatal Deflection. The accompanying figure (Fig. 17, bottom of diagram) illustrates the extreme range of adaptation as observed in the various Artiodactyla. The transition from the more horizontal to the more oblique position may be illustrated in the following genera.

Caribou, *Rangifer*, adult.
Moose, *Alces*, young.
Giraffe, *Giraffa*.
Barbary sheep, *Ammotragus tragelaphus*.
Hartebeest, *Bubalis*.

The Aoudad or Barbary wild sheep, *Ammotragus* (*Ovis*) *tragelaphus*, presents an extreme example of the progressive deflection of the palate, on the cranium with advancing age as shown in Fig. 17; also in the following succession of measurements:

At birth (average)	25.5°
Male (horns ½ in.)	30°
Male (horns 3 in.)	47°
Male (adult)	53.5°

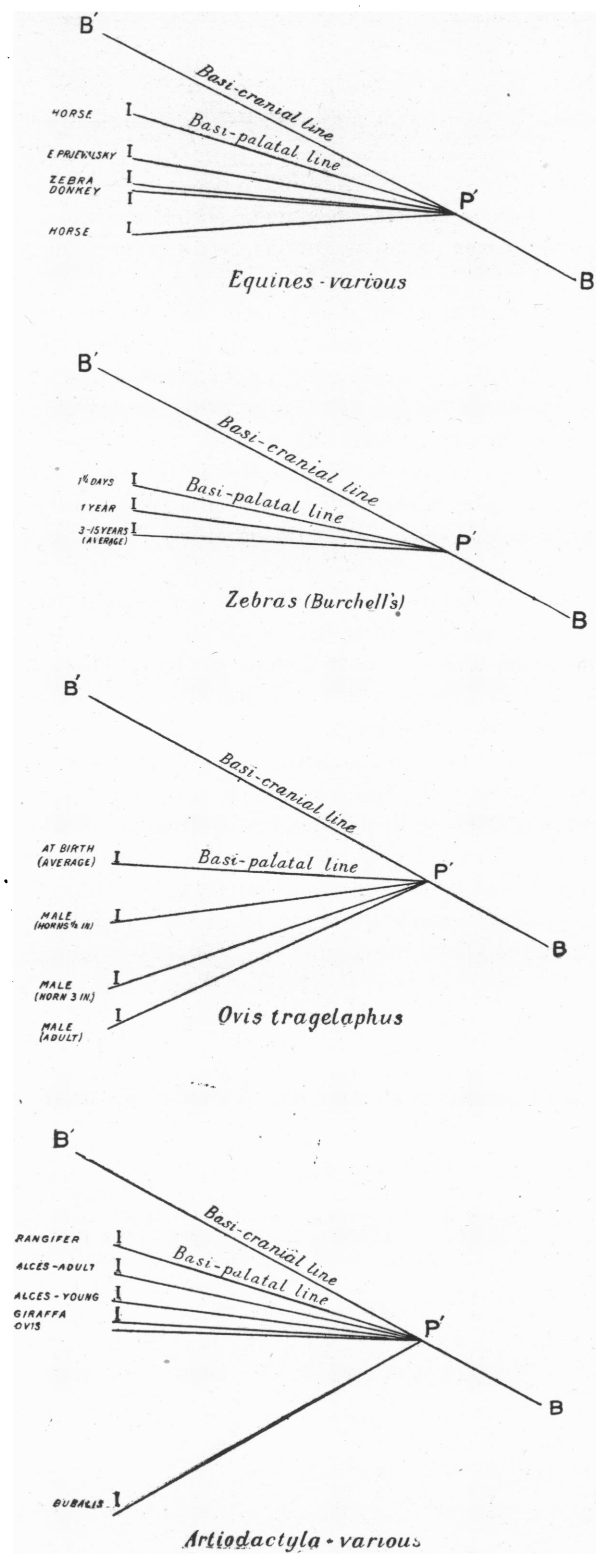

Fig. 17. ***Cytocephaly. Palato-cranial Angle in various Ungulates.***

I. Horses, Asses, Zebras. Various.
II. Burchell's Zebras. Growth stages, deflection increasing with age, 1–½ days to 15 years.
III. Aoudad, Barbary Wild Sheep. Growth stages, deflection increasing with age.
IV. Reindeer, moose, giraffe, sheep, hartebeest. Deflection characteristic of browsing (***Rangifer, Alces, Giraffa***) and grazing (***Ovis, Bubalis***) types.

Palato-Cranial Angle in Horses, Asses, and Zebras. Adults.

The existing common domesticated horses are polyphyletic, so that, as shown in Fig 17, I (top), they exhibit a range of deflection, or cytocephaly, which falls both above and below the elements presented by the Przewalsky, the zebra, and the ass. The averages are as follows:

Horse, not including *E. przewalskii*, average = 19.23°
Zebra, chiefly *E. burchelli*, " = 22.42

The range of variation is shown in the following table:

Horse:			
Percheron (Am. Mus.)	Stage	8+-about 10 years	10.°
Arab (Am. Mus.)	"	8-about 10 years	13.5°
Horse (New York, Am. Mus. No. 14132)	"	9–15 "	16.5°
Horse (Am. Mus. No. 16278)	"	9–15 "	17.°
Horse (New Mexico, Am. Mus. No. 15753)	"	3–1 "	18.5°
Horse (Indian Territory, Am. Mus. No. 19173)	"	8–5 "	20.°
Horse (Wyoming, Am. Mus. No. 16279)	"	10–25 "	20.°
Horse (New York, Am. Mus. No. 14131)	"	8+-about 10 years	21.°
Horse (Am. Mus. No. 16275)	"	9–15	21.5°
Horse (Texas, Am. Mus. No. 16613)	"	8-5 years	22.5°
Horse (Am. Mus. No. 15093)	"	9–15 "	31.°
E. przewalskii (Chubb, hybrid)	"	8–5 "	17.5°
Zebras:			
Burchell's Zebra (Am. Mus. No. 14096)	Stage	3–1 years	19.°
Grevy's Zebra (Am. Mus.)	"	5+-3 "	21.°
Burchell's Zebra (Am. Mus. No. 35153)	"	9–15 "	23°
Burchell's Zebra (A. M. No. 35167)	"	8–5 "	24.5°
Burchell's Zebra (Am. Mus. No. 45)	"	6–3½ "	25.°
Asses:			
Donkey (Mexico, Am. Mus. No. 13982)	Stage	5–2 years	20.5°
Donkey (Jamaica, Am. Mus. No. 15675)	"	5 "	23.°

Progressive Deflection with Age in Zebras. In a small collection of zebra skulls in the American Museum there appears to be evidence of progressive deflection of the palate on the cranium with advancing age as represented in Fig. 17, II, and in the following table of measurements, which, however, are less reliable because taken from different species.

Zebra, Burchell type (Chubb, No. 20)	Stage 1	36 hours old	= 15.5°
Zebra (Am. Mus. No. 14096)	" 3	3 months "	= 19.°
Zebra, Grevy's type (Chubb, No. 65)	" 5	3 years "	= 21.°
Zebra, Burchell type (Am. Mus. No. 35153)	" 8		= 23°
Zebra (Chubb, No. 47)	" 8	About 13th year	= 22.°
Zebra, Burchell (Am. Mus. No. 35167)	" 8		= 24.5°
Zebra (Chubb, No. 45)	" 6	About 4th year	= 25.°

IV. CRANIOMETRY AND ODONTOMETRY IN PALÆONTOLOGY.

In fossil skulls the *indices* lose value because the slightest degree of crushing or distortion seriously disturbs an index. Nevertheless the indices and ratios should be used wherever obtainable. Since fossil skulls and dental series are rarely complete or perfect, the palæontologist requires an additional series of detailed measurements of parts of the skull not needed by the zoölogist.

1. Measures of Equal Value in Recent and in Fossil Skulls where obtainable.

1. Vertex length
2. Basilar length
3. Frontal width
4. Cephalic index
5. Facial length
6. Facio-cephalic index
7. Cranial length
8. Cranio-cephalic index
9. Palatal index
10. Palato-cranial angle
11. Occiput vertex angle
12. Occiput height
13. Orbital index
14. Vomerine index
15. Naso-frontal suture
16. Diastema length
17. Muzzle width
18. Molar-premolar series length
19. Dental index
20. Molar index
21. Facio-cranial angle.

2. Jaw Measurements.

Identical with those in recent jaws.

3. Additional Measurements Desirable in Fossil Skulls.

22. *Zygomatic width, width across zygomatic arches.*
    This measurement in titanotheres and many other Ungulates is taken as a means of computing the general ratio between the width and length of the skull.
23. *Palatal length,* along the middle line from the incisive border to the posterior median line of the palate.
24. *Palatal width.*
    a. Between M^1 and M^1 of the opposite sides.
    b. P^2 and P^2 " " " "
    c. At narrowest point of the palate.
25. *Condylar width, i. e.,* width across the two occipital condyles at their widest part.
26. *Cranial depth,*
    a. Taken opposite posterior alveolus of M^1.
    b. Taken in a line opposite posterior alveolus of M^3.

4. Measurements of Dental Series.

The entire system of measurements of the superior and inferior dental series embraces: (1) the height and width of the crowns of each of the incisor teeth; (2) the vertical, antero-posterior, and transverse diameters of the crowns of the canine teeth; (3) the diameters and indices, antero-posterior, transverse, and vertical, of each of the grinding teeth. The entire series of measurements desirable in the grinding teeth is as follows:

18. *Molar-premolar* series (upper), P^2–M^3 (measured along the middle line of the wearing surfaces).
19. *Dental index,* as in recent skulls.
20. *Molar series,* total length (upper), measured along middle line of the wearing surfaces.
26. *Premolar series total length* (lower), P_2–P_4.
27. *Antero-posterior diameters of* P_2, P_3, P_4, M_1, M_2, M_3.
28. *Transverse diameters of* P_2, P_3, P_4, M_1, M_2, M_3 (measurements of lower teeth taken in same way as those of upper in every case).
21. *Premolar series total length* (upper), P^2–P^4 (measured along middle line of wearing surfaces).
22. *Antero-posterior diameters of* P^2, P^3, P^4, M^1, M^2, M^3 (measured along middle line of wearing surfaces).
23. *Transverse diameters of* P^2, P^3, P^4, M^1, M^2, M^3 (greatest diameter taken exactly at right angles to middle line of tooth). Approximately the same as Gidley, who measures across mesostyle and posterior half of protocone.
24. *Molar-premolar series total length* (lower), P_2–M_3.
25. *Molar series total length* (lower).

The index of each grinding tooth, that is, the ratio of the transverse to the antero-posterior diameter, is extremely important as indicative in certain mammals of the dolichocephaly and brachycephaly of the skull. In certain titanotheres, for example, we obtain 'brachycephalic indices' of each of the grinders where the width equals or exceeds the length of the grinder; also 'dolichocephalic indices' of single teeth where the length exceeds the width of the grinder.

In the horses it is extremely important to observe a fact pointed out by Gidley (1901[1])

[1] Gidley, J. W. 'Tooth Characters and Revision of the North American Species of the Genus Equus.' Bull. Amer. Mus. Nat. Hist., Vol. XIV, Art. IX, May 31, 1901, pp. 91–142.

and overlooked by Ewart, namely, that the ratios of the two diameters change with the degree of wear. Gidley observes: "Thus in the little worn condition of these teeth in a young horse especially before the teeth have worn to that stage where the transverse diameter is greatest, the antero-posterior diameter is always greater than the transverse. As the crown wears away, the antero-posterior diameter diminishes and a stage is reached where the two diameters are about equal, then, as the antero-posterior becomes still more shortened the transverse exceeds it."

Gidley's observations on *Equus* are so important in the practice of odontometry that it appears desirable to reprint his statement as a whole (*op. cit.*, pp. 96–103).

(II). *Effects of Wear on the Proportions of the Teeth.*

1. The Teeth Taken Individually.

Unlike the degree of complexity of the enamel foldings, the corresponding diameters are affected differently by wear in different teeth of the molar-premolar series. The same general rule for the change in ratio of the antero-posterior to transverse diameter may be applied to the intermediate teeth p^3 to m^2 inclusive, but the most anterior and posterior teeth (p^2 and m^3) are affected differently, in this respect, from the intermediate teeth of the series and from each other as well.

a. Laws Governing the Changes of Diameters of the Tooth Crowns.

There seems to be no exception to the following laws for the changes of diameters of the tooth crowns as they are worn away by use.

TABLE I. MEASUREMENTS ON THE TRITURATING SURFACES OF THE UPPER TEETH OF EQUUS CABALLUS AND EQUUS ASINUS.

	Description.	Approximate age.	Catalogue Number	Diameters in mm.[1]						
					p^2	p^3	p^4	m^1	m^2	m^3
Series 1.	*Large draught Horse* ♀	5 years	16274	Antero-posterior	40	32	30	30	30	29
				Transverse	27	28.5	27.5	27	26.5	21.5
				Antero-posterior, Protocone	11	14.5	15	13.5	15.5	16
	" " " ♂	8 "	14131	Antero-post	36.5	29	28	25.5	25.5	29.5
				Transverse	25.5	28	27	26.5	26	22
				Antero-post., Protocone	10.	13.5	14	13	15	16
	" " " ♂	15+ "	289	Antero-post	38.5	29.5	28.5	24	25	30
				Transverse	23	27.5	28	26	25.7	22.5
				Antero-post., Protocone	9.3	13	13	11.5	12.5	12.8
	" " " ♂	12+ "	No number	Antero-post	40	30.5	30	27	27	29
				Transverse	28	30	28.5	28	26.5	23
				Antero-post., Protocone	10	14	14	13	13.5	13
Series 2.	♀	20 ± years	16277	Antero-post	36	26	25	21.5	21.5	30
				Transverse	24	26.5	27	25	25	22.5
				Antero-post., Protocone	9	10	11	10	12.5	14.5
	♂	20 ± "	16275	Antero-post	33.5	25.5	25.5	22.5	23.5	26.5
				Transverse	23	26.3	26	25	25	23
				Antero-post., Protocone	10	12	13.5	13.5	15	14
	Thoroughbred ♀	6 "	Loaned by C. R. Knight	Antero-post	33.5	27.5	28	25	25.5	27.5
				Transverse	25	26.5	26.5	25.5	25	21.5
				Antero-post., Protocone	8.5	13	13.5	13.5	13.5	15
	Texas Pony ♂	7 "	No number	Antero-post	35	28	26	24	24.5	28.5
				Transverse	23	25.5	25	25	24	21.5
				Antero-post., Protocone	8	10.5	10.7	10.5	10.5	11
Series 3	*Domestic Ass* ♀	5 years	15675	Antero-post	33	26	25	22	23	23
				Transverse	24.7	25	24	22.5	22.5	18.5
				Antero-post., Protocone	6.5	9.5	10.5	8.5	9.5	10.5
	Mexican Burro ♂	6 "	No number	Antero-post	31	24.5	23.5	21.5	21.5	22
				Transverse	23	24.3	24	23.3	21.5	18
				Antero-post., Protocone	6.5	8.5	9	9	9	10.5

[1] In every case the transverse diameters were measured across from the exterior ridge of the mesostyle to the exterior wall of the posterior lobe of the protocone, exclusive of cement.

[Total length of three of the above skulls are as follows: No. 16274, 604 mm.; No. 14131, 573 mm.; Texas Pony, 515 mm.]

(1) The *antero-posterior* diameters of the grinding surfaces of all the intermediate teeth are greatest at the stage when the tooth has just fully come into use, that is, when about one-half of an inch, or less, of the crown has been worn away; from this point the antero-posterior diameter diminishes very rapidly for a short distance and then continues to diminish more gradually to the roots of the tooth.

(2) The antero-posterior diameter of the first premolar (p^2) remains about the same for the whole length of the crown, except that sometimes it narrows slightly near the roots.

(3) The antero-posterior diameter of the last molar (m^3), however, is relatively small at first, and increases continually as the tooth is worn away.

(4) When the teeth first come into use the *transverse diameters* of all the teeth of the series are quite narrow, owing principally to the rapid incurving of the ectoloph; this diameter increases very rapidly for about one-half to three-fourths of an inch, but from this point to the roots of the teeth the transverse diameters of p^3 to m^2 inclusive remain about the same, diminishing slightly near the roots; p^2 gradually diminishes while m^3 increases in transverse diameter as the crown wears away.

(5) The antero-posterior diameter of the protocone in all the teeth of the series remains the same for the whole length of the crown.

(6) The antero-posterior or long diameter of the incisors diminishes with age while the transverse diameter increases.

b. *Effect of Wear on the Relative Measurements of Tooth Crowns.*

(1.) *Ratio of the antero-posterior to the transverse diameter.*

It will be seen from the foregoing that owing to the very slight variation of the transverse diameters of the crowns of p^3 to m^2 inclusive, for almost their entire length, and to the great shortening of their antero-posterior diameters, the ratio of these diameters in these teeth is very different in old and in young individuals of the same species. Thus in the little worn condition of these teeth in a young horse, especially before the teeth have worn to that stage where the transverse diameter is greatest, the antero-posterior diameter is always greater than the transverse. As the crown wears away, the antero-posterior diameter diminishes and a stage is reached where the two diameters are about equal, then, as the antero-posterior becomes still more shortened, the transverse exceeds it. In every series this variation in ratio seems always to be most advanced in m^1 and m^2. This is evidently due not only to the order in which the teeth of the horse come into use, whereby the first to appear would at a given stage be most worn, but also, as is shown by an examination of Table I (p. 98), because the range of reduction of the antero-posterior diameters is greater in the molar than in the premolar teeth. M^1 is always the most advanced, as it comes into use before any of the others of the permanent set.[1]

(2.) *Ratio of antero-posterior diameter of the protocone to the antero-posterior diameter of the crown.*

The antero-posterior diameter of the protocone, being, like the transverse diameter of the crown, practically unchanged through wear, also holds to the ever-changing antero-posterior diameter of the crown in the old and much worn tooth a very different relation from what it did when the tooth first came into use. Thus, it may happen that in a little worn tooth the antero-posterior diameter of the protocone is *much less than half* that of the entire crown, but may become *greater than half* this diameter when the tooth has become much worn in consequence of this shortening of the antero-posterior diameter of the crown.

2. On the molar-premolar series as a whole.

The shortening of the antero-posterior diameters of all the other teeth in the series, except p^2, is not nearly compensated by the lengthening of this diameter in m^3, hence it results that the series, as a whole, becomes much shortened and the teeth from behind crowd forward toward p^2 which retains the same relative position in the skull, so that m^3 shows the greatest displacement and the discrepancy in length is all taken from the posterior end of the series. The gap which would otherwise be left in the maxillary bone behind m^3 becomes gradually filled in with a new growth of bone, as the teeth shift forward, leaving a flattened ridge which is continuous with the rugose prominence or ridge which marks the posterior extension of the maxillary bone beyond m^3; hence the length of this posterior extension of the maxillary depends principally upon the age of the horse. In passing from the young to the old stage, there is also a marked change in the relative position, with respect to the molar teeth, of the anterior projection of the maxillary ridge, the post-palatal foramina, and the anterior projection of the post-palatal notch,— all appearing relatively more posterior in the old individual. . . .

b. *Effect of individual variability on dimensions of the teeth.*— It has been shown under the topic of age variations that the transverse diameters of all the superior molars and premolars, except p^2 and m^3, the antero-posterior diameters of the protocones of all the teeth and the antero-posterior diameter of p^3 are measurements which change but slightly for

[1] The order of appearance or eruption of the permanent teeth of the large species from Texas (*E. scotti*) is the same as Owen has given for *E. caballus*, and is: first, m^1, second, m^2, third, p^2, fourth, p^3, fifth, p^4, sixth, m^3. This is probably the order in all other fossil species of this genus.

much the greater length of the crown; hence, unless specimens of the same age are taken for comparison, it is in these measurements that one should look for evidence of individual variability. Careful measurements of the teeth of more than ten specimens of *E. caballus* have led to the following conclusions: (1) The transverse diameters of the corresponding teeth for p^3 to m^2 inclusive are remarkably constant, especially in skulls of nearly the same size; the greatest difference in a certain series of four skulls of large draught horses examined not exceeding 2.5 mm., and in another series of three skulls belonging to animals about the size of carriage horses being less than 1 mm. (See table of measurements, p. 98).

The transverse diameters of m^2 of the large series vary only .8 mm., while in the small series all the transverse measurements for this tooth are the same. The greatest difference in the transverse diameter of m^2, including both series of skulls, is only 1.5 mm., and adding a skull of the Texas pony to the list the extreme difference between the transverse diameter of m^2 of this whole lot of skulls, ranging in size from the large draught horse to the small Texas pony, is only 2.5 mm. It will be seen by reference to the table of measurements (p. 98) that the average variation of the corresponding transverse diameter for all these teeth is very small considering the great difference in size of the animals represented.

It seems reasonable that much greater variations of the comparatively constant characters of the teeth would be found in *E. caballus* than in the extinct species, since in this species domestication and breeding have caused such a very wide range in size and proportions of the individuals; hence, when, in two lots of fossil horse teeth, the difference between the transverse diameters of corresponding teeth is on the average greater than that between the large and small varieties of *E. caballus*, it would seem that the teeth of the two lots could scarcely belong to the same species, and although the character of size, alone, could hardly be considered sufficient ground for establishing a species, yet where this difference exists, it seems reasonable to expect that when skulls which represent such two lots of teeth are known, other differences will be found which will clearly mark them as distinct species.

It has been shown that the antero-posterior diameter of the protocone is very little affected by wear; Table I (p. 98), makes it clear, however, that the range of individual variability of this diameter is very great, and cannot be depended upon as a distinguishing character even in corresponding teeth of individuals of the same size.

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