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Article III.—STUDIES IN COMPARATIVE MYOLOGY AND OSTEOLOGY, NO. V.—ON THE ANATOMY OF THE PREORBITAL FOSSÆ OF EQUIDÆ AND OTHER UNGULATES

By W. K. Gregory

Plate XVIII

CONTENTS

INTRODUCTION

In certain extinct Equidæ (Pl. XVIII) there are two fossæ on the side of the bony face in front of the orbit. The upper one of these is partly on the lacrymal bone and has therefore been called the "lacrymal fossa" by Gidley (1906) and Osborn (1918). The lower one, when present, is located partly on the anterior part of the malar and is therefore termed by Gidley and Osborn the "malar fossa." Each of these fossæ differs widely in the genera and species of fossil Equidæ, and have therefore been used by systematists as generic and specific characters.

Concerning the function of the upper, or "lacrymal," fossa, the older interpretation was that of Gaudry (1862), Lydekker (1884, pp. 13, 14) and others, who thought that it served to hold a "larmier" or facial gland, similar to that of ruminant artiodactyls. Another explanation was that of Prof. Studer (1911, p. 109), who held that the "preorbital groove" of certain extinct hippoids was essentially similar to

that of mammals having a proboscis, and that the groove served to lodge the levator muscles of a proboscis, with which he supposed *Onohippidium* and *Hipparion proboscideum* to have been provided. A third explanation was tentatively considered by Professor Osborn, who in conversation with me suggested that the preorbital groove might have lodged a backward extension of the nasal diverticulum, a structure which is vestigial or reduced in modern Equidæ. Professor Osborn also invited me to investigate the subject and generously placed at my disposal the great collection of recent and fossil horses in this Museum. A fourth explanation, advanced by Dr. W. D. Matthew, was that the development of the preorbital fossæ was correlated with the upraising of stiffening ridges and eminences above and below the fossæ and with the hollowing out of the parts not so strengthened.

The main conclusions at which I have arrived may be briefly summarized as follows:

(1) The upper, or "lacrymal," fossa probably did not lodge a "larmier" or facial gland, nor did it serve for the muscles of the snout; nor did *Onohippidium* and *Hipparion proboscideum* have a proboscis or anything like it. On the contrary, the fossa in question probably did lodge a greatly enlarged nasal diverticulum as suggested by Professor Osborn.

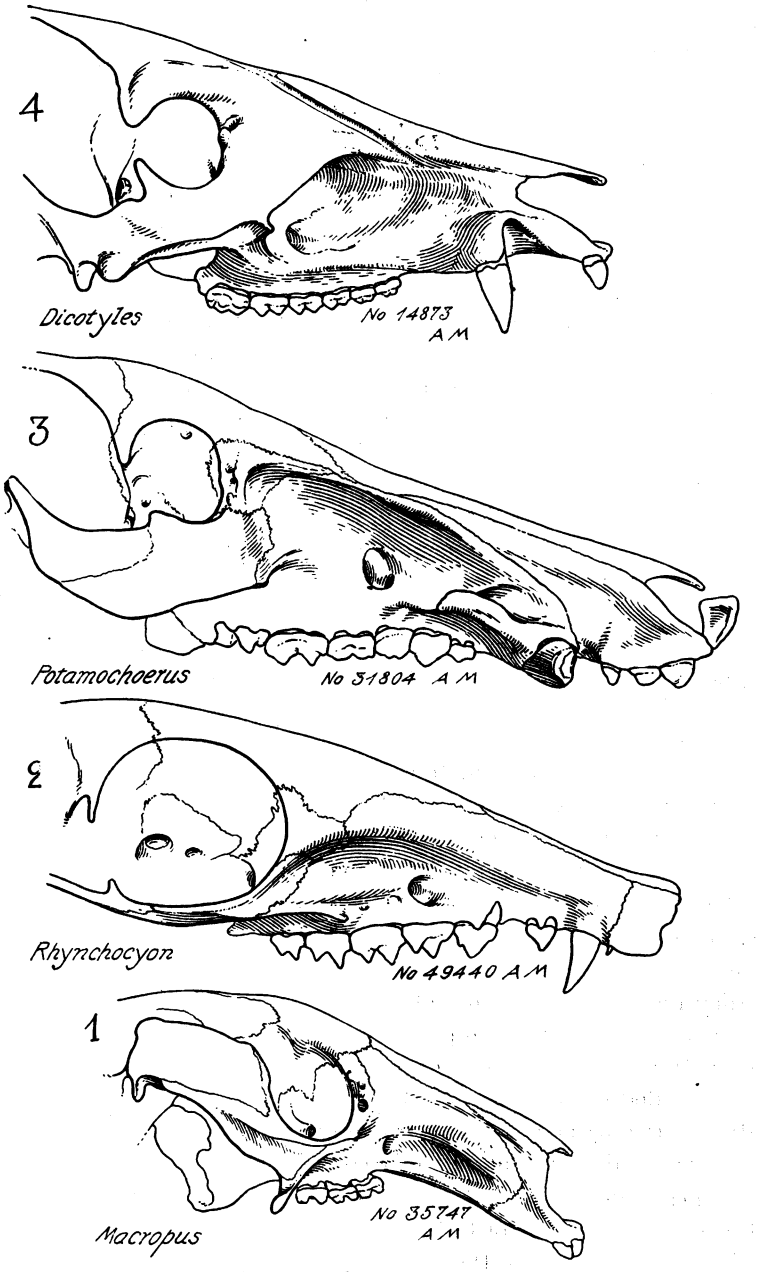
(2) The lower or "malar" fossa, when present, lodged the proximal end of the "maxillo-labialis superior," or levator labii superioris, muscle.

(3) The existence of these and of similarly placed fossæ in other ungulates is also partly conditioned by the further subsidence of certain depressed areas lying between areas or tracts that have been upraised or strengthened to resist stresses and partly by the lack of support beneath the subsided areas, due to the presence of great underlying sinuses in the maxilla, malar, and lacrymal bones.

Mr. S. H. Chubb and Mr. Erwin S. Christman have taken great interest in the present investigation and have assisted greatly by their critical comments and observations. The illustrations are by Mr. Christman.

THE PREORBITAL FOSSÆ OF *RHYNCHOCYON* AND THE SUIDÆ

Early in the course of the present investigation I thought that the preorbital fossa of *Rhynchocyon* (Fig. 2) and the Suidæ (e. g., *Potamochœrus*, Fig. 3) was more or less analogous with that of such extinct Equidæ as *Merychippus* (Pl. XVIII) and that a study of its function in the first two might give a clue to its function in the latter. In *Rhynchocyon* and the Suidæ (Fig. 5) the fossa in question lodges the muscles of the



Figs. 1-4. Preorbital fossæ of various mammals.

1. *Macropus.* Skull of a very old kangaroo, with a deep fossa in front of the infraorbital canal. This fossa lodges a part of the buccinator muscle which also extends up on the side of the face beneath the superficial muscles. (Von Boas and Paulli, 1908, Pl. XIII.)
2. *Rhynchocyon.* The preorbital fossa lodges the muscles of the long snout.
3. *Potamochœrus.* The preorbital fossa, for the muscles of the snout, is sharply defined above and leads directly forward toward the protruding snout.
4. *Dicotyles.* The preorbital fossa and snout muscles are much shorter anteroposteriorly than in *Potamochœrus.*

snout (the "maxillo-labialis superior" and "maxillo-labialis inferior") and the inference was that the preorbital fossæ of Equidæ probably also lodged homologous muscles. I afterward found that Professor Studer (1911, pp. 199, 200), arguing from similar grounds, had reached a similar conclusion with regard to the preorbital fossæ of *Hipparion proboscideum* and *Onohippidium*. Nevertheless, I was later compelled to reject this conclusion for the following reasons.

First, it can be shown conclusively that the fossæ in question in the Equidæ arose within the family and are not truly homologous with those of Artiodactyla, that there were no such fossæ in the primitive placental mammals of the Paleocene and Eocene, and that the Artiodactyla and Perissodactyla were not derived from a common stem family but are widely distinct orders. Hence, it is not permissible to assume that non-homologous fossæ in these two widely separated groups arising in different ways were yet filled by homologous structures.

Secondly, the preorbital fossæ in Suidæ (Figs. 3, 4), as well as in *Rhynchocyon* (Fig. 2), are associated with a tapering bony muzzle and a cylindrical protruding snout. Such characters certainly may not be assigned to *Pliohippus lullianus* (Pl. XVIII) which, although it had deep preorbital fossæ, is very close to a modern horse in the bony supports of the muzzle.

Thirdly, the preorbital fossæ in Suidæ lead forward toward the snout, whereas in the Equidæ (Pl. XVIII), when well developed, they are produced forward and downward toward the diastema between the canine and the first premolar.

Finally, as will be shown below, the conclusion that the preorbital fossæ of extinct Equidæ functioned, as in Suidæ, solely to lodge the muscles of the snout is at variance with the far more direct evidence afforded by the soft anatomy of existing Equidæ. And it is shown by experience that in all attempts to reconstruct missing parts either of a given extinct animal or in a phylogenetic scheme, the more direct evidence afforded by apparently homologous parts or conditions in closely related types outweighs in value the more indirect evidence derived from widely removed types and possibly convergent conditions.

Hence, I do not regard it as safe to pass from the known function of the preorbital fossæ of Suidæ to the unknown function of possibly non-homologous fossæ in the Equidæ, although other and more reliable evidence has convinced me that the preorbital fossæ of Suidæ are functionally analogous in part only with the lower preorbital, or "malar," fossæ of certain Equidæ. In the Suidæ the preorbital fossæ lodged both

the maxillo-labialis superior and the maxillo-labialis inferior, while in the Equidæ the latter muscle was entirely below the fossa and was attached to the anterior end of the masseteric ridge (Figs. 9, 19, and Pl. XVIII).

THE LOWER OR "MALAR" FOSSÆ OF THE EQUIDÆ

In recent horses (Figs. 9 to 12 and Pl. XVIII, *Equus*) there is, on the side of the face in front of the orbit, a muscle called the maxillo-labialis superior by von Boas and Paulli and the levator labii superioris by other authors. This runs from the side of the maxilla immediately above the masseter ridge obliquely forward and upward into a long, thin tendon which, passing the anterior tip of the nasal bones and joining its fellow of the opposite side, is prolonged forward in the midline above the nostrils and downward to the upper lip. About the middle of its course, and well behind the notch between the nasals and premaxillæ, the muscle in question passes immediately above the infraorbital canal (Pl. XVIII, *Equus caballus*). A line drawn just below the tip of the nasals, through the upper border of the infraorbital canal and continued back to the lacrymal above the masseter ridge, will always give the general course of this muscle in recent Equidæ.

In many skulls of horses, zebras, and asses preserved in the large collection made by Mr. Chubb for this Museum, there is a slight depression, or fossa, at the site of the origin of the maxillo-labialis superior (Fig. 12 and Pl. XVIII, *Equus*). In many fossil Equidæ there is a more or less well-defined fossa at this point. Sometimes, as in *Protohippus niobrarensis*, the lower, or "malar" fossa is but slightly indicated; in other specimens it is very deep (*Pliohippus lullianus*); and in still others it is barely visible (*Kalobatippus*). I conclude that, although this lower fossa is more or less variable, it always marks the site of origin of the maxillo-labialis superior, which, as shown by the whole configuration of the fore part of the skull, must have been located substantially as in modern Equidæ. (See Plate XVIII.)

Considerable difficulty was caused for a long time by the fact that in extinct Equidæ this lower fossa is often confluent with the upper or lacrymal fossa (Pl. XVIII, *Pliohippus lullianus*, *Merychippus*, *Parahippus*) and that the two together sometimes bear some resemblance to the preorbital fossa of the Suidæ and of other mammals having strongly developed muscles of the snout.

A second difficulty arose from the fact that some extinct Equidæ (*Hypohippus*, *Miohippus*) have but a single preorbital fossa, and

at first it was very difficult to determine whether this was the homologue of the upper fossa only or of both fossæ together. Comparison of these cases with that shown in *Archæohippus ultimus* indicates that in them it is only the upper, or "lacrymal," fossa which is present and that the lower fossa has not yet been formed, as in *Miohippus* and *Hypohippus*. (See Plate XVIII.)

When examined in detail, the preorbital fossæ of Equidæ differ in many particulars from those of mammals of other orders, and, as stated above, it finally seemed an unwarranted begging of the question to assume that they were occupied by homologous structures in widely different orders. It was finally realized that the safest criteria for the interpretation of fossil Equidæ were afforded by recent Equidæ and to some extent by members of other families of the same order. Comparison with recent Equidæ leaves practically no doubt that the function of the lower fossa was the lodgement of the maxillo-labialis superior; but, as this fossa is very variable among recent Equidæ in its occurrence and degree, while the muscle is constant both in occurrence and position, we may be sure that in extinct Equidæ the absence of the fossa does not imply the absence of the muscle at that point, especially since the form of the nasals and premaxillæ were extremely horse-like in all these Equidæ.

THE UPPER OR "LACRYMAL" FOSSA OF THE EQUIDÆ

The "Lacrymal" Fossa not a "Larmier"

Lydekker, in his description of *Hippotherium antilopinum* (1884, pp. 13, 14), describes two preorbital fossæ; the first, designated by Lydekker as "B," is homologous with the so-called "lacrymal" fossa of Osborn and the second (Lydekker's "A") is homologous with the "buccinator" fossa (Fig. 12) of the present paper.

After noting that Gaudry (1862, p. 221) had called the fossa "B" a "larmier" Lydekker says:

> The smooth form of these cavities in the Perim skull (*H. antilopinum*) leaves little or no doubt that they once contained a sebaceous gland, like the 'larmier' of the deer and antelopes. In all deer and in most antelopes the larmier is single, and placed almost entirely in the lachrymal; having of course no connection with the infra-orbital foramen. In some antelopes, however (e. g., *Cephalopus maxwelli* [sic], and *C. pygmæa*)[1] a similar cavity is present in the maxilla, which sometimes coexists with the lachrymal cavity, and sometimes replaces it. "In the African waterhogs (*Potamochærus*) a naso-maxillary pit opens between the eye and the snout, rather nearer the eye."[2] In *Oreodon*[3] there is a single cavity which is confined to the lachrymal.

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[1]See Owen, Anatomy of Vertebrates, III, p. 633.
[2]Owen, *op. cit.*, p. 634.
[3]Gaudry, Les Enchainements—Mam. Tert., p. 81, fig. 90.

These observations indicate pretty clearly that the maxillary cavities of *Hippotherium* are homologous with those of the Artiodactyla; and are very noteworthy as being one of the very few evidences among the later forms of an original connection between the artiodactyle and perissodactyle modifications of the Ungulata.

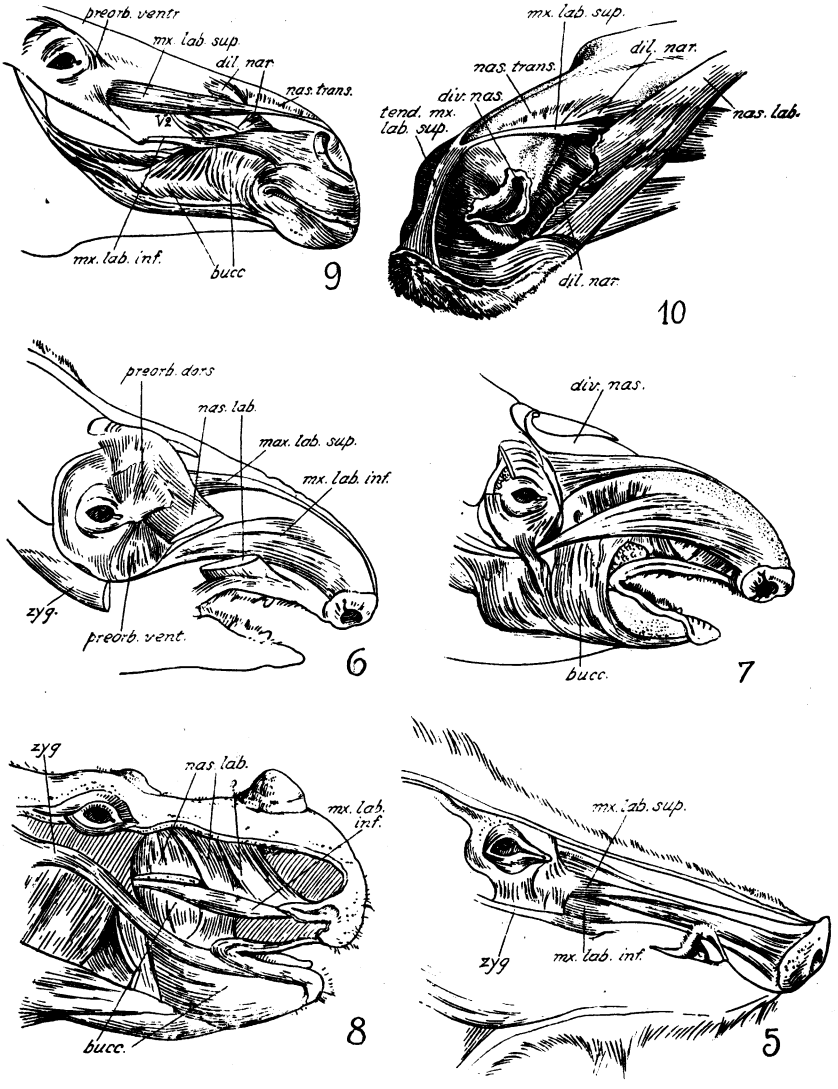
Notwithstanding these conclusions by Lydekker, I am led to believe that the "lacrymal" fossa of extinct Equidæ did not lodge a sebaceous gland like the "larmier" of the deer and antelopes. The fossa in question is extremely different in form from that which contains the "larmier" in ruminants and oreodonts, as shown in figures in my recent paper on the lacrymal region of mammals. The true "larmier" fossa is more or less circular in form and is bounded by a well-defined rim. The "lacrymal" fossa of extinct Equidæ, on the other hand, is totally different in appearance and is often continued forward and downward (Pl. XVIII) toward the buccinator fossa.

The "Lacrymal" Fossa not for the Maxillo-labialis Superior Muscle

The first reason for believing that the "lacrymal" fossa is not for the maxillo-labialis superior muscle is that this muscle has been pretty certainly allocated to the lower one of the two preorbital fossæ; secondly, the "lacrymal" fossa is produced forward and downward toward the buccinator fossa, while the maxillo-labialis superior muscle itself runs obliquely forward and upward, so that it crosses the anterior prolongation of the lacrymal fossa. This is well indicated in the type of *Archæohippus ultimus* (Pl. XVIII).

The "Lacrymal" Fossa not for the Naso-labialis (Levator Labii Superioris Alæque Nasi) Muscle

At one time I tried the hypothesis that the preorbital groove, or lacrymal fossa, of fossil Equidæ might have served as the place of origin of the "levator naso-labialis" muscle. This hypothesis is rendered improbable, however, by the following considerations: in all mammals figured by von Boas and Paulli and others the naso-labialis muscle is superficial in position and never rises from a deep fossa. Arising from the surface above and in front of the eye (Figs. 6, 8, 10), it passes over the maxillo-labialis superior muscle and runs obliquely forward and downward to be inserted in the back part of the lips. As the lower, or "malar," fossa was pretty surely occupied by the maxillo-labialis superior, we found it impossible to put the naso-labialis anywhere along the whole extent of the upper, or "lacrymal," fossa and bring it over the maxillo-labialis superior. It seems, on the contrary, highly probable that in fossil



Figs. 5–10. Facial muscles of ungulates.

5. *Sus scrofa*. Adapted from von Boas and Paulli.
6. *Tapirus terrestris*. Adapted from von Boas and Paulli.
7. *Tapirus terrestris*. Deep muscles. Adapted from von Boas and Paulli.
8. *Rhinoceros sumatrensis*. Adapted from Beddard and Treves.
   ?, *mx. lab. sup.* ?
9. *Equus caballus*. Adapted from von Boas and Paulli.
10. *Equus caballus*. Adapted from Ellenberger and Baum.
    Showing the nasal diverticulum and the muscles of the snout.

Equidæ (Pl. XVIII) the naso-labialis arose in precisely the same place as in recent Equidæ, i. e., on the very surface of the bone immediately above and in front of the eye and immediately in front of the preorbicularis dorsalis muscles. Even in the elephant and in the tapir, which have a fully developed proboscis, the naso-labialis does not run from a deep fossa but from the surface of the bone (von Boas and Paulli, plates). In *Hypohippus osborni* (Pl. XVIII), for example, it is plainly impossible to put the naso-labialis in the very deep preorbital groove and have it at the same time pass above the maxillo-labialis superior, which runs from the maxillary bone, behind the infraorbital canal, obliquely forward and upward to the tip of the nasals.

The "Lacrymal" Fossa not for a Dorsal Extension of the Buccinator Muscle

Von Boas and Paulli, in their beautiful figures of the variations of the buccinator muscles in many mammals, show that among the ungulates there is a transverse part of the buccinator which wraps around a longitudinal bundle that extends backward along the side of the cheek teeth. As may be seen by comparison with the skeletal parts, this transverse portion of the buccinator comes opposite the diastemata in the upper and lower jaws. In the lower jaw the longitudinal ridge of the mandible in the region of the diastema lies between the tongue on one side and the transverse portion of the buccinator on the other. Similarly, in the upper jaw the ridge or crest along the diastema separates the tongue on the one side from a fossa for the transverse part of the buccinator on the other.

Since the lacrymal fossa in many fossil Equidæ is continued downward and forward toward the buccinator fossa, I at one time thought that the former might serve for some strange backward and upward development of the buccinator, analogous in some ways to the cheek pouches of rodents.

In the kangaroo also, as figured by von Boas and Paulli, the buccinator extends well up on the side of the face beneath the maxillo-labialis superior and the naso-labialis muscles, and the lower part is received into a deep fossa (Fig. 1). In *Archæohippus* (Pl. XVIII) and other fossil Equidæ, however, the buccinator fossa is clearly separated by a ridge from the anterior (or subnasal) extension of the "lacrymal" fossa.

Finally, in dissecting a Grévy's zebra (Fig. 11), from the New York Zoological Park, we found that the buccinator muscle and its fossa were well defined above and had nothing to do with the anterior extension of the lacrymal fossa.

RELATIONS OF THE PREORBITAL FOSSÆ TO UNDERLYING SINUSES, TO THE DENTAL ALVEOLI AND TO STRENGTHENING RIDGES AND EMINENCES

Cross-sections of the skull of recent Equidæ in front of the orbits made by Mr. S. H. Chubb show that the outer wall of the face is very thin and that beneath it are greatly expanded sinuses in the lacrymal and

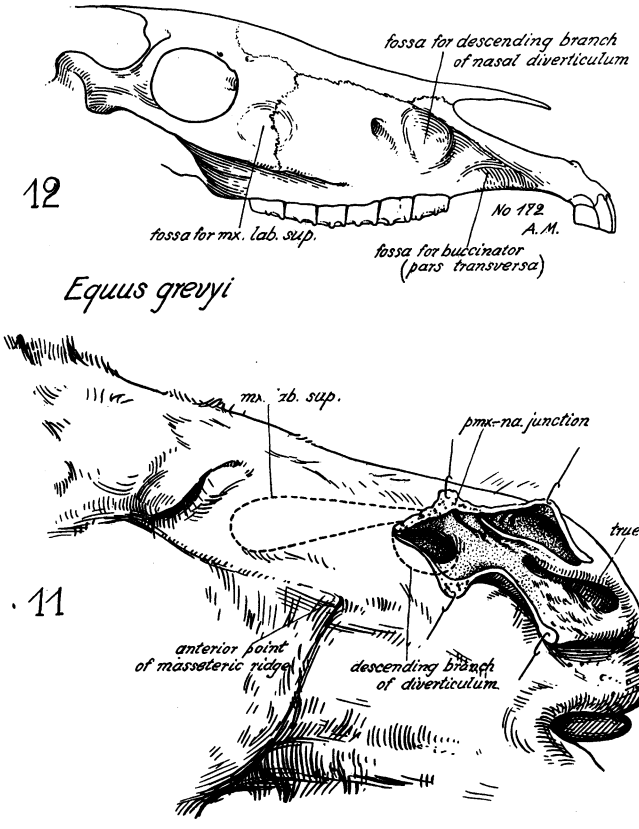


Fig. 11. *Equus grevyi.* Dissection of nasal diverticulum.
Fig. 12. *Equus grevyi.* Skull of the same individual, showing the "malar," "subnasal," and "buccinator" fossæ.

maxillary bones. A sinking in of the outer wall forms the "malar" and "lacrymal" fossæ at the expense of the underlying sinuses but does not interfere in the least with the nasal passage, which in all Equidæ is a high and rather compressed chamber. It is very probable that the

presence of these fossæ is partly conditioned in fossil Equidæ by the thinness of the external walls bounding the underlying sinuses.

It is a widespread principle in the construction of the skull among vertebrates that bones often tend to be strengthened along certain lines of special stress and to thin out between these lines. This principle is beautifully illustrated in the formation of the temporal fenestræ of reptiles. It is also illustrated in the lacrymal region of *Cervulus*,[1] where the pedicles of the horns are strengthened by prominent ridges on the lacrymal bone. In many Equidæ the thin walls between the naso-frontal ridge above and the malar-masseter ridge below have, in fact, collapsed beneath the maxillo-labialis superior muscle and the nasal diverticula, as described below.

The dorsad extension of the alveolar portion of the maxilla has also perhaps conditioned the collapse of the outer wall of bone immediately above it.

Finally, in the modern *Equus* the vertical deepening of the skull has apparently had a tendency to flatten out these fossæ so that even the "malar" fossa is but feebly preserved.

THE NASAL DIVERTICULA OF UNGULATES AND THEIR RELATIONS WITH THE LACRYMAL FOSSA

Murie (1872) has shown that in the Indian tapir the deep fossæ alongside of the nasal bones and above and in front of the orbits are filled with cartilaginous diverticula of the nose (Figs. 7, 14, 15, 16), while von Boas and Paulli (plates) show that the same is true in *Tapirus terrestris*. At first I thought that in the tapirs these deep fossæ were for the muscles that move the trunk, but von Boas and Paulli show that these muscles, especially the maxillo-labialis superior, are lateral to the deep fossæ in question, and located on or in front of the bony rim above the orbits (Figs. 6, 7). So, too, in the elephant these powerful muscles are more on the surface and not located in deep fossæ. In tapirs the fossæ in question show an extraordinary resemblance to the deep "lacrymal" fossæ in front of the eye in *Onohippidium* (Fig. 17) and other extinct Equidæ.

In recent Equidæ (Figs. 10, 11, 13) the true nasal passage is complicated by the addition of lateral diverticula (*div. nas.*), giving rise to the so-called false nostril, which is a blind passage usually not very extensive in domestic horses. Mr. Chubb has found it to be better developed, however, in a Burchell's zebra, and in a domestic ass (Fig. 13),

[1]See Fig. 154 of the preceding article.

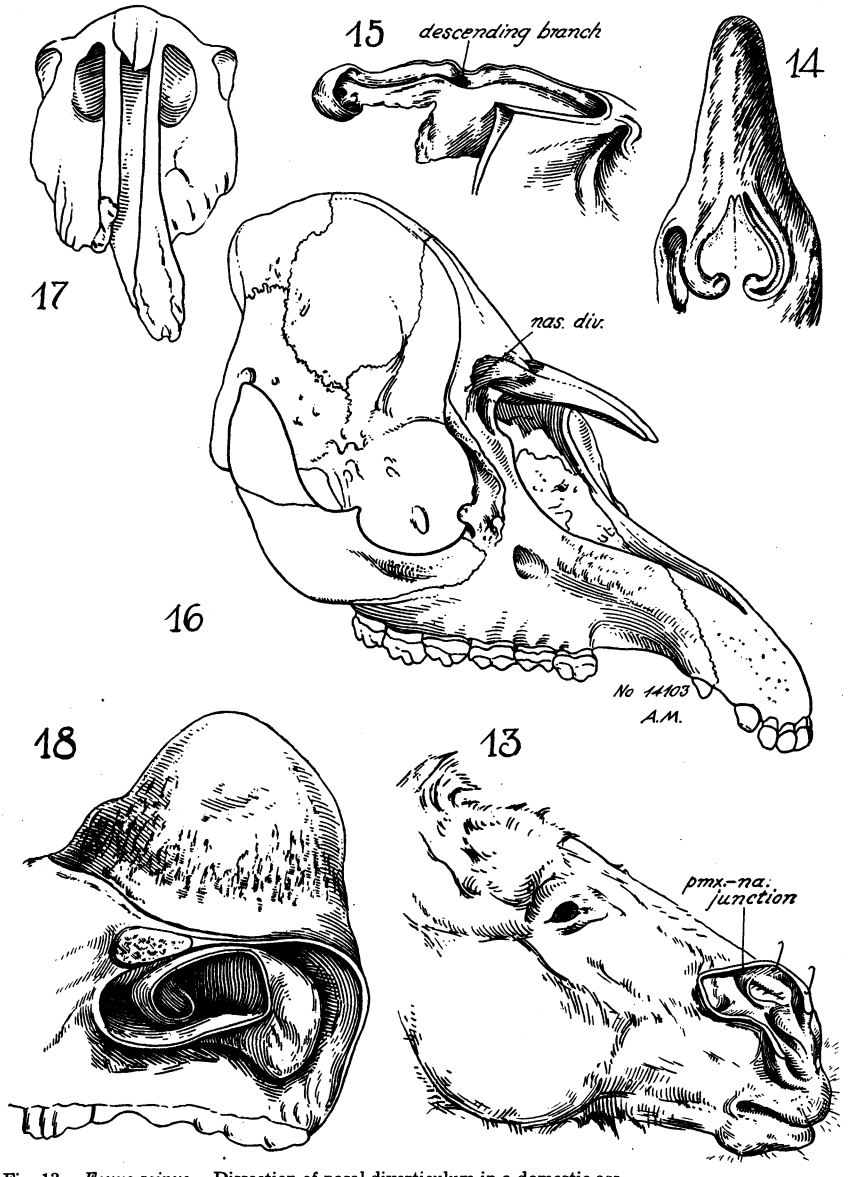
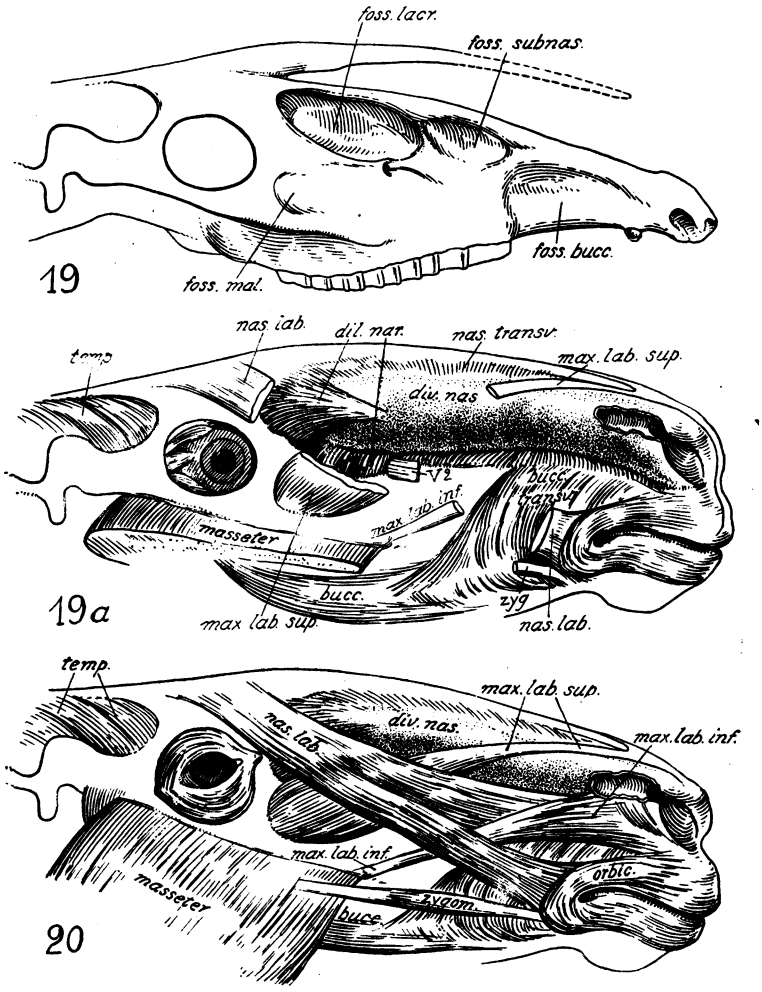


Fig. 13. *Equus asinus*. Dissection of nasal diverticulum in a domestic ass.
Fig. 14. *Tapirus* (*Rhinochœrus*) *indicus*. Nasal diverticula and snout, dorsal view. After Murie.
Fig. 15. *Tapirus* (*Rhinochœrus*) *indicus*. Left nasal diverticulum and septum seen obliquely from the right. After Murie.
Fig. 16. *Tapirus terrestris*. Oblique front view of skull showing preorbital fossa for nasal diverticulum.
Fig. 17. *Onohippidium muñizi*. Front view of type skull showing deep preorbital fossæ, presumably for nasal diverticula. Adapted from Sefve.
Fig. 18. *Rhinoceros sumatrensis*. Cartilages of nasal diverticulum, partly cut away to show interior of sac. After Beddard and Treves.



Figs. 19, 19*a*, 20. *Onohippidium muñizi.* Fore part of skull and semi-diagrammatic restorations of facial muscles.

19. Type skull, adapted from Lydekker, showing slight "malar" fossa, very large and deep "lacrymal" and "subnasal" fossæ, and a well-marked "buccinator" fossa.

19*a*. Attempted restoration of deep structures, showing supposed position of enlarged nasal diverticulum and surrounding muscles.

20. Attempted restoration of superficial muscles.

and we have lately had the opportunity of exploring this region in a Grévy's zebra, with the results shown in Figs. 11 and 12. The nasal diverticulum shows an extensive development lying above and well behind the inner opening of the true nostrils and below the tendon of the maxillo-labialis superior muscle. The upper and back part of the diverticulum gave off a descending branch which was lodged in a conspicuous depression on the side of the maxilla in front of the infraorbital foramen and above and behind the buccinator fossa. This fossa in recent Equidæ, then, is evidently homologous with the anterior extension of the "lacrymal" fossa in extinct Equidæ (Pl. XVIII).

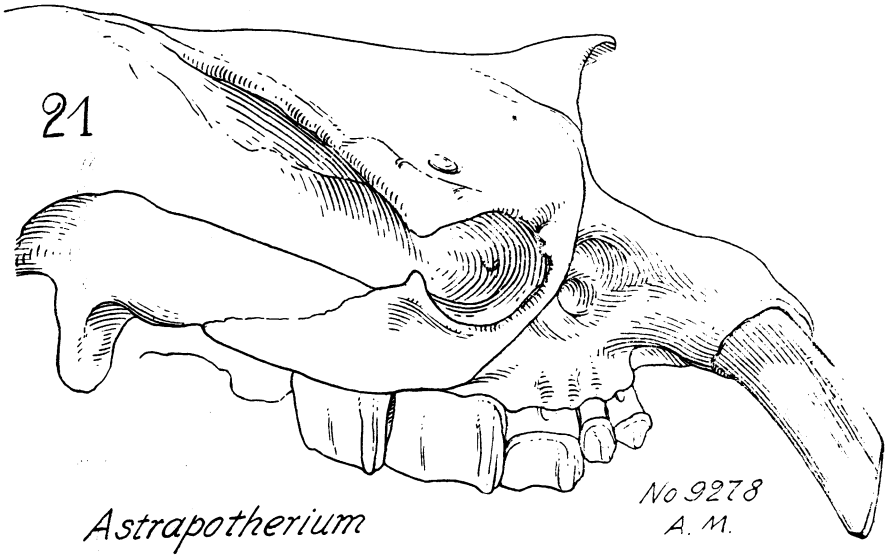


Fig. 21. *Astrapotherium* sp. Skull, showing deep preorbital fossa. ¼.

At first we sought to fill this fossa with the muscles (dilator nasi, etc.) surrounding the nasal diverticulum, but these muscles, even in the tapir and elephant, never occupy deep fossæ, and in *Hypohippus* (Pl. XVIII) the fossæ in question would be deep enough to lodge as heavy a muscle as the gastrocnemius. The presence of such a large muscle for dilating the nose would be quite inconsistent with the generally horse-like character of the front part of the skull of the extinct Equidæ.

In *Onohippidium*, also, the anterior, or "subnasal," extension of the "lacrymal" fossa (Pl. XVIII) is precisely homologous with the similarly placed fossa in the Grévy zebra, which is known to lodge a branch of the

nasal diverticulum. Accordingly, in our semi-diagrammatic restorations of fossil Equidæ (Pl. XVIII) we have filled the lacrymal fossa and its anterior, or subnasal, prolongation with an enlarged nasal diverticulum, above and around which we have placed the normal muscles of the nose and lips.

In *Astrapotherium* (Fig. 21), which, from the conformation of the nasals was very probably supplied with a proboscis, the "lacrymal"

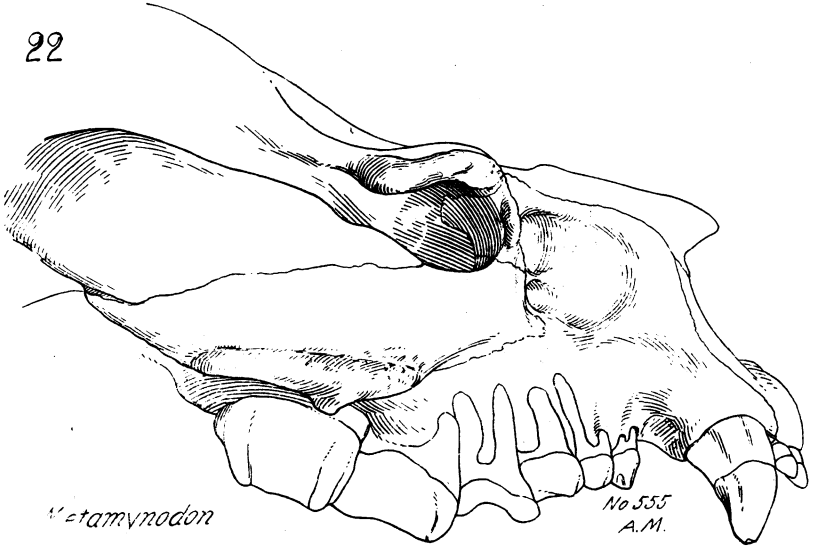
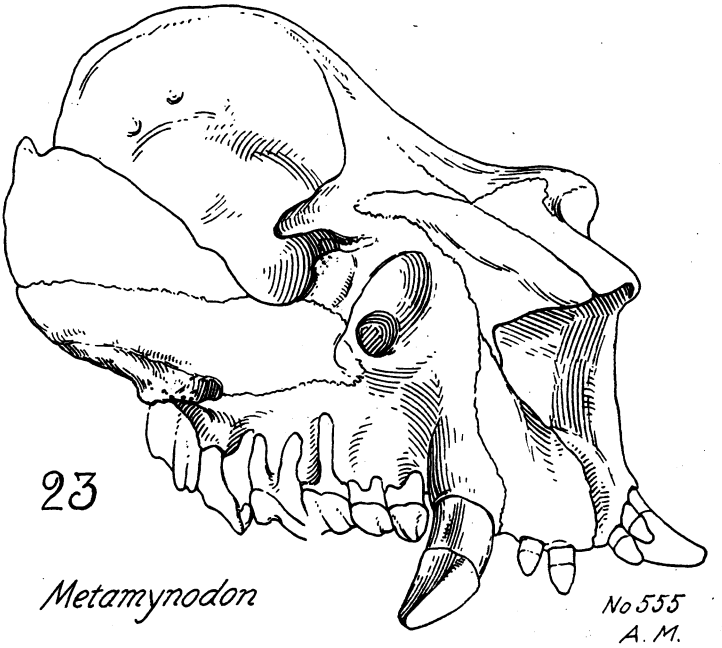


Fig. 22. *Metamynodon planifrons*. Skull, showing large preorbital fossa. × ⅛.

fossa is placed much as it is in the tapirs, and the same is true in *Metamynodon* (Figs. 22, 23), so that in these animals also these fossæ were probably occupied by nasal diverticula. There is plenty of room for the muscles of the trunk on the bony rim around the orbits lateral to these fossæ. In *Amynodon* (Fig. 24), which is ancestral to *Metamynodon*, the same fossa is extended on the side of the maxilla in front of the orbit and this gives the key to the function of a similar fossa in many of the Eocene titanotheres.[1]

In the skulls of the recent *Rhinoceros indicus* (Fig. 25) and *Ceratotherium simum* (Fig. 26) there are shallow fossæ above the infraorbital canal, which may lodge part of the nasal diverticulum (Fig. 18).

[1]Our attempted restorations of the anatomy of the face of these animals will be published in Professor Osborn's U. S. Geol. Surv. Monograph on the Titanotheres.



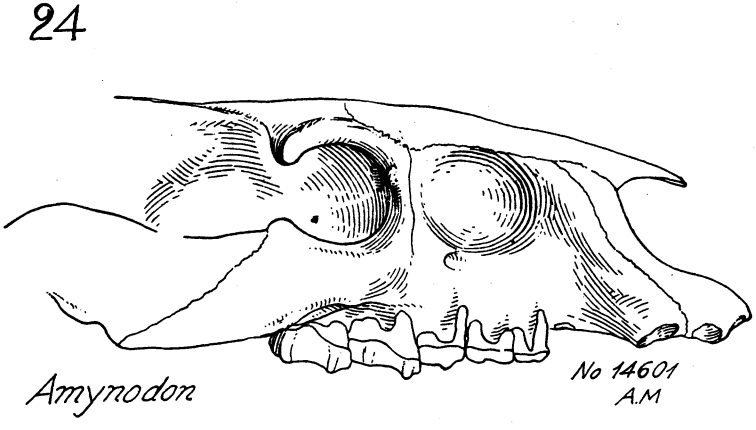
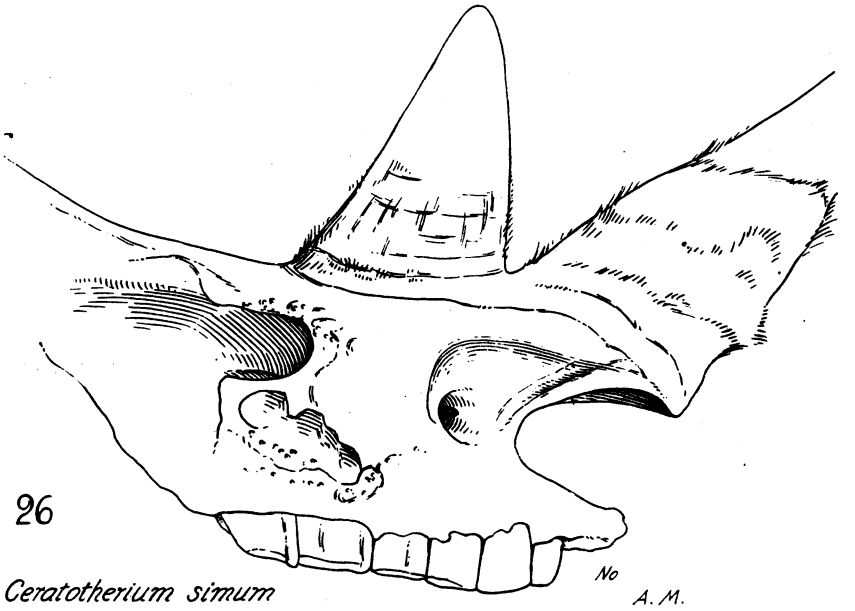


Fig. 23. *Metamynodon planifrons.* Oblique front view of skull showing preorbital fossa. (Compare *Onohippidium, Tapirus.*) × ⅜.
Fig. 24. *Amynodon intermedius.* Skull, showing large preorbital fossa. × ¼.



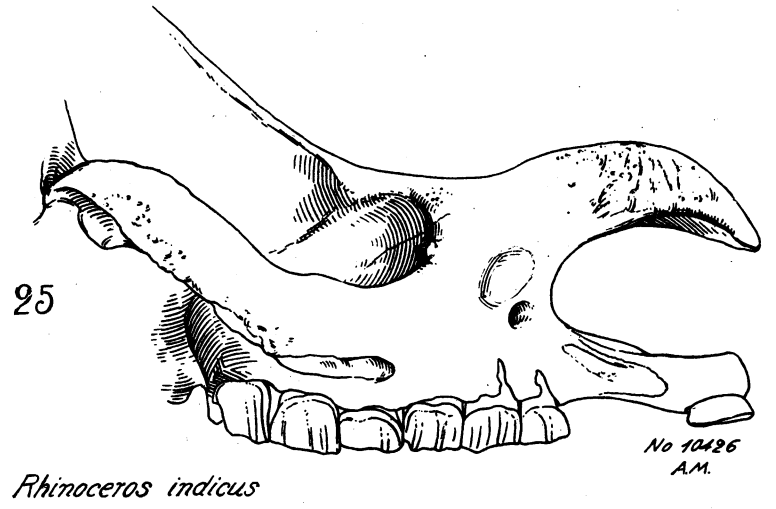


Fig. 25. *Rhinoceros indicus*. Skull, showing shallow preorbital fossa. × *circa* ⅙.
Fig. 26. *Ceratotherium simum*. Skull, showing shallow preorbital fossa. × *circa* ⅙.

In all such cases it seems highly probable that the fossæ in question were partly occupied by nasal diverticula, although the bony rims above them may well have been strengthening ridges and eminences and not directly caused by the presence of the diverticula.

In *Palæotherium* the general conformation of the front part of the skull is more or less tapiroid in character but neither in this genus nor in *Paloplotherium* were the preorbital fossæ pronounced

SUMMARY AND CONCLUSIONS

Although the preorbital fossæ of *Rhynchocyon* and the Suidæ are filled by the muscles of the snout, it is not deemed safe to infer from this alone that the same was true of the preorbital fossæ of the Equidæ, for reasons advanced on pages 266,268 above.

More direct evidence, afforded by recent Equidæ, indicates that the lower or "malar" fossa was probably filled by the maxillo-labialis superior muscle.

With regard to the upper or "lacrymal" fossa, it probably did not lodge a "larmier" or facial gland for the reason that it differs markedly in appearance from the true "larmier" fossæ of ruminants. The fossa in question probably did not lodge the maxillo-labialis superior muscle chiefly for the reason that that muscle has been pretty surely allocated to the lower fossa. It did not lodge the "naso-labialis" for the reason that that muscle in recent mammals is essentially superficial in position and could not be beneath, or deep to, the maxillo-labialis superior, which runs from the "malar" fossa forward, above the infraorbital canal, and upward toward the tip of the nasal bone. The "lacrymal" fossa probably did not serve for the lodgement of a dorsal extension of the buccinator, not only because there is no direct evidence in favor of such an hypothesis, but chiefly because in many Equidæ the buccinator fossa is sharply delimited from the anterior prolongation of the "lacrymal" fossa and especially because there is more direct evidence for the conclusion stated below. Finally, the "lacrymal" fossa probably did lodge a greatly expanded nasal diverticulum, because the remnants of this structure are actually found at the anterior or subnasal extension of the "lacrymal" fossa in existing Equidæ and because the posterior extension of the "lacrymal" fossa is often extremely similar, except in size, to its anterior extension (cf. *Onohippidium*, Pl. XVIII).

The existence of both the "lacrymal" and "malar" fossæ is probably conditioned by the thinness of the outer tabula of the malar and maxillary and by the subsidence of these areas into the underlying sinus,

which subsidence is further emphasized by the upraising of strengthening ridges and eminences around the depressed areas.

In other extinct ungulates the preorbital fossæ, when present, were probably occupied by nasal diverticula, as they are in existing tapirs.

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Plate XVIII

Skulls of various recent and extinct Equidæ, with semi-diagrammatic reconstructions, showing, in the extinct forms, the supposed backward extension of the nasal diverticulum into the "lacrymal" fossa and the positions of the maxillo-labialis superior and other muscles.

Onohippidium muñizi. Type skull, adapted from Lydekker, showing deep "lacrymal," "subnasal" and shallow "malar" fossæ.

Equus caballus. Skull, showing faint remnants of both preorbital fossæ.

Equus caballus. Semi-diagrammatic representation of the facial muscles and nasal diverticulum. Based on Ellenberger and Baum's figures and our own dissections.

Pliohippus fossulatus. Type skull, showing pronounced "lacrymal" and small but deep "malar" fossæ. After Osborn.

Pliohippus lullianus. Type skull, showing deep "lacrymal" and "malar" fossæ, partly confluent. From Osborn, somewhat modified.

Pliohippus lullianus. Restoration. The deep "lacrymal" fossa is covered by the enlarged nasal diverticulum.

Protohippus niobrarensis. Fore part of skull showing deep "lacrymal" and very shallow "malar" fossa. The buccinator fossa is deep and well defined.

Merychippus sejunctus, with restoration of muscles, etc. The "lacrymal" is confluent with the "malar" fossa.

Hypohippus osborni. Modified from Osborn. The "lacrymal" fossa is extremely deep and leads forward and downward into the subnasal fossa. There is no "malar" fossa.

Parahippus nebrascensis primus. Modified from Osborn. The shallow "lacrymal" is confluent below with the "malar" fossa. The subnasal fossa is comparatively deep.

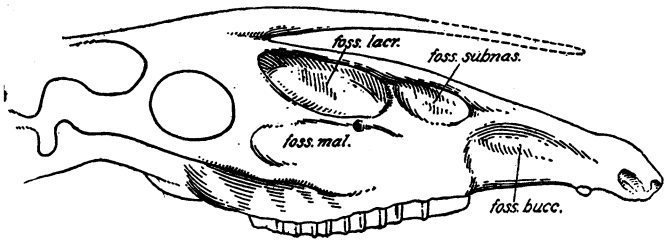
Parahippus nebrascensis primus. Diagrammatic reconstruction.

Kalobatippus præstans. Modified from Osborn. Very shallow "malar," tending to be confluent with the "lacrymal" fossa. Subnasal fossa large but shallow.

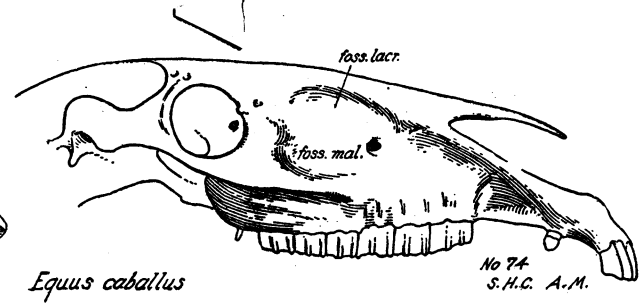
Archæohippus ultimus. Incomplete type skull, after Osborn, showing large "malar," "lacrymal" and "subnasal" fossæ.

Miohippus meteulophus. Skull, modified from Osborn, showing deep "lacrymal" and no "malar" fossa (Compare *Hypohippus*).

Miohippus meteulophus. Diagrammatic reconstruction.



Onohippidium muñizi



No 74
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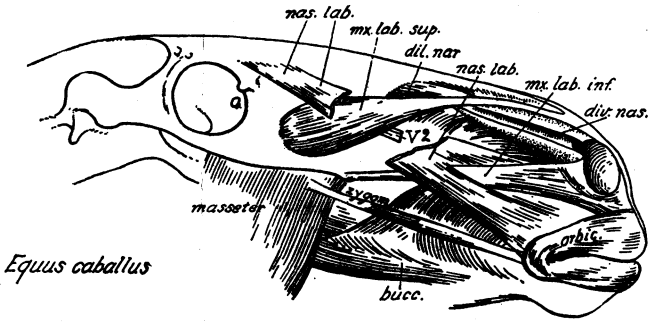
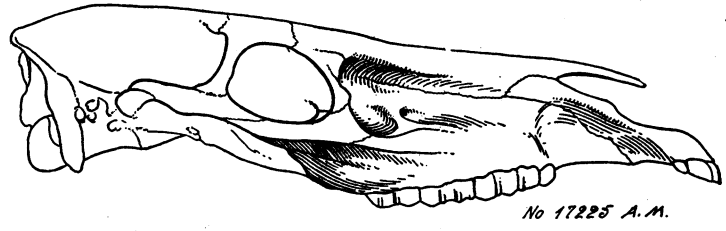
Equus caballus



Equus caballus

Pliohippus fossulatus

Type Univ. Tex.



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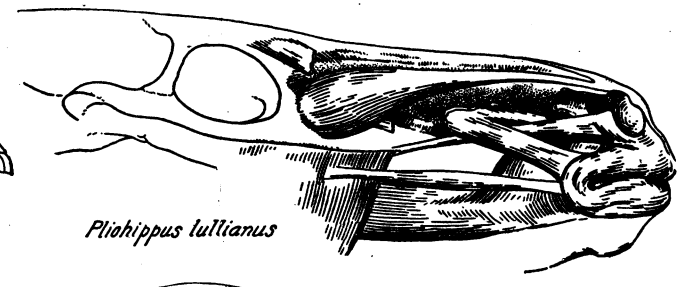
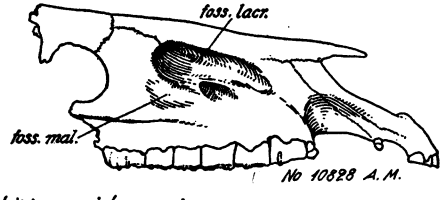
Pliohippus lullianus



Pliohippus lullianus



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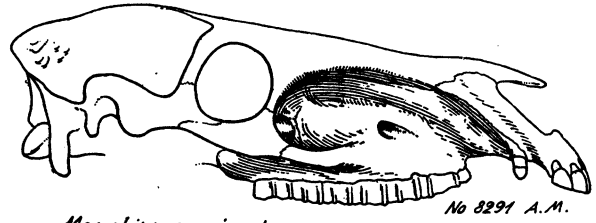
Protohippus niobrarensis



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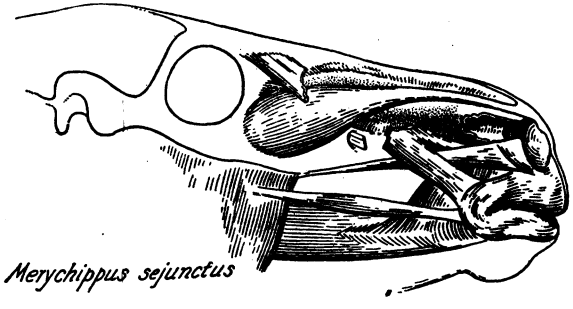
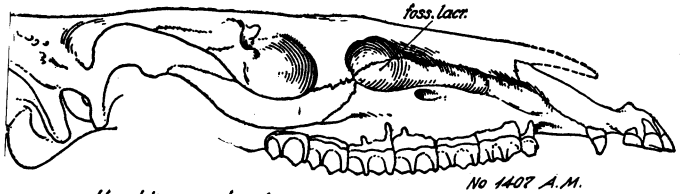
Merychippus sejunctus



Merychippus sejunctus



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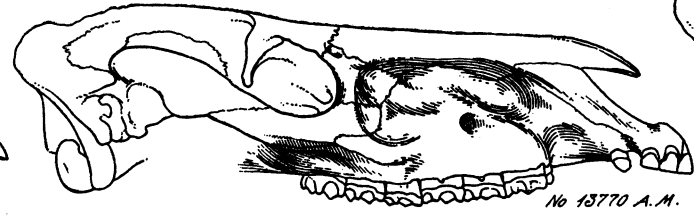
Hypohippus osborni



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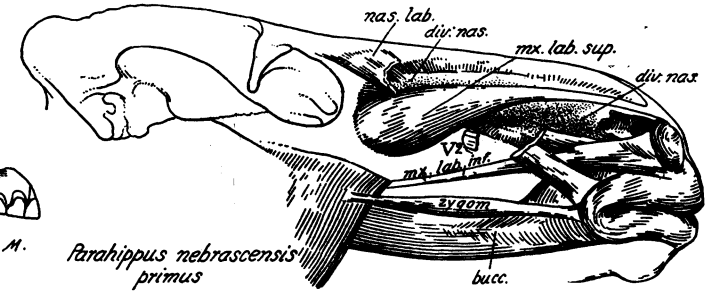
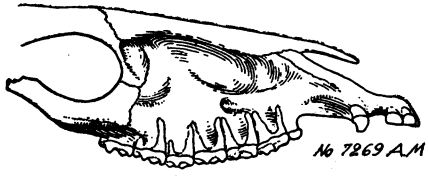
Parahippus nebrascensis primus



Parahippus nebrascensis primus



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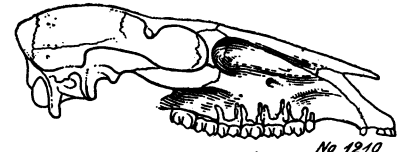
Kalobatippus praestans

No 8174 A.M.

Archaeohippus ultimus



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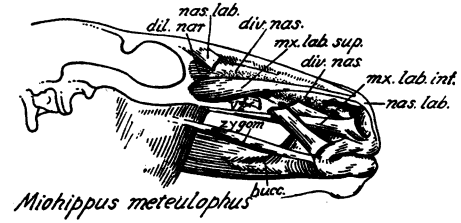
Miohippus meteulophus.



Miohippus meteulophus